

of bullies and buddies

**socio-spatial behavior and emotional regulation drives
primate-like social complexity *in silico***

Ellen Evers

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OVER BULLIES EN BUDDIES

Sociaal-ruimtelijk gedrag en op emoties gebaseerde gedragsregulatie genereren
op primatengroepen lijkende sociale complexiteit *in silico*

(met een samenvatting in het Nederlands)

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I General Introduction

Complexity in social animals

Understanding animal behavior within its social context is challenging. Individuals are situated within an intricate network of many interaction partners. Each individual's behavior affects and is affected by the behavior of its group members. Such properties are characteristic for a complex system (Bar-Yam, 1997). A complex system generally consists of interconnected parts. The parts are often linked in a non-linear fashion (feedback loops) and generate phenomena at higher organisational levels. Such phenomena can only be described and explained by considering all parts of the system in relation to each other. Thus, the complexity of social animal life becomes apparent when looking at the behavior of individuals and their interactions in relation to the dynamical structure of the whole group.

Some striking examples of complex *spatial* group structure can be observed in insect colonies (Goss et al., 1990), fish schools (Partridge, 1982) and bird flocks (Davis, 1980), where the concerted movement of the group almost seems to lead a life of its own. Within such a group, individuals often appear to be sorted by size, speed or other characteristics (Pitcher et al., 1985; Krause, 1993; Hemelrijk, 2000; Ballerini et al., 2008). Yet, the position of each individual within the group is usually not following the instructions of a *centralized organizer* or a *blueprint* (Camazine et al., 2001; Couzin et al., 2002).

Groups of animals may also display a *social* structure (Hinde, 1976). Individuals can, for instance, be categorized in age or sex classes or in kin groups. More interestingly, some types of social structure may dynamically change depending on the interactions between the individuals. As an example, the dominance rank of an individual depends not only on physical characteristics (strength, weight), but also on the number of (available) kin members and/or coalition partners, and (the outcomes of) previous interactions with others (so-called *winner-loser effect*, Hock and Huber, 2009) (Chase et al., 2002). Similarly, affiliative bonds between (non-kin) individuals are developed and maintained depending on the amount and the frequency of earlier affiliative interactions, such as grooming (Silk, 2002b; Massen et al., 2010a; Massen and Sterck, 2013). While dominance hierarchies have been documented throughout the whole animal kingdom (insects: Honk and Hogeweg, 1981; crustaceans: Goessmann et al., 2000; fish: Gorlick, 1976; Grosenick et al., 2007; birds: Piper, 1997; Schjelderup-Ebbe, 1922; reptiles: Greenberg and Crews, 1990; mammals: Hall, 1983; Holekamp and Smale, 1991; Savin-Williams, 1980), studies of affiliative relationships seem to be restricted to birds (Emery et al., 2007; Stamps et al., 1990) and mammals (Kimura, 1998; Silk et al., 2012; Sato et al., 1993). Both, dominance and affiliation, have been extensively studied in primates (Hausfater et al., 1982; Adishan et al., 2011; Silk et al., 2010a; Singh et al., 2006; de Waal, 1986; Kaplan and Zucker, 1980). Specifically, the genus macaca has been subject of extensive comparative behavioral research (Thierry et al., 2004), e.g. unraveling the variation in dominance behavior and the resulting hierarchy, ranging from a steep and strict (*despotic*) to a flat and relaxed (*egalitarian*) hierarchy (Butovskaya, 1993; de Waal and Luttrell, 1989; Thierry et al., 2008; Sueur et al., 2011b).

In animal groups, the social structure of the group may be reflected in the spatial group structure. Group members may be distributed in space according to age or sex classes, kinship, dominance relationships or affiliative bonds (Busse, 1984; Fairbanks, 1976; Hirsch, 2007; Janson, 1990; Jensen and Tokuda, 1974; Langergraber et al., 2009). For instance, in a range of primate species, dominants occupy spatial locations more central within the group compared to peripheral subordinates, i.e. a *central-peripheral distribution* (macaques: Imanishi, 1960; Itani, 1954; Jensen and Tokuda, 1974; Kaufmann, 1967; Lopez-Lujan et al., 1989; Rasmussen and Farrington, 1994; Southwick et al., 1965; Sugiyama and Ohsawa, 1982; Wada and Matsuzawa, 1986; Yamada, 1966; capuchins: Hall and Fedigan, 1997; Janson, 1990; Robinson, 1981; baboons: Busse, 1984; Hall and DeVore, 1965; Washburn and DeVore, 1961). Similarly, individuals spend more time in proximity of specific group members (e.g. affiliates or kin) than others (Silk, 2002b). Such relations between social and spatial properties of group members may be described by the so-called *socio-spatial group structure*.

Thus, social and spatial group properties are affected by the behavior of the individuals within a group. As a result of attractive and repulsive movements, related to characteristics of specific group members, some individuals are more often in each other's proximity than others. Similarly, frequently grooming dyads may maintain stronger affiliative relationships than occasionally grooming ones. In turn, social and spatial group properties may also affect the behavior of the individuals (Bode et al., 2011). For instance, individuals that encounter each other only occasionally, simply have fewer opportunities to interact with each other compared to individuals that are often in each other's proximity. Similarly, occasionally grooming dyads may have weaker affiliative relationships and may, as a consequence, approach each other less often. This interrelation between the interactions of low-level entities (individuals) and higher-level organization (group properties) is yet another common phenomenon in complex systems (see above), which can give rise to self-reinforcing structures and complex epiphenomena.

Underlying mechanisms of complex patterns in social animals

It is difficult to disentangle the mechanisms underlying complex group structures in social animals. Explanatory approaches differ extensively in the assumptions that are made about the cognitive mechanisms used by the interacting entities of the system, i.e. the individuals, ranging from highly cognitive to (overly) simple. As an extreme case, some (quite remarkable) hypotheses assumed that for instance bird flocks employ *thought transference* (Selous, 1931) or follow the *instructions* of one *leader* individual (Heppner and Haffner, 1974), to coordinate their concerted movements. Such complex capacities seem very unlikely to be present within (individual) animals. Computational model research has shown that many complex group patterns can simply emerge through self-organization (Camazine et al., 2001), which requires only minimalistic cognition and only very limited (perceived) information (e.g. via pheromones) of the local social environment. Such hypotheses are extremely elegant and appealing, as they offer explanations for a great degree of the complexity found in some part of the animal kingdom (e.g. social insects). Yet, they may not capture the entire process going on in species that have been shown to possess more elaborate cognitive capacities.

As an example, different approaches have been followed to explain why and how a *central-peripheral distribution* with central dominants and peripheral subordinates as found in many primate species, may come about. From an ultimate point of view, Hamilton (1971) argued that individuals may have evolved an instinctive preference for the group center (*centripetal instinct*) to lower predation risk (*selfish herd theory*). Taking a proximate perspective, such a spatial preference may then cause individuals to seek the group center, with dominants

succeeding in monopolizing it. On the other hand, computational model studies have shown that no preference for any particular spatial location is required (Hemelrijk, 1998b; Bryson et al., 2007). In these minimalistic models, a central-peripheral distribution emerged through self-organization, as a side effect of aggressive dominance interactions and subsequent fleeing by the subordinates. Subordinates flee away from the dominants and, thus, end up at the group periphery.

Similarly, several different mechanisms have also been proposed to explain complex social group patterns observed in primates, such as cooperation, coalitions, post-conflict affiliation and, in particular, reciprocity (Schino and Aureli, 2009; Dunbar, 1998; Cords, 1997; Byrne and Whiten, 1988; Barrett et al., 2007; de Waal and Luttrell, 1988; Brosnan et al., 2010; Whiten and Byrne, 1997; Schino and Aureli, 2010a). Reciprocity, for instance, concerns the exchange of beneficial behaviors, such that the given benefits match the ones that are received (Trivers, 1971). Particularly, grooming is typically exchanged for grooming in primates, such that grooming episodes are time-matched (Barrett et al., 1999; Manson et al., 2004; Chancellor and Isbell, 2009) or that partner choice is reciprocal (Leinfelder et al., 2001; Schino et al., 2003; Payne et al., 2003). Besides its hygienic function, grooming has been shown to be rewarding and stress relieving in the receiver of grooming and, to a smaller degree, in the grooming individual itself (Boccia et al., 1989; Spruijt et al., 1992; Shutt et al., 2007). Nonetheless, giving grooming is costly, as it requires time and attention and investing in unpredictable future behavior of group members is uncertain (Russell and Phelps, 2013). Yet, in a many primate species grooming is reciprocated and even time-matched to a remarkable degree.

Proposed mechanisms underlying grooming reciprocity in primates again range from cognitively simple to complex. For instance, individuals may simply prefer grooming partners based on symmetries inherent in dyadic relationships, such as mutual association, age similarity or kinship. This *symmetry-based reciprocity* (as proposed by de Waal and Luttrell, 1988 and Brosnan and de Waal, 2002) is cognitively very simple and only requires recognition of the symmetric characteristic in others. Yet, such a tag-based mechanism (similar to a *green beard*, Dawkins, 1976; Hamilton, 1964) is vulnerable to cheaters and, thus, seems improbable to have evolved. Moreover, primates have been shown to develop differentiated affiliative relationships with individuals of similar age or rank classes, which also vary over time (Silk, 2002b; Brent et al., 2014). A cognitively more complex mechanism may be *attitudinal reciprocity* (de Waal, 2000; Brosnan and de Waal, 2002), where an individual's behavior towards a partner is based on the earlier behavior received from this partner. This mechanism, thus, requires individual recognition and a partner-specific attitude based on earlier received behaviors. The partner-specific attitude may for instance only concern the last interaction with the partner (similar to a *tit-for-tat* strategy, Dugatkin and Alfieri, 1991), but may also consist of an emotionally mediated summary of several earlier interactions with the partner, i.e. *emotional bookkeeping* (Schino and Aureli, 2009). Emotional bookkeeping has been proposed to mediate social relationships (Aureli and Schino, 2004; Aureli and Schaffner, 2002; Aureli and Whiten, 2003) and does not require a conscious valuation or scorekeeping of earlier events. A cognitively very complex mechanism to explain grooming reciprocity in primates may be *calculated reciprocity* (de Waal and Luttrell, 1988) or mental scorekeeping. However, even in humans this seems too taxing a mechanism to be used on a day-to-day basis.

Over the last few decades, mounting evidence led to the consensus that primates possess sophisticated cognitive abilities, with the degree of sophistication varying across different primate species (Tomasello and Call, 1997). Correlations between brain size and group size among primates suggest that these cognitive abilities evolved in response to increasing social complexity (*social brain hypothesis*, Dunbar, 1998). Consequently, it is expected that primates employ

their cognitive abilities especially in the social domain. Yet, to empirically study primates' use of sophisticated cognition in a social setting is difficult, since simpler cognitive explanations cannot be easily dismissed (Barrett et al., 2007).

While parsimonious explanations of social complexity are preferred (*Occam's razor*), we may still take into account the cognitive capacities that the studied species has been shown to employ (Dunbar, 1980). For instance, many primate species seem capable of individual recognition, know third-party relationships and even employ elements of episodic-like memory or theory of mind (Byrne and Bates, 2010). Thus, instead of finding the simplest possible mechanism to explain certain group phenomena, it may be more interesting to explore what specific cognitive capacities (known to be employed by the study species) may add to a phenomenon, when compared to simpler mechanisms (Petit, 2011). Admittedly, this may be difficult to achieve in empirical studies, while avoiding potential anthropomorphism. Moreover, there are ethical, financial and methodological limits to which degree we can control for the use of certain cognitive capacities employed by individuals in empirical studies. Last, but not least, social complexity itself forms a huge obstacle in being explored empirically. The many individuals within a group affecting each other and the different organizational levels affecting each other would require sophisticated methods of data recording of all individuals simultaneously and at different organizational levels. Moreover, studying only isolated components of the complex system (e.g. single individuals or small subgroups) will not suffice to grasp the system's full complexity. Fortunately, computer simulation models offer a promising perspective, as they do not face many of the above-mentioned constraints. For instance, controlling for specific factors (by simply excluding them from the model) and recording of many output data on multiple levels is no problem.

Simulation models as research tool

A suitable approach to explore complex patterns in social animals lies in theoretical modeling. Translating hypothesized processes into model algorithms demands an abstract, but explicit description of these processes, which allows us to test the hypotheses' (internal) consistency, i.e. if a hypothesis may work (at least hypothetically). It also presents the opportunity to reveal gaps in the theoretical framework that may remain unnoticed otherwise.

In general, we can distinguish between *analytical* models and *simulation* models. Analytical model solutions, e.g. of differential equations, rely on static equilibria and may not always exist or may be very hard to find, especially in complex systems. In contrast, simulation models can be seen as a set of (probabilistic) rules that define the system's future behavior given its current state, allowing the study of the dynamic changes within the system over time. Thus, hypotheses about the underlying mechanisms of a system are implemented, i.e. translated into model algorithms, which then can be simulated, systematically explored and altered experimentally. Simulation models are ideal to understand when, i.e. under which circumstances and settings, specific patterns are to be expected. A wide range of parameter settings can be thoroughly analyzed within a particular model and alternative models (e.g. with specific model components switched on or off) can be compared. Model parameters are fully controllable and can be manipulated experimentally, even towards very hypothetical values, without methodological, financial or ethical constraints. Typically, multiple simulation runs are computed for the same parameter setting, but with differing *random seed*, i.e. random processes will be comparable concerning the probabilities, but not identical. This ensures that observed patterns of a specific parameter setting are not due to unique random coincidences, but inherent to the model at this parameter setting. All model output is accessible to be recorded and analyzed.

Traditionally, simulation models focus on the dynamics of the entire system (*system dynamics*). In this case, system-level processes are represented in terms of well-mixed aggregates (of individuals) and flows between different (types of) aggregates. As a consequence, individuals within the same aggregate are indistinguishable. Another type of simulation models concerns *agent-based models* (ABM, sometimes also referred to as individual-oriented models, IOM). As can be already deduced from the name, the focus lies on the elements that a system consists of, e.g. the individuals within a group. Individuals and their behavioral rules are implemented and modeled from the perspective of the individual. This proximate, process-oriented approach allows us to gain insights into how specific group-level patterns may come about. In fact, no global patterns or dynamics at the group-level are predefined in ABMs (Hogeweg and Hesper, 1985). Instead, group patterns emerge as a result of the interactions between the individuals, *generating* the model system (Epstein and Axtell, 1996; Epstein, 2006) from the bottom up. Thus, known (or proposed) processes at the individual level are implemented into the model, resulting in observable patterns at the group level. Representing a system in such a *multi-level* way (Hogeweg and Hesper, 1990; Grimm, 2005) allows a better understanding and better validation of the system compared to models that concern only the group-level dynamics (*system dynamics*). Similarly, multiple timescales may be represented in a model. For instance, next to incorporating the proximate mechanisms underlying a system's dynamics, a model may also include evolutionary processes (e.g. mutations and natural selection) to represent and investigate the (possible) evolution of specific individual- or group-level properties (e.g. see Campenni and Schino, 2014 for an ABM of reciprocal partner choice and the evolution of cooperation). In ABMs, individuals may be situated on a spatial grid, to account for spatial constraints that are found in real animal groups, which are mostly not well-mixed, but spatially structured. Moreover, as individuals are modeled as discrete entities, low group sizes may have different, i.e. more realistic, consequences (e.g. concerning reproduction, extinction or the transmission of information or diseases) as compared to system dynamics models. Lastly, individuals in ABMs are distinguishable, as they may all have different properties and states, which may depend on their individual history. Thus, ABMs are a powerful theoretical tool to study how dynamic, complex group-level patterns may emerge from the interactions of the individuals (Bryson et al., 2007). Complementing empirical research with ABM studies is a promising venture (Petit, 2011), as many methodological constraints of working with real animals, concerning for instance the manipulation of specific abilities in the animals, do not apply to research *in silico*.

Agent-based models of primate social behavior

Considering the potential value of agent-based models (ABM), it is not surprising that many questions concerning animal behavior have been explored using this model formalism. Especially when studying collective motion and collective decision making of groups of insects (ants: Pratt et al., 2005; honey bees: de Vries and Biesmeijer, 1998; cockroaches: Jeanson et al., 2005), birds (Hemelrijk and Hildenbrandt, 2011), fish (Couzin et al., 2002) or mammals (primates: King et al., 2011; humans: Fridman and Kaminka, 2010), ABMs have become widely accepted as a research tool. Concerning primate social behavior, ABMs are not yet that established as investigation method and make up only a small part of the research as compared to empirical research (Hemelrijk, 2000; Hemelrijk and Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). Nonetheless, primate social behavior is well suitable to be investigated by agent-based models. Primate groups display a variety of complex group-level phenomena, are spatially heterogeneous (i.e. not well-mixed) and socially structured (i.e. not indistinguishable), and consist of numerous interacting individuals whose behavior may be described by behavioral rules. Recognizing this, a number of researchers took the lead in studying primate

behavior by means of ABMs, which has often led to unexpected insights and newly generated hypotheses.

For instance, aggregations of male chimpanzees were postulated to benefit the individuals through shared cost of territory defense and inclusive fitness, where male relatedness was concluded from the migration of adult females. In this line of argumentation, unpredictable fluctuations in party structure have traditionally been interpreted as measuring errors or “noise”. However, te Boekhorst and Hogeweg (1994) generated very similar party structures in an ABM, where model entities simply looked for food, travel mates and mating partners, while male relatedness and competition with other parties was not necessary. Similarly, Ramos-Fernandez et al. (2006) showed that fission-fusion dynamics and selective non-random associations may arise in an ABM with simple foraging rules and no social interactions or tendency to join others whatsoever, given that the environment shows intermediate food patch heterogeneity. Van der Post and Hogeweg (2006) developed another ABM in which model individuals (with a tendency to join others) forage and learn what to eat. In this model, a heterogeneous environment resulted in homogeneous diets within groups, diet differentiation between groups and, subsequently, in increased (within-)group cohesion. Others have used ABMs to test and validate proposed mechanisms underlying collective decision-making (e.g. concerning when and where to move) in baboons and macaques (Sellers et al., 2007; King et al., 2011; Sueur et al., 2009). For instance, in a very elegant paper, Sueur et al. (2009) implemented four different hypothesized mechanisms into an ABM, namely that the individual decision to move would be independent of others or would depend on the number or characteristics (kin, preferred partners) of others moving. Comparing multiple resulting group-level patterns to empirical data of Tonkean macaques, it seemed most likely that individual macaques join moving groups depending on their preferred partners.

Probably one of the most extensively published agent-based models of primates (macaques) is the so-called *DomWorld* model by Hemelrijk (2000). In (most versions of) this model, individuals prefer to stay near (any) other group members, perform dominance interactions and flee after losing such contests. Originating from a model of bumblebees (Hogeweg and Hesper, 1985), these simple behavioral rules have shown to result in interesting group-level phenomena. In this model a so-called *winner-loser effect* was implemented. Individuals either attack or flee from potential opponents, depending on their expected chances of winning the contest (based on the perceived dominance of the opponent). Depending on the actual outcome, which may by chance differ from the expected outcome, both opponents' dominance is subsequently updated. In this way, dominance hierarchies develop and stabilize over time even when all individuals start initially with equal dominance. Depending on the strength of the feedback from contest outcomes on updating of dominance, corresponding to the intensity of aggression, a more or less strict hierarchy may emerge (Hemelrijk, 2000).

More interestingly, as lower-ranking individuals more often lose and subsequently flee from dominants, a central-peripheral group structure (i.e. centrality of dominants, as described further above) emerges in this model. This socio-spatial group structure arises simply as a side effect of the spatial movements of the individuals (Hemelrijk, 1998b). Moreover, the spatial structure reinforces and is reinforced by the social dominance structure (Hemelrijk, 2000). Analyzing and discussing the *DomWorld* model in detail, Bryson et al. (2007) also developed a modified version of the model in which a stable hierarchy, as opposed to a dynamically updating hierarchy, was implemented. Even with a stable hierarchy, a central-peripheral group structure emerged in the model. As dominance hierarchies in macaques can be stable over long time periods up to several years (Bernstein, 1969; Rhine et al., 1989; Ostner et al., 2008; Silk, 1988), this may be a better representation of how such a socio-spatial group structure arises in established groups.

In the DomWorld model, an array of group level patterns has shown to co-vary with the strictness of the hierarchy; matching and possibly explaining observed differences in macaque species with a strict (*despotic*) or less strict (*egalitarian*) dominance hierarchy. For instance, compared to a less strict hierarchy, a strict hierarchy also entails greater differentiation and stability of dominance, greater uni-directionality and reduced frequency of aggression, more spread out groups and a clearer central-peripheral group structure (Hemelrijk, 1999b). The DomWorld model has been extended with several additional features, generating interesting new hypotheses. For instance, two sexes (with initially lower-ranking females) were implemented in the model (Hemelrijk, 2002a). Investigation of this extended model revealed, that unexpected occurrences of female co-dominance (often observed in typically male-dominant species) may result from sexual attraction or an increase in cohesion, intensity of aggression, competition for food, and, surprisingly, the percentage of males within a group (Hemelrijk et al., 2003, 2008; Hemelrijk, 2002a).

The so-called *GrooFiWorld* model (Puga-Gonzalez et al., 2009) is a more recent variation of the DomWorld model in which also affiliative behavior and some underlying emotional processes have been implemented. In the GrooFiWorld model, individuals may execute not only agonistic behaviors, but also affiliative behavior, i.e. grooming. The model individuals' emotional state is represented as anxiety, which increases over time and in response to aggression and which is decreased in response to grooming. In turn, high anxiety results in increased probabilities to groom encountered individuals, given that the chance of winning a dominance interaction from such an individual is low. As a result, the model yielded several interesting phenomena that match observations in real macaque groups. For instance, given a strict hierarchy, grooming was directed up the hierarchy and towards individuals of similar rank, grooming was reciprocated at group level, after a fight opponents engaged in grooming sooner compared to matched-control periods (so-called *conciliatory tendency*), grooming after a fight was more often directed to those group members that were also mostly groomed outside of aggressive contexts (i.e. valuable partners) and agonistic support was more reciprocated (Puga-Gonzalez et al., 2009; Hemelrijk and Puga-Gonzalez, 2012). In *FriendsWorld* (Puga-Gonzalez, 2014), the most recent variation of the GrooFiWorld model, those group members with whom an individual engages most in grooming (top quartile) have been defined as "friends". Such "friendships" than affect the individuals' movements such that individuals preferably approach "friends". Preference for grooming or grooming partner choice is not affected by these "friendships". As a result, reciprocation and interchange of social acts was reinforced as compared to the GrooFiWorld model, due to more frequent interactions between "friends" than between "non-friends".

Objectives and overview of this thesis

Generally, primate social behavior is more sophisticated than represented in many ABMs of primate social behavior. Such features of actual primate behavior may be considered redundant or unimportant, since even systems with very simplistic model entities can give rise to very complex epiphenomena. Still, a system of more complex model entities may generate different epiphenomena and may better explain, reveal or disentangle certain underlying mechanisms. Therefore, we explored the consequences of equipping model entities with more *primate-like* behavior (i.e. behaviors known to be employed by primates) towards potentially aggressive group members, namely avoiding and social vigilance, and investigated the effect on spatial and interaction patterns. In addition, based on an extensive array of empirical data, we formulated a new model in which we implemented the underlying emotional regulation processes of primate behavior, considering not only agonistic, but also affiliative behavior. Using this model, we explore how affiliative relationships differ depending on whether model entities

possess more or less cognitive abilities, such as (different degrees of) emotional bookkeeping or a simple preference for similar-ranking group members. In this thesis, I present the results of these endeavors in form of a series of ABM studies.

The first part (Chapter 1-2) focuses on the mechanisms underlying the socio-spatial group structure in primates, particularly in macaques, elaborating on the well-established DomWorld model (described further above). The DomWorld model provided an elegant hypothesis on how spatial centrality of dominants may simply arise without any preference for central locations: subordinates typically lose dominance interactions and subsequently flee away from dominants (Hemelrijk, 1998b). In fact, individual variation in fleeing tendency structures the spatial composition of the group.

Carefully examining the movement rules implemented in DomWorld, we felt skeptical about the implications and consequences of some of these rules. In DomWorld, an individual's movement within the group is affected by other group members only through encounters. An encounter, i.e. the perception of a group member within close proximity, results in a dominance interaction and subsequently causes the loser to move away from its opponent. In other words, subordinates first need to short-sightedly *bump into* dominants, before being able to move away from them. In macaques (and most other primates), animals are able to individually recognize group members and their dominance rank also at greater distances (Sugiura et al., 2014). Preventing the potential risk of costly conflicts is crucial, especially in aggressive, intolerant species and species lacking formal submission signals (Bernstein and Ehardt, 1985; de Waal, 1986; Isbell and Pruettz, 1998; Kutsukake and Clutton-Brock, 2008; Rowell and Olson, 1983; Kaplan and Zucker, 1980). This risk prevention can be easily achieved by simply avoiding close proximity towards potential aggressors, i.e. by already moving away from such individuals before being in very close proximity. Moreover, individuals may even actively look out for potential aggressors. Such *social vigilance* can be achieved by regularly scanning the social environment to detect potential aggressors and by monitoring the whereabouts of specific potential aggressors that should be avoided. Indeed, avoidance, scanning and monitoring behavior have been reported for a number of primate species (baboons: Alberts, 1994; capuchins: Hall and Fedigan, 1997; Pannozzo et al., 2007; gorillas: Watts, 1998; humans: La Freniere and Charlesworth, 1983; langurs: Jay, 1965; Sommer et al., 2002; macaques: Bernstein and Ehardt, 1985; Furuchi, 1983; Mori, 1977; Pitcairn, 1976; Haude et al., 1976; Deaner et al., 2005; mangabeys: Blois-Heulin and Girona, 1999; Blois-Heulin, 1999; meerkats: Kutsukake and Clutton-Brock, 2008; patas monkeys: Isbell and Pruettz, 1998; Rowell and Olson, 1983; McNelis and Boatright-Horowitz, 1998; squirrel monkeys: Caine and Marra, 1988; talapoin: Keverne et al., 1978 and vervets: Isbell and Pruettz, 1998) and the behavioral rates are often inversely related to dominance rank (baboons: Alberts, 1994; capuchins: Pannozzo et al., 2007; humans: La Freniere and Charlesworth, 1983; langurs: Jay, 1965; macaques: Chance, 1956; Haude et al., 1976; Deaner et al., 2005; patas monkeys: McNelis and Boatright-Horowitz, 1998; squirrel monkeys: Caine and Marra, 1988 and talapoin: Keverne et al., 1978). Similarly to individual variation in fleeing tendency (see above), individual variation in the tendency to avoid, to scan or to monitor are therefore likely to be important potential determinants of the spatial (and social) structure within a group. Nonetheless, researchers have not yet investigated the role of avoidance or social vigilance in this specific context, neither empirically nor theoretically.

In Chapter 1, we introduce the *avoidance model* and investigate the effect of individual variation in avoidance of potential aggressors (at a distance) on the socio-spatial group structure, particularly concerning the spatial centrality of dominants. To do this we specifically analyze the range of two parameters determining avoidance behavior in the model. The parameter *avoidance-dominance difference* describes the minimum difference in dominance between two

individuals that elicits avoidance behavior in the subordinate. The parameter *avoidance distance* describes the spatial distance within which subordinates avoid aggressors. We compare the results of the different settings in the avoidance model, to a control model without avoidance, the *fleeing model*. Our fleeing model resembles many aspects of the original *DomWorld model* by Hemelrijk (1998b) and also shows very similar dynamics. Yet, the model is not an exact replication of the DomWorld model. On one hand, this is due to the fact that the program code of the DomWorld model is not publicly available. On the other hand, we simply felt that some of the modeled behaviors may be implemented in a way that better represents primate behavior. An overview of those model differences will be given in Table 6.1 in the Summarizing Discussion. Additionally, Chapter 1 investigates a very simple and more general mechanism that may potentially underlie spatial centrality of dominants, namely individual variation in velocity.

In Chapter 2, we added social vigilance mechanisms to the avoidance model. Next to avoiding potential aggressors, model individuals may also scan the environment to locate potential aggressors (*scanning model*) or monitor the whereabouts of specific potential aggressors (*monitoring model*) to facilitate avoiding their proximity. Contrasting the avoidance model (of Chapter 1, without social vigilance) with the scanning model and the monitoring model, we describe the resulting consequences for the socio-spatial group structure, in particular the spatial centrality of dominants. Thus, while Chapter 1 compares the effects of individual variation in different movement properties (fleeing, avoidance, velocity) on the socio-spatial group structure, Chapter 2 focuses on individual variation in different perception properties (scanning and monitoring). Investigating this by means of ABMs allowed us to disentangle the effects of each of these factors, by including them in or excluding them from the model, which is not possible in empirical research.

The second part of this thesis (Chapter 3-5) explores the mechanisms underlying affiliative structures within groups of primates, particularly in macaques, with respect to the emotional regulation of behavior and cognition. Note that throughout this thesis, we refer to *emotional processes* without implying accompanying conscious, subjective states that are inaccessible to measurement in non-human animals (Paul et al., 2005; Panksepp, 1998; LeDoux, 1999; Berridge and Winkielman, 2003). Taking neurobiological and ethological perspectives, a great extent of empirical studies has unraveled the importance of emotional processes in behavior regulation, in primates and other species (Aureli and Smucny, 2000; Boissy et al., 2007; Berridge and Kringelbach, 2008; Aureli, 1997; Aureli and Whiten, 2003).

Emotional processes are considered a prompt response to relevant (social) stimuli allowing an individual to quickly react in an appropriate, adaptive way (Panksepp, 1998; Rolls, 1999). The emotional response is marked by a concerted set of changes at the physiological (peripheral and central) and behavioral level (Paul et al., 2005) and affects subsequent behavioral reactions (Aureli and Whiten, 2003). A number of studies have investigated the role of emotional processes in the social context of primates (Aureli, 1997; Aureli and van Schaik, 1991; Schino et al., 2007b; Spruijt et al., 1992; Boccia et al., 1989; Shutt et al., 2007). Yet, to empirically study this in an intact social group of many individuals remains methodologically difficult. The use of ABMs seems more promising, but has only to a limited extent been applied in this context (Puga-Gonzalez et al., 2009; Hemelrijk and Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2014; Puga-Gonzalez, 2014).

In order to capture the emotional regulation of behavior in the social context, we developed a new agent-based model, dubbed the *EMO-model*. The implementation of those emotional regulation processes was based on a large array of empirical data. In the model, an individual's emotional state, described by an activating, aversive and attractive component (i.e.

arousal, anxiety and satisfaction), is affected by social interactions and in turn affects the individual's general behavioral probabilities. For instance, receiving aggression increases arousal and anxiety levels, which in turn results in higher probabilities of active behavior (as opposed to resting) and social vigilance, more risk-sensitive agonistic behavior and a higher motivation to employ grooming. Over time, arousal and anxiety decrease towards baseline levels. Engaging in grooming causes a faster decrease of arousal and anxiety, and increases satisfaction levels. Over time, when not engaging in grooming, satisfaction levels decrease to baseline levels, which in turn results in an increased motivation to groom. Via such basic feedback mechanisms, emotional processes in the EMO-model regulate spontaneous behaviors as well as appropriate responses to received behaviors on a short-term basis.

Some elements of the emotional regulation of behavior in our EMO-model resemble the *GrooFi-World model* (Puga-Gonzalez et al., 2009) and the *FriendsWorld model* (Puga-Gonzalez, 2014) (described further above). However, in contrast to those models, we aimed to represent the multi-dimensionality of emotional processes (including not only anxiety, but also arousal and satisfaction) and fully integrated them into the behavioral framework (including not only aggression, but also affiliation, social vigilance and movement). Such a less simplistic implementation allows for a better translation of empirical data to model data and vice versa. In contrast to FriendsWorld, the EMO-model explicitly models how individuals process and direct affiliative behaviour. A summary of correspondences and differences between GrooFiWorld, FriendsWorld and the EMO-model is summarized in Table 6.2 in the Summarizing Discussion.

Emotional processes mediate (social) behavior, but are only short-lived. Maintaining a summarizing *memory* of the emotional responses to earlier social stimuli, e.g. in the form of partner-specific *emotional attitudes* that are associated with each other group member and updated regularly, would allow for emotionally based (implicit) *learning* of the value of these group members, without causing an excessive cognitive load. This mechanism of *emotional bookkeeping* has been proposed to underlie grooming reciprocity, as emotional attitudes may guide behavior and partner selection and, this way, promote affiliative reciprocal relationships (Schino and Aureli, 2009). As mentioned earlier, primate affiliative relations between non-kin individuals are of a dynamic nature and have been shown to reflect earlier dyadic interactions. In primates, affiliative relations are developed and maintained through grooming, and grooming is often reciprocated. Whether grooming reciprocity and long-term affiliative bonds in primates are indeed regulated via emotional bookkeeping is difficult to investigate empirically and has not yet been studied in simulation models. A number of ABMs have shown that grooming reciprocity may simply arise from the socio-spatial structuring of the group and emotional bookkeeping may not be necessary (Puga-Gonzalez et al., 2014; Hemelrijk and Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). However, considering the mediating role of emotions in social behavior and the fact that primate behavior is not purely determined by spatial group structure (Chapter 1-2), it is worthwhile to explore the further implications of emotional bookkeeping, with respect to grooming reciprocity and the nature of long-term affiliative relationships. To do this, our EMO-model presents a suitable framework, since it allows us to compare different model versions, in which emotional bookkeeping can be excluded or included (to varying extents).

In the EMO-model, emotional bookkeeping concerns socio-positive emotional responses to affiliation (i.e. grooming). Model individuals associate partner-specific emotional attitudes (*LIKE*, *FEAR*) with each group member. *LIKE* attitudes represent an individual's affiliative valuation of a group member, depending on the frequency and duration of earlier received grooming. *LIKE* attitudes are, thus, dynamically updated, according to the change in emotional state in response to received grooming. Over time, *LIKE* attitudes slowly decrease, mimicking a "fading" of the emotional memory. In other words, receiving grooming from individual A increases the

LIKE attitudes towards individual A. In turn, this results in increased probabilities to direct affiliative behavior (approach, affiliative signaling, grooming) towards individual A. In contrast to LIKE attitudes, FEAR attitudes in our model do not change over time, as they resemble the known dominance relations within dyads, which are stable throughout the course of a simulation run. However, FEAR attitudes also affect partner-specific behavioral probabilities in the model. A high FEAR results in decreased probabilities of aggression and increased probabilities of submission towards the respective individual. Thus, while the emotional state affects an individual's general behavioral probabilities, emotional attitudes towards group members regulate social behavior in a partner-specific way.

In Chapter 3, the EMO-model is introduced and its implementation is described in detail. We present the extensive body of literature that was reviewed to substantiate and parameterize the model. General behavioral patterns emerging in the model, e.g. differences between subordinates and dominants, or between similar- and distant-ranking dyads, are validated using empirical data. Moreover, the causation of those general behavioral patterns is explained, unraveling the underlying regulation processes at work. Chapter 3 proposes the EMO-model as a new research framework to study animal social behavior in the light of emotional regulation and emotional bookkeeping.

Supposing that primates use emotional bookkeeping, they may choose between several potential grooming partners, depending on the partner-specific attitudes associated with these individuals. Thus, valued individuals would be preferred over less valued ones. The question arises, whether and to which degree valued individuals should be preferred over others, for grooming reciprocity to emerge. To explore this, we systematically varied the degree to which model individuals prefer *LIKEd* grooming partners over less *LIKEd* ones, i.e. *LIKE-partner selectivity* (LPS), in the EMO-model in Chapter 4. We investigated the consequences for the emerging affiliative relationships, analyzing group-level reciprocity and the average rank-distance between affiliative partners at different setting of LPS. The most extreme case (LPS=0) constitutes a *null model*, where LIKE attitudes do not have any effect on interaction partner choice and grooming partners are chosen arbitrarily. In Chapter 4, the EMO-model with dynamic LIKE attitudes (*dynamic attitude model*) is also compared to a cognitively simpler control model, the *fixed attitude model*. Here LIKE attitudes do not represent an emotional memory of earlier grooming interactions. Instead of being updated dynamically, they are fixed and depend on rank-distance. Thus, the fixed attitude model presents an alternative hypothesis of how grooming reciprocity may be regulated, i.e. *symmetry-based reciprocity*. Comparing the fixed attitude model to the dynamic attitude model allows us to identify the specific group-level patterns that may only arise when emotional bookkeeping is included in the model.

Emotional bookkeeping allows individuals to keep an updated summary of earlier interactions with each specific group member. The further implications of the timeframe over which emotional bookkeeping works, are still unclear. Intuitively, one might expect that emotional bookkeeping over longer timeframes would yield more stable long-term relationships. To explore this, we systematically vary the temporal dynamics of emotional bookkeeping in the EMO-model in Chapter 5. In our model, when updating the LIKE attitudes, earlier and current experiences are combined to a new value. Here, earlier experiences are given a higher weight (*LIKE-HISTORY WEIGHT* or LHW) compared to the current emotional experience, which results in a slow decrease of LIKE over time when no grooming is received. Higher LHW results in a longer-lasting emotional memory of earlier grooming events. We investigated the effect of the duration of the emotional bookkeeping timeframe on the emergent affiliative group structure. For different durations of this timeframe, we additionally investigated different settings of partner selectivity (LPS: LIKE-partner selectivity). Specifically, we analyze the distribution, duration and reciprocity of specific grooming-partner preferences (affiliative bonds).

Finally, the Summarizing Discussion recapitulates the main results of this thesis and examines how our results (and implemented mechanisms) differ from other simulation studies. Attention is drawn to empirical studies that are still needed to further validate or adapt the models presented in this thesis. Moreover, I suggest how the models presented in this thesis may be further investigated and which control models may still be explored, to fully grasp our models' behavior. I conclude that the models presented in this thesis provide a useful framework to investigate primate social complexity *in silico*.

1

Better safe than sorry - Socio-spatial group structure emerges from individual variation in fleeing, avoidance or velocity in an agent-based model

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ABSTRACT

In group-living animals, such as primates, the average spatial group structure often reflects the dominance hierarchy, with central dominants and peripheral subordinates. This central-peripheral group structure can arise by self-organization as a result of subordinates fleeing from dominants after losing a fight. However, in real primates, subordinates often avoid interactions with potentially aggressive group members, thereby preventing aggression and subsequent fleeing. Using agent-based modeling, we investigated which spatial and encounter structures emerge when subordinates also avoid known potential aggressors at a distance (*avoidance model*) as compared with the model which only included fleeing after losing a fight (*fleeing model*). A central-peripheral group structure emerged in most conditions. When avoidance was employed at small or intermediate distances, centrality of dominants emerged similar to the *fleeing model*, but in a more pronounced way. This result was also found when fleeing after a fight was made independent of dominance rank, i.e. occurred randomly. Employing avoidance at larger distances yielded more spread out groups. This provides a possible explanation of larger group spread in more aggressive species. With avoidance at very large distances, spatially and socially distinct subgroups emerged. We also investigated how encounters were distributed amongst group members. In the *fleeing model* all individuals encountered all group members equally often, whereas in the *avoidance model* encounters occurred mostly among similar-ranking individuals. Finally, we also identified a very general and simple mechanism causing a central-peripheral group structure: when individuals merely differed in velocity, faster individuals automatically ended up at the periphery. In summary, a central-peripheral group pattern can easily emerge from individual variation in different movement properties in general, such as fleeing, avoidance or velocity. Moreover, avoidance behavior also affects the encounter structure and can lead to subgroup formation.

INTRODUCTION

Understanding animal behavior within its social context remains a challenge, since individuals are situated in a complex social environment that consists of many interacting entities and is typically structured, both spatially and socially (Hinde, 1976; Krause and Ruxton, 2002; Whitehead, 2008; Wilson, 2000). A socio-spatial group structure (or pattern) describes how social and spatial properties of individuals, e.g. dominance rank and spatial position within the group, relate to each other (Hemelrijk, 1998b, 2000). In this paper we aim to identify some general mechanisms, which generate socio-spatial group structures. Our theoretical results, obtained via agent-based modeling, are applicable to group-living species, where the dominance hierarchy plays a prominent role in determining the spatial group structure. Here, we will mainly focus on primates and relate our findings to empirical primate studies.

A particular socio-spatial structure often reported in primate studies is a central-peripheral group pattern, i.e. dominant individuals are at the center of the group and subordinates populate the periphery (macaques: Imanishi, 1960; Itani, 1954; Jensen and Tokuda, 1974; Kaufmann, 1967; Lopez-Lujan et al., 1989; Rasmussen and Farrington, 1994; Southwick et al., 1965; Sugiyama and Ohsawa, 1982; Wada and Matsuzawa, 1986; Yamada, 1966, capuchins: Hall and Fedigan, 1997; Janson, 1990; Robinson, 1981, baboons: Busse, 1984; Hall and DeVore, 1965; Washburn and DeVore, 1961). Concerning this centrality of dominants, different theories have been put forward to explain how or why this group pattern may come about. From an ultimate point of view, individuals may have evolved an instinctive preference for the central position within the group to lower predation risk ('selfish herd theory', Hamilton, 1971). On the proximate level, this spatial preference may cause dominants to monopolize this preferred central position. Another, purely social, proximate explanation suggests that the average spatial pattern is a side-effect of the movements of all individuals relative to each other. By means of an agent-based model called DomWorld, Hemelrijk (1998b) showed that aggressive dominance interactions and subsequent fleeing by the loser gives rise to a central-peripheral spatial structure. This spatial pattern emerged through self-organization, meaning that the model individuals had no preference for any spatial location whatsoever. Such a cognitively minimalistic proximate mechanism is likely to extend far beyond the primates.

The crucial element in Hemelrijk's model is the flight of the loser after an aggressive encounter. However, in contrast to these model entities, real primates often try to reduce or prevent aggression within a group, which results in less aggressive encounters and less fleeing. To reduce negative consequences of aggressive conflicts, primates follow numerous strategies either during or after the conflict, e.g. fleeing, policing, redirection or post-conflict affiliation (Aureli et al., 1993, 2002; Aureli and de Waal, 2000; Bernstein and Ehardt, 1985; Koski et al., 2007a; Silk, 2002a; Thierry et al., 2008; de Waal, 1986). However, aggression may also simply be prevented in the first place through conflict avoidance (Aureli et al., 1995; Aureli and de Waal, 1997; Wolkenet et al., 2006). When maneuvering within the group, individuals can adjust their spatial position with respect to potential aggressors to reduce the chance of encounters and the ensuing risk of receiving aggression (Bernstein and Ehardt, 1985; Furuichi, 1983; Hall and Fedigan, 1997; Isbell and Pruett, 1998; Jay, 1965; Judge, 2005; Kutsukake and Clutton-Brock, 2008; McBride, 1971; Mori, 1977; Rowell and Olson, 1983; Sommer et al., 2002). Primate species can be characterized by their dominance style (de Waal and Luttrell, 1989). Vehrencamp (1983) distinguished between egalitarian and despotic styles and Thierry (2000) suggested a whole continuum of dominance styles. Despotic species are characterized by a steeper dominance hierarchy, more unidirectional aggression, higher variance of within-group aggressiveness, lower levels of tolerance and a more pronounced centrality of dominants compared to egalitarian species. Avoidance of potential aggressors is especially important in

aggressive, intolerant species and in species that lack formal submission signals (Bernstein and Ehardt, 1985; Isbell and Pruettz, 1998; de Waal, 1986; Kutsukake and Clutton-Brock, 2008), such as patas monkeys (Kaplan and Zucker, 1980; McNelis and Boatright-Horowitz, 1998; Rowell and Olson, 1983; Loy et al., 1993). Especially in species with a despotic dominance hierarchy, the rank distance between two individuals is reflected in avoidance behavior (Chance, 1956; Jay, 1965). Avoidance behavior is therefore likely to be an important determinant of spatial structuring within a group, however, researchers have not yet investigated this specific potential role of avoidance behavior.

We integrated avoidance behavior into an established model framework to investigate its effect on the socio-spatial properties of a group of individuals. To study this we constructed an agent-based model. Agent-based models (ABMs, also called individual-based models or IBM) are especially helpful to systematically study and understand the structuring mechanisms in a complex system (Hogeweg and Hesper, 1979; Judson, 1994; Villa, 1992). Whereas empirical results from behavioral observations and experiments provide the ingredients for a theoretical model, ABMs can complement and provide feedback on this empirical research itself and on the underlying theory (Bryson et al., 2007; Grimm and Railsback, 2005; Hemelrijk, 2002b; de Vries and Biesmeijer, 1998). In contrast to empirical methods to find explanations, ABMs may help understanding a phenomenon by *generating* it (Epstein, 2006; Epstein and Axtell, 1996). An advantage of models is that distinct factors can be manipulated separately and under controlled conditions, including factors that cannot easily be accessed in real animal groups. ABMs have proven to be well suited to investigate the link between individual behavior and resulting group level patterns in primates (te Boekhorst and Hogeweg, 1994; Bryson et al., 2007; Hemelrijk, 1998b, 2000, 1999a; van der Post et al., 2009; van der Post and Hogeweg, 2004; Puga-Gonzalez et al., 2009; Sueur et al., 2009) and other species (birds: Hildenbrandt et al., 2010, fish: Hemelrijk et al., 2010; Viscido et al., 2005; Oosten et al., 2010; Couzin et al., 2002, insects: Becher et al., 2010; Johnson, 2009; Hogeweg and Hesper, 1983; de Vries and Biesmeijer, 1998).

The agent-based model we present here is adapted from the DomWorld model of Hemelrijk (1998b), which in turn was inspired by Hogeweg (1988). The DomWorld model concerns individual variation in dominance rank and dominance-related variation in fleeing frequency. We replicated a simplified version of this model, adding some modifications and extensions. Irrespective of these modifications, our version still exhibits the same characteristics as the DomWorld model. Replicating DomWorld allowed us to compare different models to the DomWorld model, especially with respect to model properties that have not been measured or described previously. In particular, we measured the distribution of encounters among the group members, since the spatial distribution of individuals may affect with whom individuals interact. Our adapted version of DomWorld is, hereafter, referred to as the '*fleeing model*'.

We contrasted the *fleeing model* with a model that additionally includes avoidance behavior (*avoidance model*), to investigate how aggressor avoidance, and thus fewer aggressive encounters and less frequently subsequent fleeing, may give rise to different forms of socio-spatial structure. We varied two determinants of avoidance behavior (the rank-difference above which an individual is avoided and the spatial distance within which avoidance is employed). Furthermore, we investigated the isolated effect of avoidance behavior on the socio-spatial structure: by removing individual variation in fleeing frequency from the *avoidance model* we control for any structuring effect that may result from fleeing subsequent to aggressive encounters (*avoidance with fleeing-control model*). An additional goal of this paper is to identify general mechanisms underlying a central-peripheral group pattern. Both the *fleeing model* and the *avoidance model* concern individual variation in movement characteristics, i.e. frequency and

direction of fleeing or of spatial avoidance at a distance. In both models subordinates move, i.e. flee or avoid, more frequently than dominants. In a third model (*velocity model*) we test whether individual variation in velocity alone is already sufficient to generate a central-peripheral group pattern.

By investigating how several movement characteristics (fleeing, avoidance and velocity) that may vary across a social group, may result in consistent spatial and encounter structures, a more complete understanding of the emergence of spatial and social group structure and their inter-relatedness is obtained. We present a new, general mechanism and explanation for one of the main questions in primate literature: what causes centrality. More specifically, we investigate the effects of a specific primate behavior: aggressor avoidance at a distance.

METHODS

The models

Our basic model, the *fleeing model*, is adapted from DomWorld, but differs in the following points. First, we implemented a stable dominance hierarchy (similar to the model in the appendix of Bryson et al., 2007). In primates, dominance hierarchies are stable over long periods of time (up to several years, macaques: Bernstein, 1969; Rhine et al., 1989; Ostner et al., 2008; Silk, 1988, gorilla: Robbins et al., 2005, baboons: Samuels et al., 1987; Hausfater et al., 1982, capuchins: Bergstrom and Fedigan, 2010, vervets: Bramblett et al., 1982) and are altered only incidentally, e.g. after changes in the group composition due to birth, death or migration of individuals (Missakian, 1972; Robbins et al., 2005). Moreover, we do not aim to study the development of the hierarchy within a group. Instead, we assume that in our group a hierarchy has been already established and does not change over the timeframe of our simulation. Second, we chose to model a larger group than earlier models (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003; Puga-Gonzalez et al., 2009), consisting of 30 instead of 8, 10, 12 or 20 individuals. This more accurately represents group size in many primate species (Lehmann et al., 2007; Sueur et al., 2011a) and furthermore results in more informative data regarding the spatial group structure. Third, our adapted grouping procedure allows strayed individuals to find back the group and to move towards it quickly (see section Grouping and movement below). This ensures fast grouping and does not artificially prolong the time spent at the group periphery. Fourth, we restricted the maximum spread of the group to prevent eventual group split-up, while still allowing for flexibility with regard to group spread, individual spatial positions within the group and subgrouping patterns (see section Grouping and movement below). This allowed us to analyze all group members as a single group. Fifth, our model differs from DomWorld in the decision-making procedure subsequent to an encounter. In our model both opponents may decide whether to engage in a fight, as a fight only takes place if both opponents agree to it (see section Social interactions below). This is in contrast with DomWorld where the encountered individual always takes part in the fight, if the encountering agent decided to start a fight (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003; Puga-Gonzalez et al., 2009). Sixth, we implemented a sigmoid win chance function (Hsu et al., 2005) (as suggested by de Vries, 2009), instead of a relative win chance function. The latter two adaptations ensured that escalated fights between two individuals distant in rank are rare (see Text S1.1), as has been suggested by empirical and theoretical work (Alexander and Bowers, 1969; Bernstein and Sharpe, 1966; Maynard-Smith and Parker, 1976). Last, in our model, when individuals move within the group they employ a random walk. This contrasts with the DomWorld model, where individuals move straight (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003). In fact, in DomWorld, individuals may only change their

heading direction, after an encounter or when other individuals are too far away and need to be approached. An evaluation of the effect of the random movement is discussed below (see Section Robustness of the model).

In the *fleeing model*, individuals behave as follows: (1) Individuals move and orient themselves to have at least three other group members in sight. (2) If this condition is fulfilled, individuals move around randomly. (3) On encounter, individuals may engage in dominance interactions. Each individual's dominance strength determines its ability to win dominance interactions and individuals differ in dominance strength. The loser of a dominance interaction flees from the winner. To investigate the implications of avoidance behavior for the socio-spatial group structure, we compared a model without avoidance behavior (*fleeing model*) to a model that includes avoidance behavior (*avoidance model*). In the *avoidance model*, individuals follow the same rules as in the *fleeing model*, yet additionally, individuals may avoid potential aggressors at a distance. Thus, the effects of fleeing and avoidance behavior are combined in the *avoidance model*. We also investigated the isolated effect of avoidance by excluding variation in fleeing frequency (*avoidance with fleeing-control model*). Thus, in the *avoidance with fleeing-control model* the structuring effect of fleeing was removed. To assess whether individual variation in velocity alone may be sufficient to generate a central-peripheral group pattern, we constructed another model (*velocity model*), in which individuals differ merely in their average velocity. In this model, individuals have a tendency to group (rules (1) and (2) above), but there is no variation in fleeing frequency and individuals do not employ avoidance behavior.

Simulations were run using NetLogo 4.0.3 (Wilenski, 2007). For our models, we extensively modified an earlier publicly available replication of the DomWorld model by Bryson et al. (2007). The program code of all our models is available for download via the website of the first author¹. Definitions and values of the model parameters can be found in Table 1.1. Below, we describe all model procedures in more detail.

Environment, initialization and timing regime

The modeled environment is a continuous two-dimensional grid (300×300 grid units) with a torus shape to exclude disturbing border effects. One grid unit is scaled to 1 meter. We chose the size of the grid to be large enough to hold a group with a maximum group spread of around 110 meters (see section Grouping and movement below), while ensuring that real distances between group members were always smaller than distances between group members when measured around the torus. We did not explicitly implement ecological features of the environment; in the model an individual's environment is purely social. This also implies that our model individuals do not engage in foraging behavior. Thus, we model a group that is not traveling.

At the initialization of each simulation run, the x-coordinates and the y-coordinates of all individuals are drawn from a normal distribution around an arbitrarily chosen position on the spatial grid (standard deviation = 10 grid units), independent of their dominance strength. Their initial heading was set to a random number between 1 and 360 degrees.

Our model is event-driven. During a simulation run, individuals' activations are regulated by a timing regime. One time step in the simulation resembles 1 "second". Agents are activated in a cyclic, asynchronous way. Each time, the agent with the lowest schedule time is activated first. After activation, this agent's next activation is scheduled. The remaining time until its

¹<https://sites.google.com/site/elleneversutrecht/models>

Parameter	Description	Value
General parameters		
D	Grid unit	1 m
T	Time step	1 s
$GRID_SIZE$	Grid size	300×300 m
N	Number of individuals in group	30
$PERS_DIST$	Maximum distance, within which others can be encountered	4 m
$NEAR_DIST$	Maximum preferred distance to the group	20 m
MAX_DIST	Maximum distance monkeys are able to see	50 m
FAR_DIST	Maximum preferred distance to the furthest group member	$NEAR_DIST * \sqrt{N} \approx 110m$
MIN_OTHERS	Minimum preferred number of conspecifics within $NEAR_DIST$	3
MAX_DOM	Maximum dominance strength	1.0
m_iDOM_i	Dominance strength of individual i	$(i * MAX_DOM)/N$
η	Parameter determining the steepness of the sigmoid function of win chance	$6 / MAX_DOM$
$VIEW_ANGLE$	Default view angle	120°
$ChaseD$	Distance the winner of a fight chases the loser	1 m
$FleeD$	Distance the loser of a fight flees from winner	2 m
$WalkD$	Default distance an individual walks forward	1 m
Avoidance parameters		
$AvoidD$	Distance an individual moves away from <i>avoider</i>	2 m
AV_DOM_DIFF	Avoidance dominance difference; difference in strength, above which an agent is considered a potential aggressor and consequently avoided	0.2, 0.4, 0.6
AV_DIST	Avoidance distance; spatial distance within which potential aggressors are avoided	5, 15, 25, 35 m
Velocity parameters		
$MAX_VELOCITY$	Maximum possible velocity	1, 5, 10, 20, 30 m/s
$m_iVELOCITY_i$	Velocity of individual i	$MAX_VELOCITY/i$

Table 1.1: Parameters, definitions and values of the fleeing, avoidance and velocity model.

next scheduled activation is randomly drawn from a negative exponential distribution with a mean of 10 time steps:

$$ScheduleTime_{new} = ScheduleTime_{old} + (-10 * \ln(RND(0, 1))). \quad (1.1)$$

In other words, events are randomly distributed in time. Scheduled times are on a continuous range. If an action involves other individuals as well, each participant gets scheduled anew for its next action.

Perception and action-selection

On activation, individuals execute an action-selection protocol (Figure 1.1). This protocol goes through a number of decisions to produce the behavior appropriate to the social situation. The decisions are structured hierarchically according to urgency, e.g. interactions have priority over grouping and grouping has priority over avoidance.

First, individuals check whether other individuals are encountered, i.e. whether other individuals are within a personal distance of 4 m (*PERS_DIST*), which will lead to an interaction (see Interactions section below). If no one is encountered, individuals turn and move towards the group if necessary (see Grouping and Movement section below). In the *avoidance model*, if grouping is not necessary, individuals may further choose to avoid others (see section Avoidance below). If none of the above actions were selected, individuals move randomly within the group (see Grouping and Movement section below).

The identity and spatial position of other group members affects an individual's behavior. Individuals are capable of perceiving the spatial distance and the dominance strength of others that are dwelling within a view angle of 120 degrees and a maximum perceivable distance of 50 m (*VIEW_ANGLE* and *MAX_DIST* in Figure 1.2). Parameter choices for *PERS_DIST*, *VIEW_ANGLE* and *MAX_DIST* were adapted from (earlier replications of) DomWorld (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003).

Grouping and movement

To stay relatively close to group members, individuals check whether at least three group members (*MIN_OTHERS*) are situated within a distance of 20 m (*NEAR_DIST*) within their view angle (Figure 1.2). The parameter choice for *MIN_OTHERS* was adapted from van der Post and Hogeweg (2004, 2006, 2008, 2009); van der Post et al. (2009) and the parameter choice for *NEAR_DIST* was adapted from an earlier replication of the DomWorld model (Bryson et al., 2007). If less than three group members were detected within 20 m, individuals try to find another group member within the maximum distance they can see (50 m), or else within a broader view angle (360 degrees) by looking around (Figure 1.2). Of the perceived individuals, one is selected randomly and approached by 1 m (*WalkD*). The parameter choice for *WalkD* was adapted from DomWorld (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003).

Furthermore, individuals always check the distance towards the furthest group member. If at any time the distance towards the furthest group member exceeds a certain value, *FAR_DIST*, ego will immediately turn towards a randomly selected group member and approach it (for 1 m). *FAR_DIST* depends on the number of individuals in the group (*N*) as follows:

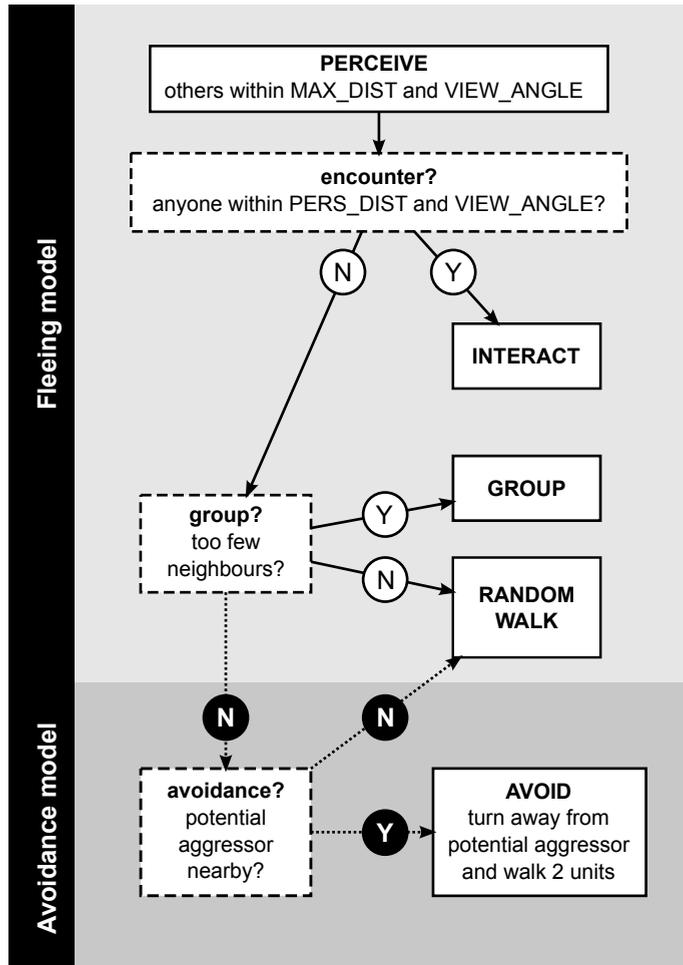


Figure 1.1: Interaction rules. Model individuals employ a hierarchically organized decision tree. The protocol is starting at the top and resulting in only one of three or four (depending on the model) possible behaviors, depending on the social situation of the individual and the priority of the behaviors. Note that this decision tree does not reflect any temporal order of the behaviors.

$$FAR_DIST = NEAR_DIST * \sqrt{N}, \quad (1.2)$$

thus, for a group of $N = 30$ individuals, $FAR_DIST \approx 110$ m. The parameter value for FAR_DIST was chosen arbitrarily. Note that by approaching a random group member, the probability of selecting another individual that just walked away from the group itself is small. This grouping procedure ensures that all group members remain within a certain distance from each other. Subgroups may form, but eventual group split-up is prevented in our model.

Movement of the model individuals is either motivated by explicit social factors, such as grouping, fleeing, chasing or avoidance, or is else implemented as a random walk. When executing

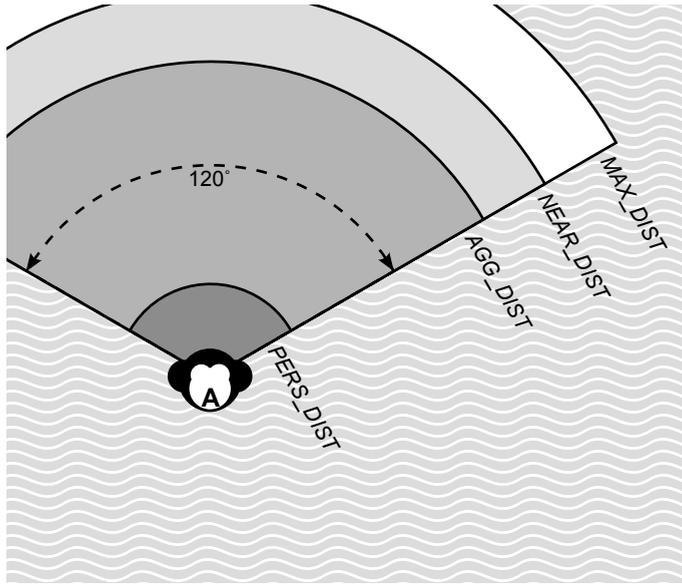


Figure 1.2: Perception. Model individuals perceive other group members within a default view angle of 120 degrees. The maximum distance within which another can be seen is *MAX_DIST*. Distances in the figure are not to scale.

a random walk, individuals simply move forward (for 1 m) and with a chance of 0.5, they then turn randomly up to 180 degrees to the right or left.

Social interactions

When other group members are perceived within a personal distance of 4 m, ego chooses the nearest individual as an interaction partner. In our models interactions are always dyadic. For each interaction, the partner choice is recorded and scored as an encounter. Thus, encounters are directed from one individual (ego, who perceived the other first) to another (chosen partner).

On encounter, ego may either challenge its interaction partner or flee from it for 2 m (Figure 1.3). This decision depends on the chance of winning a fight with the opponent. This win chance is dependent on both opponents' dominance strength. When initializing a simulation run, each model individual gets assigned a fixed value for its dominance strength (*myDOM*), ranging from $1/N$ (for the lowest-ranking individual) to 1.0 (highest-ranking). Note that this choice of scaling the dominance values between 0 and 1 is arbitrary and does not affect our results. The chance of individual *A* winning against individual *B*, w_{AB} , is then calculated as:

$$w_{AB} = \frac{1}{(1 + e^{-\eta(myDOM_A - myDOM_B)})}, \quad (1.3)$$

where the parameter η describes the steepness of the sigmoid win chance function and $myDOM_i$ is the dominance strength of individual *i*. Note that by definition the win chances of both opponents add up to 1 and the opponents win chance is thus: $w_{BA} = 1 - w_{AB}$. A higher

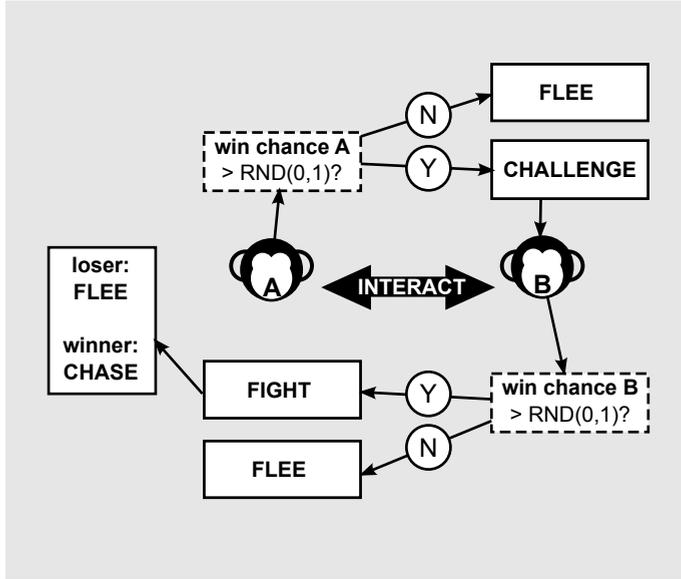


Figure 1.3: Interaction rules upon encounter. Upon encounter, an agent may either challenge or flee from the opponent. After being challenged, the opponent may either flee or agree to a fight.

difference in dominance strengths results in a higher chance of winning the fight for the dominant individual. Note that the win chance w_{AB} in our model is the same whenever the difference in dominance strengths, $DOM_A - DOM_B$, is the same (de Vries, 2009). Note further that we chose η such that the distribution of win chances among the group members is comparable to the DomWorld model, with win chances ranging from $w_{AB} \approx 0.003$ (for $myDOM_A = 1/30$ and $myDOM_B = 1$) to $w_{AB} \approx 0.997$ (for $myDOM_A = 1$ and $myDOM_B = 1/30$).

On encounter, ego challenges its opponent when its expected win chance is higher than a randomly drawn number between zero and one:

$$w_{AB} > RND(0, 1), \quad (1.4)$$

and flees when it is lower. As a response to a challenge, the opponent may either reject or agree to engage in a fight, depending on its own expected win chance (Figure 1.3). If the opponent's win chance w_{BA} is higher than a new randomly drawn number, a fight will start, otherwise the individual declines and flees. As soon as one of the two interacting individuals declines and subsequently flees, the conflict is settled and no fight takes place.

If no fight took place, the fleeing individual turns away from its opponent. With a chance of 0.5, its opponent visually orients towards a random direction. Staying oriented towards the opponent would result in repeated interactions. However, since the fleeing individual acknowledged its opponent's higher status, the opponent can orient elsewhere.

In our models, only if both individuals agree to a fight does an actual fight take place (Figure 1.3). The winner of a fight is stochastically determined: individual A wins from B, when its win

chance, w_{AB} , is higher than a new randomly drawn number between zero and one (Equation 1.3 and 1.4).

After a fight, the loser flees from the winner for 2 m (*FleeD*), while the winner chases the loser by running after him for 1 m (*ChaseD*) (Figure 1.3). Parameter choices for *FleeD* and *ChaseD* were adapted from DomWorld (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003). Bryson et al. (2007) proposed to reinterpret the fight and subsequent fleeing behavior in the DomWorld model as displacement behavior. Our model implements an even richer behavioral differentiation. When individual *A* perceives *B* nearby and immediately flees, we may call this unprovoked fleeing. When individual *A* flees only after *B* signaled its fighting intention, we may call this fleeing after threat. When both individuals signaled their fighting intention, a real fight takes place.

In contrast to the DomWorld model, we did not implement so-called “wiggling” in which the winner turns about a certain angle after chasing the loser. This was implemented in the DomWorld model to (artificially) prevent too many repeated interactions between the same individuals (Hemelrijk, 1998a,b). However, we found that this work-around can affect the socio-spatial structure. For a short analysis of the effect of “wiggling” see the Text S1.2.

Outcomes of fights have no further implications for the behavior or for the dominance strength of the participants. Thus, we model a primate group with a stable dominance hierarchy where dominance strength is not updated after a fight (like the model in the Appendix of Bryson et al., 2007; but unlike the DomWorld model of Hemelrijk, 1998b).

The interaction procedure described above results in low-ranking individuals losing and fleeing more often than high-ranking ones. In the *avoidance with fleeing-control model* and in the *velocity model* we controlled for individual differences in fleeing rate by simply assigning a win chance of 0.5 to each individual, independent of its actual dominance strength. In this way, fleeing rates were equal among individuals, while other properties, such as avoidance behavior or velocity, did still differ.

Avoidance

In addition to all procedures described above, individuals in the *avoidance model* may avoid known potential aggressors at a distance. This contrasts with earlier models where individuals may flee from a dominant only directly after encountering it (Bryson et al., 2007; Hemelrijk, 1998b, 2000; Hemelrijk et al., 2003; Puga-Gonzalez et al., 2009). How and to what extent avoidance behavior is employed is determined by two parameters: AV_DOM_DIFF and AV_DIST , which will be explained below.

Whether an individual identifies another as a potential aggressor depends on the difference of both individuals’ dominance strength. The parameter AV_DOM_DIFF (avoidance dominance difference) describes the minimum difference in dominance strength between two individuals that elicits avoidance behavior in the subordinate. Thus, individual *A* avoids individual *B*, if:

$$myDOM_A < myDOM_B - AV_DOM_DIFF. \quad (1.5)$$

Values for AV_DOM_DIFF may be varied from zero to one. A high value for AV_DOM_DIFF represents a system where only the lowest-ranking subordinates avoid only a few highest-ranking individuals. A low value for AV_DOM_DIFF means that subordinates avoid most higher-ranking

individuals, mimicking a more despotic group with more pronounced aggression and frequently employed avoidance.

Whether ego avoids a detected potential aggressor is dependent on the spatial distance to that animal. The parameter *AV_DIST* (avoidance distance) describes the spatial distance within which subordinates avoid aggressors (Figure 1.2); ego avoids potential aggressors that are perceived at a distance smaller than *AV_DIST*. Values for *AV_DIST* may be varied from zero to *MAX_DIST* (Table 1.1). A low *AV_DIST* value would result in subordinates avoiding only those potential aggressors that were already very close. A high value for *AV_DIST* would result in subordinates avoiding also those potential aggressors that were still at a large distance, mimicking a more despotic group with more pronounced aggression and frequently employed avoidance. Therefore, the number and the identity of potential aggressors may differ among individuals, depending on their dominance strength and their spatial position within the group.

The actual avoidance behavior of detected potential aggressors is implemented in the following way: Reacting on another individual directly after encounter, i.e. after perceiving any other individual within *PERS_DIST* still has the highest priority. If no encounter took place, ego checks whether there are too few neighbors perceived within *NEAR_DIST*, which would result in grouping behavior. When no encounter takes place and no grouping behavior is necessary, ego checks whether there is a potential aggressor within *AV_DIST* (Figure 1.1). If potential aggressors are detected, the nearest one is selected and avoided: ego turns away from this individual and walks away for 2 m.

Velocity

In the fleeing model and the avoidance model, subordinates flee from or avoid dominants. This suggests that on average subordinates move over larger distances, compared to dominants. To check, whether this variation in the amount of movement may be sufficient to generate a central-peripheral group pattern we developed the velocity model, where individuals merely differ in their average velocity, i.e. the average distance they walk per time interval (in meters/second). In this model, we made velocity directly dependent on dominance strength, thus subordinates walk greater distances in the same time interval compared to dominants. Velocity of individual *i* is calculated as follows:

$$myVelocity = \frac{MAX_VELOCITY}{myDOM_i * N} = \frac{MAX_VELOCITY}{i}, \quad (1.6)$$

where, $myDOM_i$ is the dominance strength of individual *i*, *N* is the total number of individuals within the group and *MAX_VELOCITY* is the maximum possible velocity within the group. Note that in the *velocity model*, individuals do not differ in their fleeing rates nor do they employ any avoidance behavior (see section Social interactions above).

Data collection and parameter settings

To assess socio-spatial group properties within each model, we used several measures. To measure how individual differences in fleeing frequency, avoidance tendency and velocity were related to the individuals' spatial position within the group, we calculated each individual's distance to the arithmetic center of the group. The coordinates of the arithmetic center of the group were calculated as follows:

$$(\bar{x}, \bar{y}) = \left(\frac{1}{N} \sum_i^N x_i, \frac{1}{N} \sum_i^N y_i \right), \quad (1.7)$$

where N is the number of individuals in the group and x_i and y_i are the spatial coordinates of individual i . When the group was wrapped around a border of the field in the direction of the x or y -axis, the respective coordinates (x or y) of the individuals at the low end of the field were increased by the length of the field in the respective direction for the calculation. We also calculated centrality-peripherality using circular statistics and the mean spatial direction of all others around an individual. This procedure is described and discussed elsewhere (see Mardia, 1972; Fisher, 1996; Christman and Lewis, 2005 and Figure 4a in Hemelrijk, 2000). Values for centrality-peripherality are similar to the distances to the arithmetic center of the group, except that the centrality-peripherality measure is normalized and scaled to values between 0 and 1. Here, we only discuss the results for the distances to the arithmetic center of the group, as they are more informative considering the group spread and as group size is the same in all the models presented here.

We measured differences in spatial group spread by recording the furthest neighbor distance within the group (the distance between the two individuals in the group that are furthest away from each other).

We assessed how dyadic distances, as well as the number of encounters were distributed among all possible dyads. The spatial dyadic distances were simply recorded over time. To measure the total number and direction of encounters, i.e. the encounter structure, we recorded the identity of those group members that ego had selected as opponents.

A single simulation was run for 72 000 time steps, which resembled 20 observation “hours”. We recorded data during the last 10 “hours”, to avoid transient spatial and social group effects due to the initial random placement. This time period is sufficiently long to measure patterns emerging from the short-term scale (inter)actions in the model. All measures of the socio-spatial group structure (distance to arithmetic center of the group, centrality-peripherality, spatial group spread, dyadic distances and encounter structure) were recorded every 900 time steps which was equivalent to 15 “minutes”. All measures, except the number of encounters per dyad, were averaged over recorded time for each simulation run. For the number of encounters per dyad all occurrences were recorded. For each model 50 independent simulations were run per parameter setting.

In the *avoidance model*, the parameter *AV_DOM_DIFF* was varied between 0.2 and 0.6, and the parameter *AV_DIST* was varied between 5 m and 35 m. In the *velocity model*, the parameter *MAX_VELOCITY* was varied between 1 m/s and 30 m/s. See Table 1.1 for an overview of all parameters used in our models.

Experimental set-up

First, we confirmed whether the properties of our *fleeing model* were similar to earlier results published on the DomWorld model. To then assess the effect of avoidance behavior on socio-spatial group properties, we contrasted the *fleeing model* to the *avoidance model*. The *fleeing model*, where individuals do not employ any avoidance behavior, would correspond to groups where avoidance might simply not be necessary, e.g. due to very low levels of aggression. In contrast to that, the *avoidance model* reflects a whole range from little to intensive avoidance

behavior (depending on the parameter settings), which would correspond to groups ranging from low-level to severe aggression. To investigate, whether the socio-spatial group properties that emerged in the *avoidance model* depend on the more frequent fleeing of subordinates, we implemented the *avoidance with fleeing-control model*. In this model we controlled for variation in fleeing frequency to measure the isolated effect of avoidance. Thus, in the *avoidance with fleeing-control model*, subordinates flee equally often as dominants after a fight. This model does not attempt to represent real primate groups, but it allows us to disentangle several factors and their effects, which are usually interconnected in the real system. Finally, we measured group level properties of the *velocity model*, in which individuals merely vary in their velocity. In other words no avoidance is employed and subordinates flee equally often as dominants. The *velocity model* does also not attempt to represent real primate groups. Rather, it allows us to investigate, whether variation in velocity alone may be already sufficient to generate a central-peripheral pattern in groups of entities. The experimental set-up is summarized in Table 1.2.

	Factor:	Fleeing frequency	Avoidance tendency	Velocity
1.	Fleeing model	Variable	Not employed	Equal
2a.	Avoidance model	Variable	Variable	Equal
2b.	Avoidance fleeing-control model	Equal	Variable	Equal
3.	Velocity model	Equal	Not employed	Variable

Table 1.2: Experimental set-up and characteristics of the compared models.

RESULTS

Fleeing model

As described above, the *fleeing model* is a modified version of DomWorld model (Hemelrijk, 1998b). In this *fleeing model*, a (weak) central-peripheral group structure arose with dominants more often at the group center and subordinates more often at the periphery (Figure 1.4A). The lower an individual's dominance strength, the more likely it was to lose a dominance interaction. Thus, subordinates fled more often just before or after a fight, thereby moving away from higher-ranking individuals. Since the most dominant animal (alpha animal) was the individual that most others usually fled from, the alpha was automatically found at a spatially central position in the group. Since subordinates fled from most other group members, they were found more often at the periphery of the group (see Figure 1.5A for an example snapshot). This self-sorting of the model individuals, according to their dominance strength, arose through self-organization. As a result distance from the group center, correlated with dominance strength (Figure 1.4A).

For comparison with the other models in this paper, the following results of the *fleeing model* are important. The repulsive force of fleeing counteracted the attractive force of grouping and affected how much the group was spread out and how it was patterned in space. The spread of the group in the *fleeing model* was small (Figure 1.6A): the average furthest neighbor distance was 36.4 ± 1.0 m (mean \pm standard deviation, N=50 simulation runs). Consequently, the

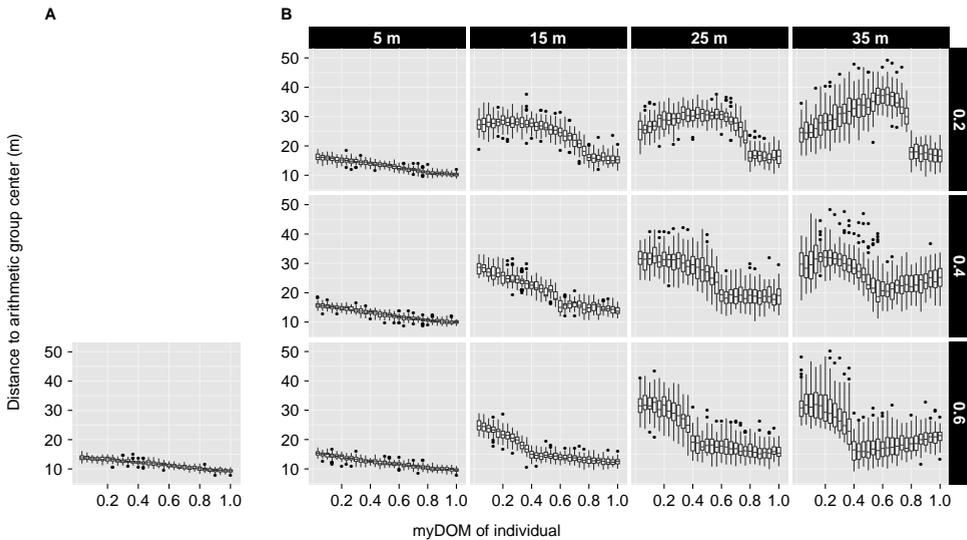


Figure 1.4: Centrality of dominants. This figure shows the relationship between an individual's dominance strength (myDOM) and its centrality (distance to the arithmetic center of the group in meters) for different models. **A:** *Fleeing model*. **B:** *Avoidance model* (with different combinations of *AV_DOM_DIFF* (vertically, 0.2 - 0.6) and *AV_DIST* (horizontally, 5 - 35 m)). Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper, centrality of dominants is more pronounced. Depending on the model, a low myDOM further implies low win chance and thus frequently employed fleeing behavior (*fleeing* and *avoidance model*) and frequently employed avoidance behavior (*avoidance model*). Boxplots show values of 50 simulation runs, averaged over time.

average dyadic distances were similarly small among all individuals (Figure 1.7A). Following from this, the frequency and direction of encounters were similar among all individuals, i.e. the encounter structure was not differentiated (Figure 1.8A).

Avoidance model: Spatial structure

To assess the effect of avoidance behavior on socio-spatial group properties, we compared the *fleeing model* to the *avoidance model*, while varying values for the distance within which an individual avoided potential aggressors (*AV_DIST*, varied from 5 m to 35 m) and the difference in dominance strength above which avoidance was employed by the subordinate (*AV_DOM_DIFF*, varied from 0.2 to 0.6). Just as in the *fleeing model*, we observed a central-peripheral distribution of animals, sorted according to their dominance rank (Figure 1.4B). When avoidance was employed at a small distance (*AV_DIST* = 5 m), the central-peripheral group structure was comparable to the *fleeing model*. Because avoidance was only employed when a potential aggressor was very close the behavioral and spatial consequences were comparable to fleeing from an opponent after encountering it within *NEAR_DIST* (4 m). When avoidance was employed at intermediate distances (*AV_DIST* = 15 - 25 m), the socio-spatial structure became more pronounced (Figure 1.4B); individual distances to the group center were more differentiated than in the *fleeing model*. This is reflected in the steeper slope in Figure 1.4B as compared to the slope in Figure 1.4A (the *fleeing model*). The spatial group structure in the *avoidance model* is illustrated in some example snapshots in Figure 1.5B. Note that in the *avoidance model*, individuals with $myDOM \geq (1.0 - AV_DOM_DIFF)$ did not avoid any other individuals

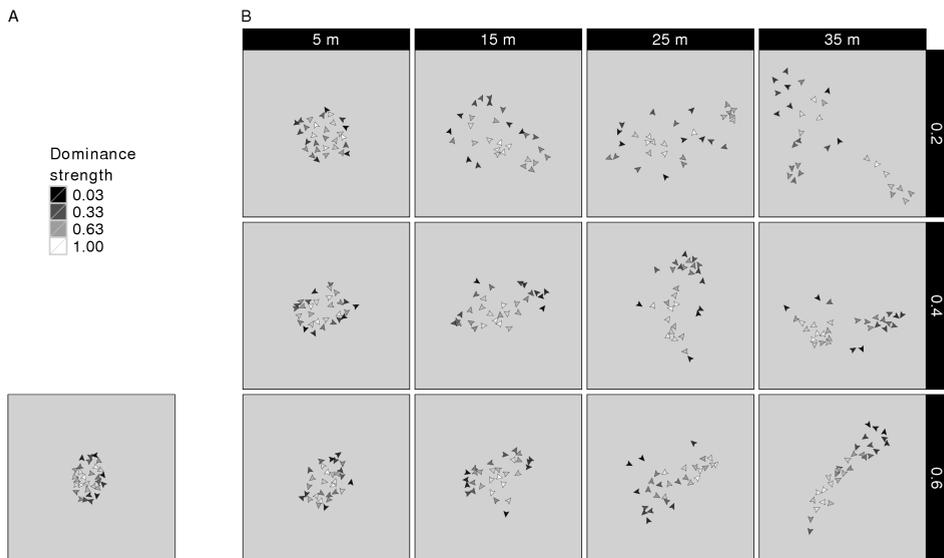


Figure 1.5: Snapshots of the socio-spatial group structure. This figure shows snapshots of the spatial composition of the group members for different models. **A:** *Fleeing model*. **B:** *Avoidance model* (with different combinations of AV_DOM_DIFF (vertically, 0.2 - 0.4) and AV_DIST (horizontally, 5 - 35 m). Shown is a 100 by 100 meters excerpt of the total grid at one arbitrary point in time. Each arrowhead represents an individual. White shade represents a high dominance strength, dark shade represents a low dominance strength. The heading of an arrowhead represents the individual's visual orientation. For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend.

by definition (see Equation 1.5). These dominant individuals formed a subgroup at the center of the group. This central subgroup showed small variation in average spatial distance to the group center (Figure 1.4B). In fact the central subgroup in the *avoidance model* behaved just like individuals in the *fleeing model*, as no avoidance was employed by these individuals and only variation in fleeing frequency structured the spatial properties within this subgroup. When avoidance was employed at very large distances ($AV_DIST = 35$ m) the central-peripheral group structure broke down (see subsection Subgroup formation below).

Groups in the *avoidance model* were more spread out compared to the *fleeing model* (Figure 1.6B). The furthest neighbor distance was ranging from 38.0 ± 0.6 m (for $AV_DOM_DIFF = 0.6$ and $AV_DIST = 5$ m) to 92.6 ± 6.0 m (for $AV_DOM_DIFF = 0.2$ and $AV_DIST = 35$ m, mean \pm standard deviation, $N=50$ simulation runs). Higher values for AV_DIST resulted in larger group spread, as potential aggressors were avoided at larger distances. Lower values for AV_DOM_DIFF yielded a larger group spread, as more group members needed to be avoided (Figure 1.6B).

To assess the isolated effect of avoidance behavior on socio-spatial group patterns, we measured the relationship between spatial distance to the group center and dominance strength in the *avoidance with fleeing-control model* (a model without individual variation in fleeing frequency). In the *avoidance with fleeing-control model*, a similar spatial structure to that of the *avoidance model* emerged (Figure S1.3), although groups were less spread out for avoidance at small and intermediate distances. The furthest neighbor distance was ranging from 30.7 ± 0.4

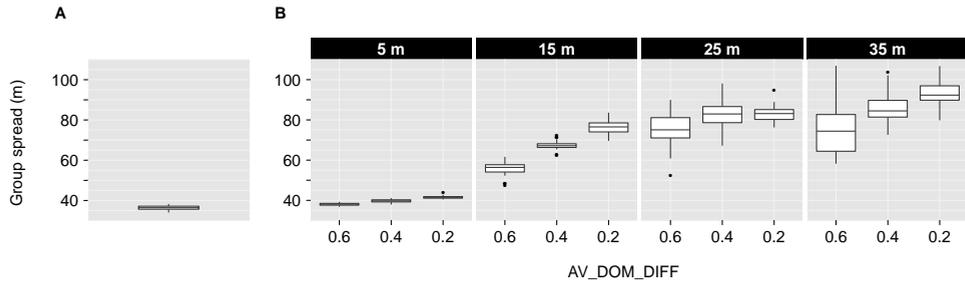


Figure 1.6: Group spread. This figure shows the group spread (in meters) for different models. **A:** *Fleeing model*. **B:** *Avoidance model* (with different combinations of AV_DOM_DIFF (x-axis, 0.2 - 0.4) and AV_DIST (horizontally, 5 - 35 m). Boxplots show values of 50 simulation runs, averaged over time.

m (for $AV_DOM_DIFF = 0.6$ and $AV_DIST = 5$ m) to 93.3 ± 9.5 m (for $AV_DOM_DIFF = 0.2$ and $AV_DIST = 35$ m, mean \pm standard deviation, $N=50$ simulation runs). Furthermore, the variation in distance to the group center among the central dominants disappeared (Figure S1.3). Because we controlled for variation in fleeing, these central individuals were in fact identical to each other and only differed in the degree to which they were avoided by others.

Avoidance model: Subgroup formation

When avoidance was employed at large distances ($AV_DIST = 35$ m), dyadic distances between avoiders and avoidees became larger. Eventual splitting-up of the group was restricted in our model (see Methods), but individuals formed subgroups that were spatially separated. Subgroups emerged, consisting of individuals of similar rank that did not avoid each other (Figure 1.7B). As a result of this spatial structure, almost no encounters took place between individuals from different subgroups (Figure 1.8B). The number and size of subgroups depended on AV_DOM_DIFF , with more and smaller subgroups for low values of AV_DOM_DIFF . For example, if $AV_DOM_DIFF = 0.2$, individuals with dominance strength higher than 0.8 formed the alpha subgroup, individuals with dominance strength between 0.6 and 0.8 formed the beta subgroup, and so on (Figure 1.7B and 1.8B).

In addition, for avoidance at large distances ($AV_DIST = 35$ m), the general central-peripheral group pattern broke down (Figure 1.4B). When avoidance at large distances ($AV_DIST = 35$ m) was combined with low AV_DOM_DIFF (0.2), lower-ranking individuals formed several subgroups (e.g. beta, gamma and delta) around the central alpha subgroup, arranged spatially according to average subgroup rank. However, the probability that a low-ranking subgroup was “driven apart” by an approaching, more dominant subgroup increased with decreasing average subgroup rank. Therefore, the lowest-ranking individuals could not aggregate as a subgroup, as they were constantly forced to avoid approaching potential aggressors. While the beta subgroup could keep a safe distance from the alpha subgroup, the still lower-ranking subgroups (e.g. gamma and delta) were forced to occupy spatial positions closer to the center, in-between the central alpha subgroup and the peripheral beta subgroup (for an example snapshot of the spatial configuration at this parameter setting see Figure 1.5B). As the maximum group spread was restricted in the model, these lower-ranking subgroups could not aggregate at an even greater distance from the higher-ranking subgroups. Without this restriction, avoidance at a

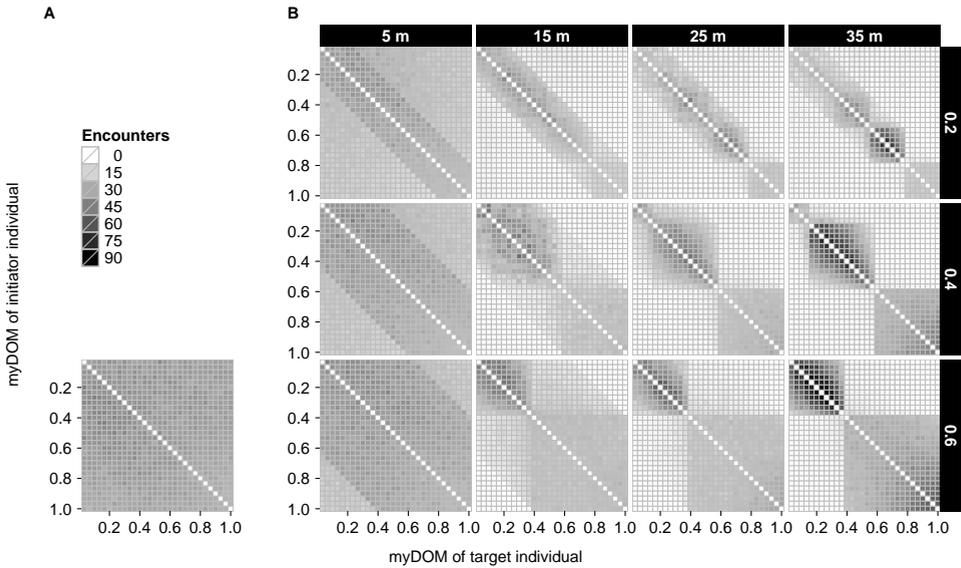


Figure 1.8: Encounter structure. This figure shows the distribution and direction of encounters among the individuals of a group for different models. **A:** *Fleeing model*. **B:** *Avoidance model* (with different combinations of AV_DOM_DIFF (vertically, 0.2 - 0.4) and AV_DIST (horizontally, 5 - 35 m). Encounters are directed from initiators (y-axis) to targets (x-axis), both are ordered by dominance strength (myDOM). For further implications of an individual’s dominance strength depending on the model, see the Figure 1.4 legend. Plots show the mean values of 50 simulation runs. Dark shades represent frequent encounters. Values at the diagonal are by default not applicable.

individuals of distant rank (darker band around the diagonal in Figure 1.8B). Note that the range of “preferred” dominance values of interaction partners (the width of the band around the diagonal in Figure 1.8B) is determined by the parameter AV_DOM_DIFF (Figure 1.8B): a lower AV_DOM_DIFF allows interactions only between individuals very close in rank. While individuals of too high a rank would be avoided by a specific individual, individuals of too low a rank would themselves avoid this specific individual.

When AV_DIST was increased to 15 m, frequent avoidees (high-ranking individuals that were avoided) at the center of the group were surrounded by frequent avoiders (low-ranking individuals) at the periphery (Figure 1.8B). While the individuals still formed a coherent group spatially (see Figure 1.5 for an example snapshot of the spatial configuration), encounters were not only restricted to similar-ranking individuals, but also to either avoidees or avoiders (Figure 1.8B). Avoidees were individuals that employed no avoidance behavior at all (as for these individuals there were simply no potential aggressors to be avoided), while avoiders were avoiding at least one individual from the group of avoidees, thereby avoiding the whole group of avoidees (given a large enough AV_DIST).

When avoidance was employed at very large distances, subgroups formed, consisting of avoiders and avoidees (see subsection Subgroup formation above). These subgroups were spatially distinct and encounters were now restricted to individuals from the same subgroup (Figure 1.8B).

Velocity model

In the very simple *velocity model*, which did not include avoidance behavior and in which there was no variation in fleeing frequency, also a central-peripheral pattern emerged: Individuals were sorted in space according to their average velocity, with fastest moving individuals at the periphery (Figure 1.9; note that in this model an individual's velocity was made inversely related to myDOM). In the *velocity model* the spread of the group was dependent on the maximum possible velocity. With a higher maximum velocity, a larger group spread (see Figure S1.4) and a more pronounced central-peripheral group structure emerged (see Figure 1.9).

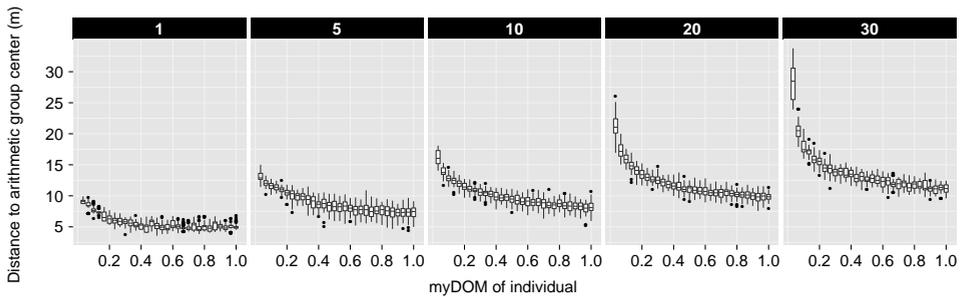


Figure 1.9: Centrality of dominants in the *velocity model*. This graph shows the relationship between an individual's dominance strength (myDOM) and its centrality (distance to the arithmetic center of the group in meters) for the *velocity model* for a range of values for *MAX_VELOCITY* (horizontally, 1 - 30 m/s). Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper, centrality of dominants is more pronounced. In this model an individual's velocity has been made inversely related to myDOM. Boxplots show values of 50 simulation runs, averaged over time.

Robustness of the model

We conducted a number of control experiments in our model, to check for implementation-based biases.

First, to ensure that our results do not depend on the specific timing regime chosen in our model, we implemented a model with a different timing regime. Here, an individual's next schedule time was a continuous random number between 0 and 20, thus also with a mean of 10 time steps. This change of the timing regime yielded the same patterns as our original model (data not shown).

Second, to check whether our results would also apply for smaller groups, we ran the model for group size $N = 10$. This model yielded similar result as the original model. However, we observed no subgroup formation when aggressors were avoided at large distances. This was due to the limited number of individuals. With only a few ("preferred") group members nearby, individuals move towards others rather than avoiding potential aggressors (data not shown).

Third, we checked whether our results were affected by the degree of randomness in the random walk procedure. This degree of randomness is determined by the random angle individuals

can turn about. With a lower turning angle, individuals move more persistently in a particular direction. The movement direction of individuals is probably highly persistent when foraging, but much less persistent when individuals are not traveling. In our original model individuals could turn up to 180 degrees to the left or right. When we ran our model with a maximum turning angle of 45, 90 and 135 degrees, we obtained similar results to the original model. However, a lower maximum turning angle, and thus more persistent movement, caused a larger group spread (see Figure S1.5 for the group spread in the *fleeing model* with different maximum turning angle). Note, that this is similar to the results obtained from the *velocity model*; if all individuals move faster (or more persistently in a particular direction) all individuals end up further away from the group center. As a result of the larger group spread, the number of encounters between individuals decreased. This in turn decreased the structuring effect of fleeing (after encounter). Therefore, when we ran the *avoidance model* with a lower maximum turning angle (45 degrees), we could still observe the spatial patterns that resulted from avoidance behavior (central-peripheral group structure or subgroups), while the spatial structuring among *avoidees* (which came about only due to fleeing) disappeared (see Figure S1.6).

Fourth, we were interested to which degree our subgrouping patterns depended on the discrete cut-off chosen in the behavioral rules for aggressor avoidance. In our model, individuals always avoided others, when their difference in dominance strength was larger than a certain value. To test how much our results depended on this assumption, we also implemented a more probabilistic way of avoidance behavior, where higher-ranking individuals were avoided according to an avoidance chance. This avoidance chance was implemented as a sigmoid function, which is characterized by its inflection point and the slope at the inflection point. For the inflection point we chose the same values as for *AV_DOM_DIFF* in the original model (namely 0.2, 0.4 and 0.6). Around these values (for difference in dominance strength) the chance of avoiding the particular individual changes (more or less rapidly, depending on the slope) from zero to one. For the slope at the inflection point we tested the values 5, 15, 30, 60 and 120. Note, that the discrete cut-off in our original model could be approximated by this sigmoid function with an infinite slope. The *avoidance model* with probabilistic avoidance behavior obtained results similar to the original model, whenever the slope of the avoidance chance function was steep enough (see Figure S1.7). Note, that for subgroup formation we needed larger avoidance distances than in the original model (see Figure S1.8), because with probabilistic avoidance chance, avoidance is less strict and thus less often employed. When the slope was very low (slope = 5), no subgroup formation was observed (see Figure S1.9). With a low slope of the avoidance chance function, individuals avoided all higher-ranking individuals with a certain probability, therefore no individuals were left to form a subgroup with. Moreover, the inflection point of the avoidance chance function had two opposing effects on subgroup formation. A very low value for the inflection point (0.2) resulted in individuals avoiding most higher-ranking individuals, while having just a few potential partners to form a subgroup with. On the other hand, a high value for the inflection point (0.6) resulted in individuals avoiding only very few higher-ranking individuals, while having many potential partners to form a subgroup with. Therefore, the most pronounced subgroup formation occurred at intermediate values for the inflection point (0.4) (see Figure S1.7). From this we can derive the following conditions for subgroup formation: a sufficient number of individuals should not avoid each other, allowing the formation of a subgroup, while a sufficient number of other individuals (and their subgroup) should be avoided at a sufficiently large distance.

Fifth, we tested whether switching off the restriction of the maximum group spread would result in spatially separated subgroups. As expected, in the *avoidance model* with large enough *AV_DIST* the group split up in separate subgroups, which tended to move away from each other (see Figure S1.10 for some example snapshots of the spatial configuration).

Last, we tested the effect of *FleeD* on the spatial group structure, in particular the group spread. We tested a range of values for *FleeD* (1m, 2m, 5m, 10m, 20m) in the *fleeing model*. As expected, larger *FleeD* resulted in groups that were more spread out (see Figure S1.11). This is again in line with the results obtained from the *velocity model*, if individuals move faster, they end up further away from the group center, thus the group is more spread out. As fleeing was mostly employed by lower-ranking individuals, and almost never by high-ranking individuals, the socio-spatial group structure became more differentiated (see Figure S1.12). The larger group spread resulted in larger dyadic distances. Similar to the original *fleeing model*, the encounter structure was not differentiated, because the spatial distances were similar among all individuals (see Figure S1.13).

DISCUSSION

Emergence of central-peripheral spatial group structure

We identified three different factors that may drive the emergence of a central-peripheral spatial structure in primates, and possibly other group-living species as well: individual variation in fleeing frequency, in avoidance behavior or in velocity.

In the *fleeing model*, the resulting spatial group structure was consistent with earlier findings (Hemelrijk, 1998b): the fleeing behavior of subordinates shaped a central-peripheral structure. In line with other model-based research (Puga-Gonzalez et al., 2009 and the model in the Appendix of Bryson et al., 2007), the emergent spatial structure did not depend on winner-loser effects, but arose also with a stable dominance hierarchy. Similar to the *fleeing model*, avoidance of potential aggressors at small or intermediate distances (*avoidance model*) resulted in a central-peripheral group structure with avoiders at the periphery and avoidees at the center, though in the *avoidance model* this spatial structure was more pronounced. Moreover, when we controlled for individual variation in fleeing frequency (by keeping win chances equal for all individuals), a similar spatial structure to that in the *fleeing* and in the *avoidance model* emerged. The self-organizing principle here is analogous to the effect of fleeing: subordinates avoid mostly dominants, which in turn remain at the center of the group. However, in contrast to fleeing upon an aggressive encounter, avoidance already operates at a distance. In the third model (the *velocity model*), we showed how even individual variation in average velocity alone is sufficient for a central-peripheral group structure to emerge, with faster moving individuals at the periphery of the group. In this model, individuals only differed in movement speed, not in fleeing frequency, and avoidance behavior was not employed. This suggests that a central-peripheral group structure can result from any behavioral mechanism that enhances differential average velocity in individuals.

A high fleeing frequency, frequent avoidance behavior and a high average velocity may be properties that are typical for subordinate individuals (Chance, 1956; Jay, 1965; Morgan et al., 2000; Watson et al., 1998). By disentangling the contribution of each of these factors within a simulation model, we showed how each property independently results in peripheral spatial positions within a group, a venture that would be impossible in real groups of animals. Our results suggest a robust spatial group structure can be generated by several mechanisms simultaneously, which can be commonly found in primate groups.

Avoidance behavior, aggressiveness and group spread

Two variables in the *avoidance model* directly influenced the degree of avoidance behavior: the minimum difference in dominance strength between two individuals that elicits avoidance behavior in the lower-ranking individual (*AV_DOM_DIFF*), and the spatial distance within which subordinates avoid potential aggressors (*AV_DIST*). In a group of primates there may be individual variation in the value of these parameters, depending on an individual's urge to avoid others. Different primate species may also differ in the degree of both overall and within-group variation of these variables, in relation to their degree of aggressiveness. Despotic species are characterized by a steeper dominance hierarchy and a higher variance of within-group aggressiveness. Within such a group, the urge to avoid dominants is higher and thus the dominance difference that elicits avoidance behavior (*AV_DOM_DIFF*) is expected to be lower within a group. Our results show that the lower this dominance difference (*AV_DOM_DIFF*), the more spatially spread out groups were. Similarly, subordinates in despotic species are expected to prefer to maintain a large distance to potential aggressors (*AV_DIST*). For avoidance at large distances our model also predicts a larger group spread. This suggests a possible mechanism for the larger group spread seen in groups of despotic animals compared to more egalitarian species, as has been shown in real primates (Richter et al., 2009; de Waal and Luttrell, 1989) and was suggested by other models (Hemelrijk, 1999a,b).

It has been suggested that avoidance behavior may be imperative in aggressive species that lack formal dominance signals (Isbell and Pruett, 1998; Kaplan and Zucker, 1980; Kutsukake and Clutton-Brock, 2008; Rowell and Olson, 1983; de Waal, 1986) and our model predicts large group spread for such species. Researchers have found that groups of patas monkeys, a species lacking formal signals of submission, are much more spread out compared to species capable of formal submission (Kaplan and Zucker, 1980; Rowell and Olson, 1983). This may result from frequently employed avoidance behavior, as predicted by our model. In a species capable of formal submission, the urge to avoid is expected to be lower. Our model suggests such a group would be less spread out; however, the effects of dominance style and formal submission on spatial structure have yet to be explicitly formulated in a model.

Avoidance behavior, aggressiveness and subgroup formation

Avoidance at a large distance (*AV_DIST* = 35 m) resulted in subgroups of avoiders and *avoidees*, which were spatially and socially distinct. In our model, the maximum group spread was restricted. Without this restriction, the group would have split into separate groups. Thus, in highly aggressive species, group split-up might occur as a result of frequent avoidance behavior among subgroups.

Modeling studies have shown how subgrouping patterns may emerge through foraging in a structured environment (Ramos-Fernandez et al., 2006) or from affiliative bonds between the individuals (Sueur et al., 2010). Our model suggests another possible mechanism causing subgroup formation. High degrees of aggression and resulting avoidance behavior may be a major driving force behind subgroup formation and eventual group split-up, with subgroups of similar rank. Subgrouping patterns may thus simply be a consequence of aggression in the group. For example, Romero and Aureli (2007) described two spatially distinct subgroups in a group of ring-tailed coatis, where aggression occurred more frequently between than within subgroups. Another study, in Barbary macaques (Prud'Homme, 1991), identified overt aggression between individuals of two subgroups as the main factor driving group split-up. Here, we present the first model that explicitly implemented and tested the effects of conflicts

and spatial avoidance of aggressors on group structure, corroborating the organizing potential of social behavior.

Aggression resulting in spatial avoidance, however, may reduce group cohesion to suboptimal levels. Under such conditions, different behaviors that reduce the effect of aggression, but do not depend on an increase of distance, may evolve. Indeed many primates employ signals of submission, policing and post-conflict affiliation (Aureli et al., 1993, 2002; Aureli and de Waal, 2000; Bernstein and Ehardt, 1985; Koski et al., 2007a; Silk, 2002a; Thierry et al., 2008; de Waal, 1986). The effects of these alternative behaviors remain to be modeled.

In our model, we identified specific conditions leading to subgroup formation and eventual group split-up in our model system: 1) Individuals are socially attracted to group members. 2) There are subsets of individuals within a group, which do not avoid each other. Such a subset of individuals may form a subgroup. 3) When avoidance is employed at large distances between members of different subgroups, these subgroups may separate from each other spatially. The validity of these conditions needs to be tested in real primate groups.

We point out, that we did not aim to model all possible mechanisms of fission-fusion. Rather, our model shows how severe aggression and avoidance of potential aggressors may contribute to socio-spatial group patterns and subgroup formation. Moreover, the subgroups in our model assorted themselves according to dominance rank. Such a pattern has not been described for primate subgroups after group fission. This emphasizes the importance of kin and affiliative relationships in primate fission-fusion dynamics, especially with respect to subgroup composition. The composition of subgroups in our model seems to be similar to patterns observed in fish shoals. Many fish species assort themselves within the shoal according to size (Hoare et al., 2000) and European minnows for example, are even able to recognize and avoid strong competitors within the shoal (Metcalf and Thomson, 1995). Although our model was inspired by primate behavior, it may be applicable more generally. Our model may explain how certain socio-spatial patterns may arise due to individual interactions in any species with a highly differentiated dominance hierarchy (or any other trait), given that the species is capable of individually recognizing this trait and responding with differentiated locomotion behavior.

Encounter structure and spatial structure

Both the *fleeing model* and the *avoidance model* with avoidance at small distances ($AV_DIST = 5$ m) demonstrated (weak) centrality of dominant individuals. Moreover, in both of these models the dyadic distances between all group members were similar. Although the spatial patterning was similar, the models differed in the frequency and direction of encounters within the group. In the *fleeing model*, encounters were almost equally distributed among all possible dyads, whereas in the *avoidance model* more encounters took place among individuals of similar rank. This shows that social group properties, such as encounter structure, are not deducible from spatial relations alone.

Conclusions

In this study we presented the group-level consequences of individual variation in movement properties. It has been shown that in some primate species group members vary in their degree of employing social vigilance: subordinates pay more attention to other group members than dominant individuals (Keverne et al., 1978; McNelis and Boatright-Horowitz, 1998; Pannozzo et al., 2007). This variation in social information uptake may also give rise to group-level

patterns, similar to the variation in movement properties presented in this paper. This will be further investigated in future models.

We could find no empirical studies in which avoidance behavior at a distance was observed. This is likely due to the difficulty of determining exactly which animal is avoided by another in a social group. Therefore, model studies can be of particular value, as they can serve as an informative tool to study the group-level consequences of such behavior, showing that difficult to observe behavior can have profound effects. This emphasizes the relevance to empirically study avoidance of aggressors in social groups.

We presented three models (*fleeing model*, *avoidance model* and *velocity model*), comparing different types of individual variation in movement characteristics within a group of model individuals. Using simulations, we assessed the effect of individual variation in fleeing tendency, in avoidance behavior and in velocity, to understand their effect on spatial and encounter structure. A central-peripheral group structure was found in all three investigated models, suggesting that any behavioral mechanism that selectively enhances movement differentiation in group members can be responsible for this specific spatial group structure, while the encounter structure is determined by the specific behavioral rules.

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SUPPLEMENTARY MATERIAL

Text S1.1: Win chance function and the distribution of fights among group members

In our model, an individual's chance of starting a fight depends on its win chance against its opponent. In contrast to the sigmoidal win chance we used here, Hemelrijk (1998b) implemented a relative win chance in her DomWorld model. With this relative win chance, individual A's chance of winning from individual B gets calculated as follows:

$$w_{AB} = \frac{myDOM_A}{myDOM_A + myDOM_B}, \quad (S1.1)$$

i.e. the win chance of an individual depends on the relative difference in dominance compared to the opponent. This has been criticized elsewhere (de Vries, 2009), because of resulting unrealistically high dominance updates in low-ranking individuals after a fight. Furthermore, with a relative win chance low-ranking individuals with a certain dominance difference differ much more in their win chances than two higher-ranking opponents with the same dominance difference (Table S1.1). On the other hand, when applying a sigmoidal win chance (as suggested by de Vries, 2009), win chance is the same whenever dominance difference is the same.

We found that the function of the win chance function may crucially affect the number of fights within a group and especially how fights are distributed among members of the group. We compared three models with different functions for the win chance: relative (as in Hemelrijk, 1998b), sigmoidal (as was used in the current paper, Equation 1.3) and absolute win chance. The latter is similar to the sigmoidal win chance, except that the curve is much steeper and

thus approximating a step function. To get an absolute win chance we simply set the parameter η (Equation 1.3) to $(60/MAX_DOM)$, instead of $(6/MAX_DOM)$ for the sigmoidal win chance.

With a relative win chance function, almost all dyads engage in fights regularly (Figure S1.1A). Only the lowest-ranking individuals restrict fights to opponents of similar rank. On the other hand, with a sigmoidal win chance, escalated fights are restricted to opponents of similar rank (Figure S1.1B). With an absolute win chance, fights are even more restricted to the diagonal (Figure S1.1C).

Note that these effects are not due to differences in group spread or encounter rates (see Table S1.2). The encounter rates in Figure S1 comply with the chance of starting a fight after encounter for each possible dyad. The chance that a certain dyad engages in a fight after encounter can simply be calculated as the product of both individuals' win chances, as in our model an actual fight takes place only if both opponents agree to a fight (see Figure 1.3). Therefore the calculated fight chances are also symmetrical for each dyad.

myDOM _A	myDOM _B	Dominance difference	Relative w _{AB}	Relative w _{BA}	Sigmoidal w _{AB}	Sigmoidal w _{BA}
0.1	0.2	0.1	0.33	0.66	0.35	0.65
0.9	1.0	0.1	0.47	0.53	0.35	0.65

Table S1.1: Differences of the relative and sigmoidal win chance functions for pairs with same dominance distance.

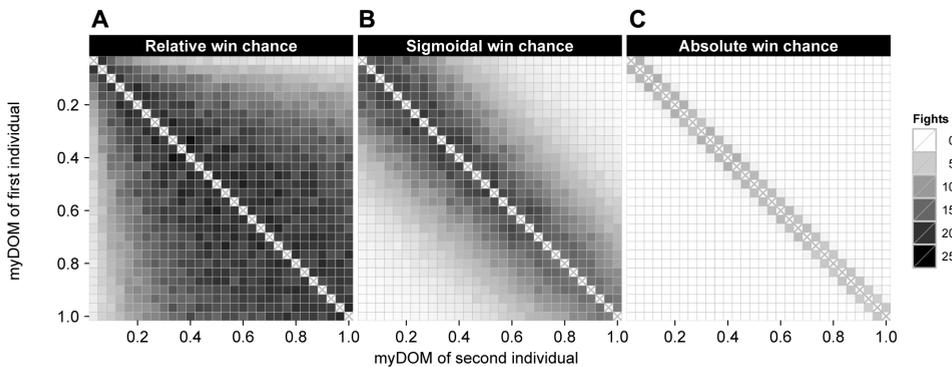


Figure S1.1: Fight structure for different win chance functions. This figure shows the distribution of fights among members of a group of individuals for the fleeing model with three different win chance functions: **A:** Relative win chance. **B:** Sigmoidal win chance. **C:** Absolute win chance. Numbers of fights are symmetrical for dyads, as both opponents have to agree to engage in a fight. Plots show the mean values of 50 simulation runs. Dark shades represent frequent fights. Values at the diagonal (x) are by default not applicable.

Win chance:	Relative	Sigmoidal	Absolute
Group spread	34.9 ± 0.6 m	36.5 ± 0.7 m	38.7 ± 0.7 m
Average number of encounters per possible dyad	37.9 ± 0.6	37.8 ± 0.9	37.7 ± 1.2

Table S1.2: Group spread and average number of encounters per dyad, for different win chance functions. Values are means ± standard deviation of the group average (N = 50 simulation runs).

Text S1.2: Centrality of dominants as a model artifact

In the original DomWorld model (Hemelrijk, 1998b) as well as in our model, individuals engage in dominance interactions. After a fight, the loser flees from the winner and the winner chases the loser. Furthermore, in the DomWorld model (but not in our model here) the winner usually turns about a certain angle after chasing. This turning, or “wiggling”, was implemented by Hemelrijk (1998b) to (artificially) prevent too many repeated interactions between the same two opponents.

Our model and the DomWorld model show that the fleeing behavior of subordinates after a fight shapes a central-peripheral spatial group structure. However, an earlier replication of the DomWorld model did not find this spatial pattern after excluding the chasing behavior of the winner after a fight (see Appendix of Bryson et al., 2007). This was quite unexpected as distances between loser and winner should increase even more than when chasing behavior is excluded from the model, this in turn should result in a more pronounced spatial structure.

After extensive examination of this case, we found that this change in spatial pattern was due to two main factors: first, individuals always engaged in an interaction when they encountered each other and second when chasing was excluded, this automatically excluded subsequent wiggling of the winner.

When individuals interact in Bryson *et al.*'s model, both opponents orient towards each other. After the loser flees, the winner is still oriented towards the loser. When chasing is included in the model, central dominants usually win and chase losers towards the periphery. However if the winner wiggles about a considerable angle, its visual orientation is directed away from its former opponent. This not only decreases the chance of renewed encounters with this same individual, it also increases the chance of perceiving others near the group center, thereby ensuring movement back towards the group center. Through this, the winner returns to the group center earlier than the loser, who cannot turn around towards the group until its next activation. In other words, wiggling gives the winner a head start in returning to the group center, while the loser has to “skip a turn”. This effect is even more exaggerated, when the individual's movement is straight instead of a random walk. The loser can now only turn back towards the group after it is perceiving too few others in *NEAR_DIST* anymore, i.e. after it reached the group periphery.

We tested a range of values for the wiggle-angle in a simplified version of our fleeing model, where individuals always fight on encounter (as in the model in the Appendix of Bryson et al., 2007). A large wiggle-angle resulted in a more pronounced central-peripheral group structure (Figure S1.2). In contrast, when the wiggle-angle was small or zero, the winner of a fight was still oriented towards the loser and presumably engaged in further interactions with the loser. This results in less central winners (dominants) compared to a model with large wiggling.

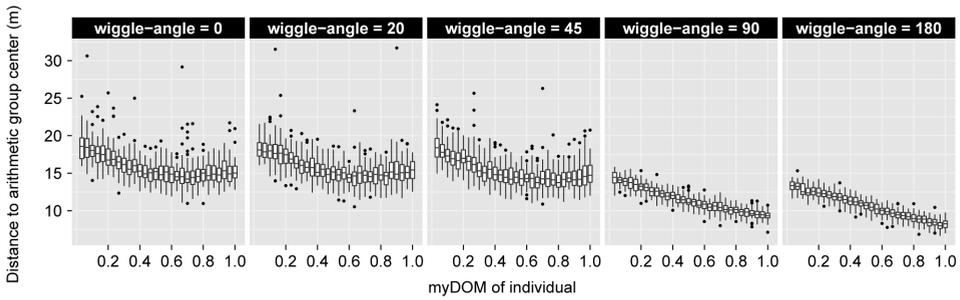


Figure S1.2: Centrality of dominants for different wiggle-angles. This graph shows the relationship between an individual's distance to the arithmetic center of the group (in meters) and their dominance strength in the fleeing model for a range of values of wiggle-angle: 0, 20, 45, 90 and 180 degrees. Wiggle-angle is the angle (in degrees) a winner turns away from its opponent after chasing it. Boxplots show values of 10 simulation runs, averaged over time.

Interestingly, the width of the wiggle-angle does not have this effect when encountering individuals do not instantaneously engage in a fight. In the DomWorld model and in our model, individuals can decide whether to fight or to flee. As a consequence, a large number of encounters resulted in fleeing behavior without an interaction taking place and before both opponents could orient towards each other. Dominants are left at the group center and did not always chase or follow the subordinates. Thus, whether winners wiggle after chasing does not have such an effect on the group structure in our model.

This elaboration of the wiggle-angle illustrates how each rule that is put into a behavioral model should preferably be motivated by the actual behavior observed in real animals. Furthermore, as far as it is feasible, the effect of each rule should be analyzed thoroughly to prevent model artifacts distorting the explanatory potential of a model.

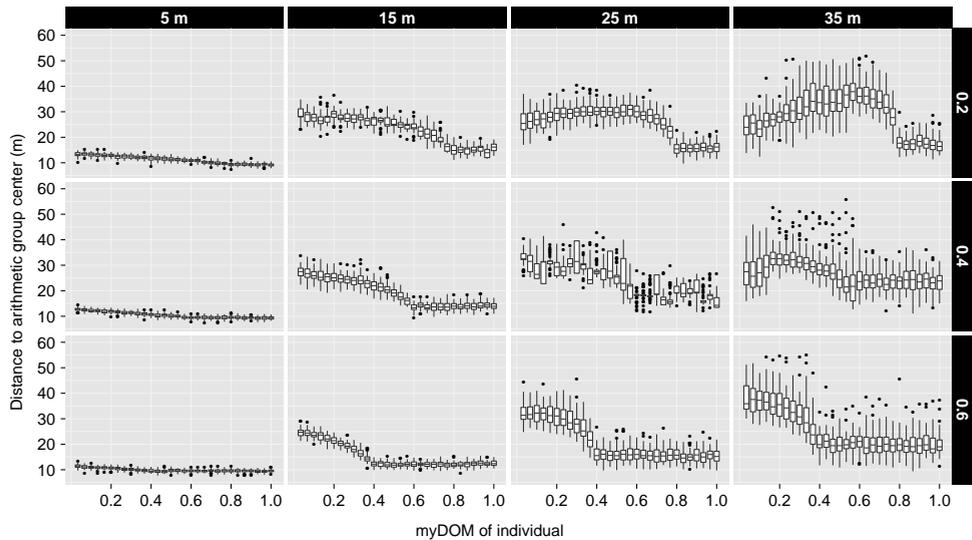


Figure S1.3: Centrality of dominants in the avoidance with fleeing-control model. This graph shows the relationship between an individual's dominance strength (myDOM) and its centrality (distance to the arithmetic center of the group in meters) for the *avoidance with fleeing-control model* (with different combinations of *AV_DOM_DIFF* (vertically, 0.2 - 0.4) and *AV_DIST* (horizontally, 5 - 35 m)). Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper, centrality of dominants is more pronounced. For further implications of an individual's dominance strength depending on the model, see the Figure 4 legend. Boxplots show values of 50 simulation runs, averaged over time.

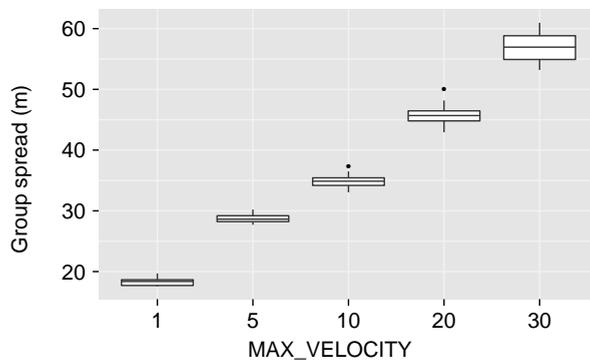


Figure S1.4: Group spread in the velocity model. This graph shows the group spread (in meters) in the *velocity model* for a range of values of *MAX_VELOCITY* (x-axis, 1 - 30 m/s). Boxplots show values of 50 simulation runs, averaged over time.

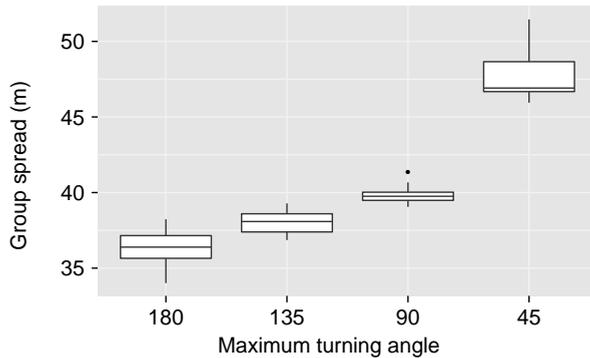


Figure S1.5: Group spread in the fleeing model with different maximum turning angle. This graph shows the group spread (in meters) in the *fleeing model* for a range of values for the maximum turning angle, used in the random walk procedure (x-axis, 180 - 90 degrees). Boxplots show values of 10 simulation runs, averaged over time.

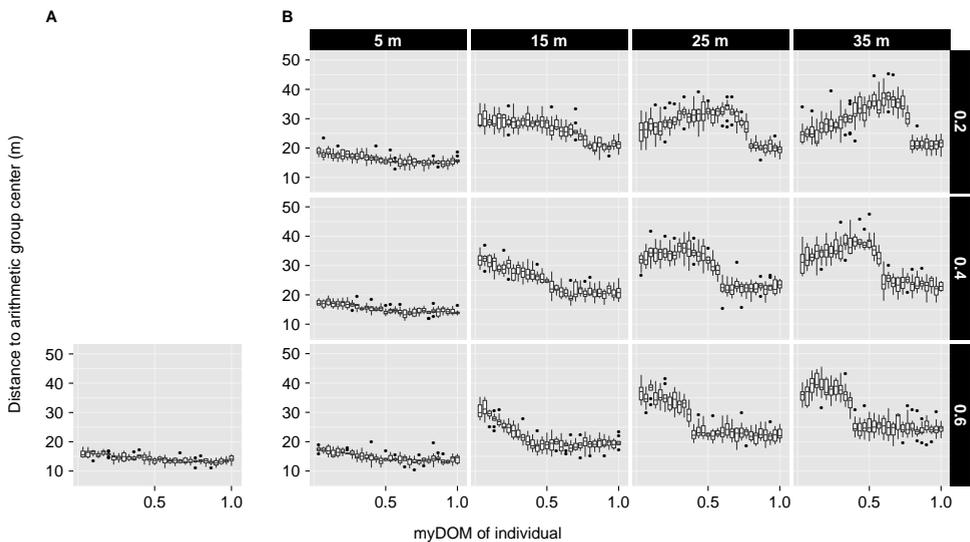


Figure S1.6: Centrality of dominants for maximum turning angle of 45 degrees. This figure shows the relationship between an individual's dominance strength (myDOM) and its centrality (distance to the arithmetic center of the group in meters) for different models with a maximum turning angle of 45 degrees, as used in the random walk procedure. **A:** *Fleeing model*. **B:** *Avoidance model* (with different combinations of *AV_DOM_DIFF* (vertically, 0.2 - 0.4) and *AV_DIST* (horizontally, 5 - 35 m)). Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper, centrality of dominants is more pronounced. For further implications of an individual's dominance strength depending on the model, see the Figure 4 legend. Boxplots show values of 10 simulation runs, averaged over time.

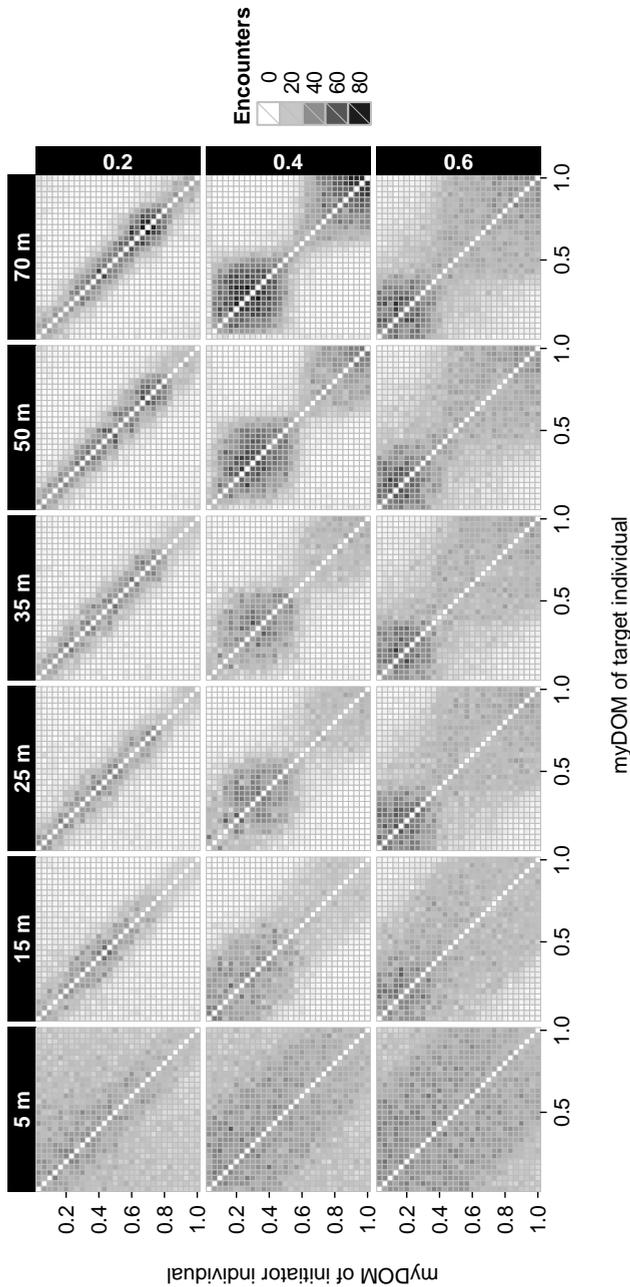


Figure S1.7: Encounter structure in the probabilistic avoidance model with slope 30. This figure shows the distribution and direction of encounters among the individuals of a group for the avoidance model with probabilistic avoidance with a slope of 30 for the avoidance chance function (with different combinations of *AV_DOM_DIFF* (vertically, 0.2 - 0.4) and *AV_DIST* (horizontally, 5 - 70 m). Encounters are directed from initiators (y-axis) to targets (x-axis), both are ordered by dominance strength (myDOM). For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend. Plots show the mean values of 10 simulation runs. Dark shades represent frequent encounters. Values at the diagonal are by default not applicable.

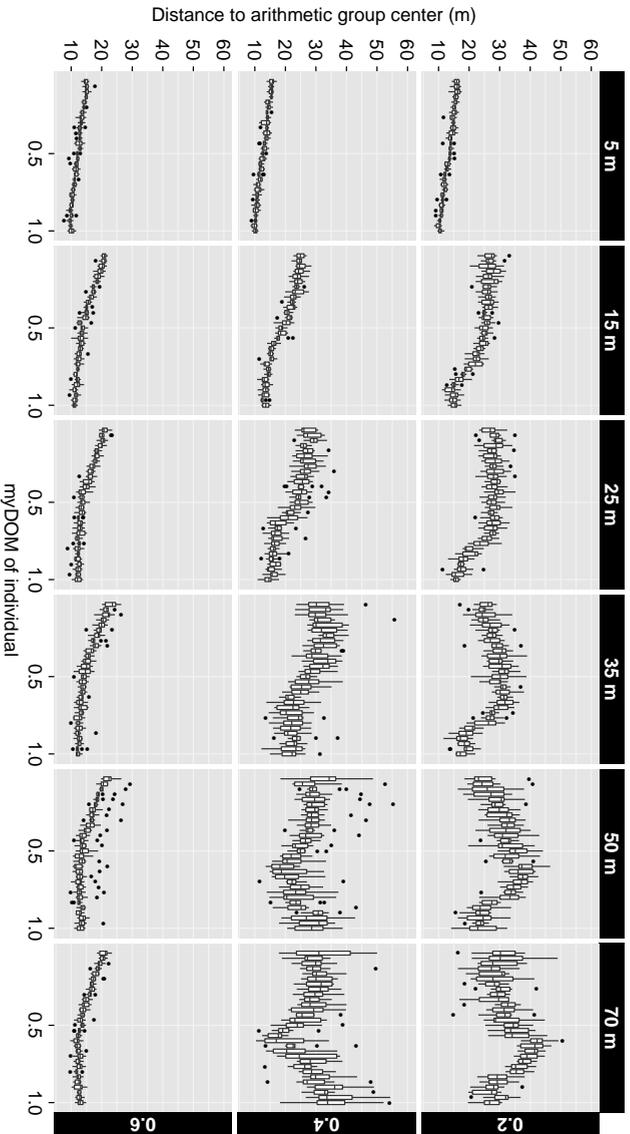


Figure S1.8: Centrality of dominants in the probabilistic avoidance model with slope 30. This figure shows the relationship between an individual's dominance strength (myDOM) and its centrality (distance to the arithmetic center of the group in meters) for the avoidance model with probabilistic avoidance with a slope of 30 for the avoidance change function (with different combinations of AV_DOM_DIFF (vertically, 0.2 - 0.4) and AV_DIST (horizontally, 5 - 70 m)). Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper, centrality of dominants is more pronounced. For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend. Boxplots show values of 10 simulation runs, averaged over time.

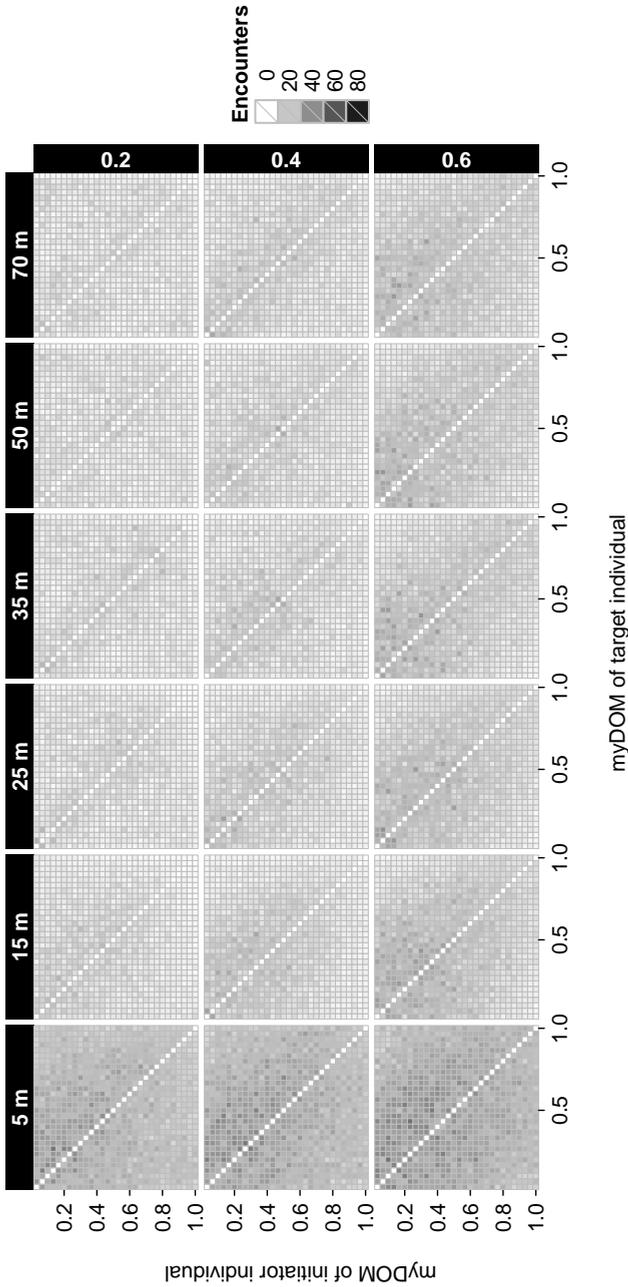


Figure S1.9: Encounter structure in the probabilistic avoidance model with slope 5. This figure shows the distribution and direction of encounters among the individuals of a group for the *avoidance model* with probabilistic avoidance with a slope of 30 for the avoidance chance function (with different combinations of *AV_DOM_DIFF* (vertically, 0.2 - 0.4) and *AV_DIST* (horizontally, 5 - 70 m). Encounters are directed from initiators (y-axis) to targets (x-axis), both are ordered by dominance strength (myDOM). For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend. Plots show the mean values of 10 simulation runs. Dark shades represent frequent encounters. Values at the diagonal are by default not applicable.

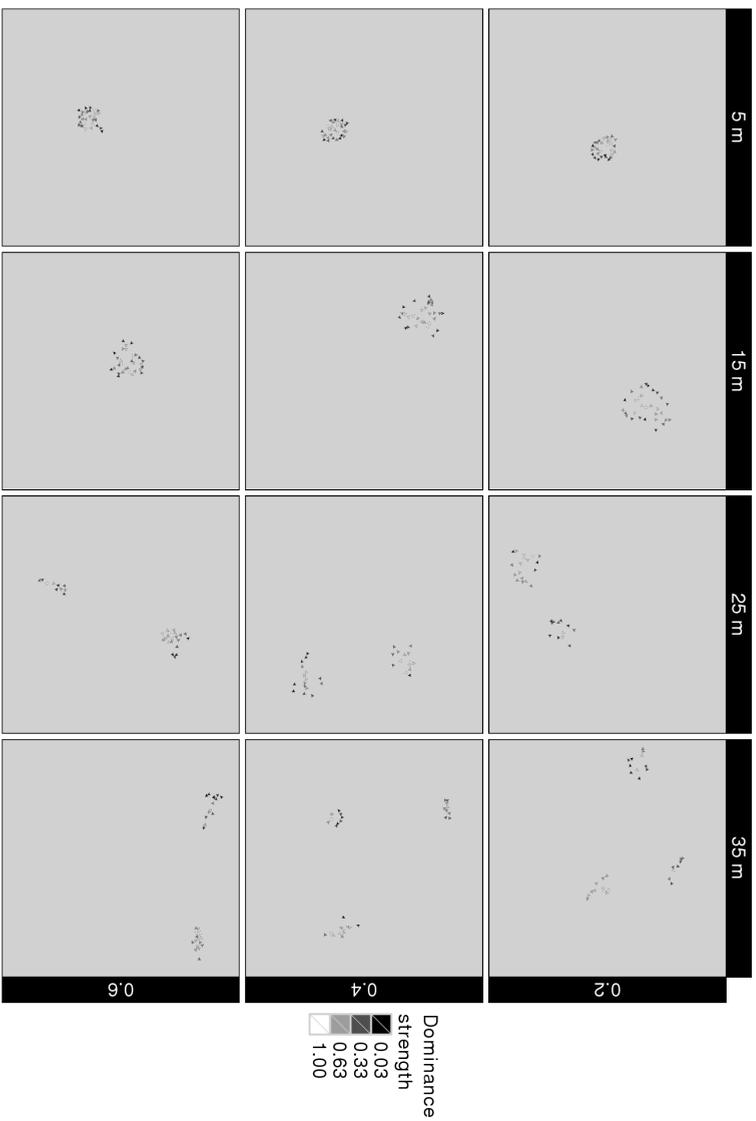


Figure S1.10: Snapshots of the socio-spatial group structure without restriction of fashion. This figure shows snapshots of the spatial composition of the group members for different models in which the restriction of the maximum group spread was switched off. (A) *Fleeing model*. (B) *Avoidance model* (with different combinations of AV_DOM_DIFF (vertically, 0.2 - 0.4) and AV_DIST (horizontally, 5 - 35 m). Shown is the total grid (300 by 300 meters) at one arbitrary point in time. Each arrowhead represents an individual. White shade represents a high dominance strength, dark shade represents a low dominance strength. The heading of an arrowhead represents the individual's visual orientation. For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend.

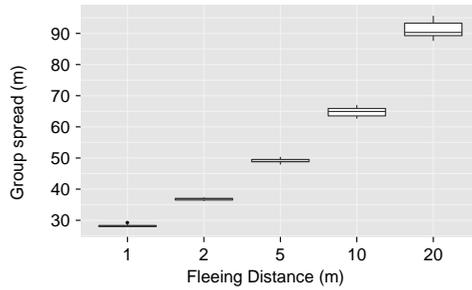


Figure S1.11: Group spread in the fleeing model with different values for fleeing distance. This graph shows the group spread (in meters) in the fleeing model for a range of values of *FleeD* (x-axis, 1 - 20 m). Boxplots show values of 10 simulation runs, averaged over time.

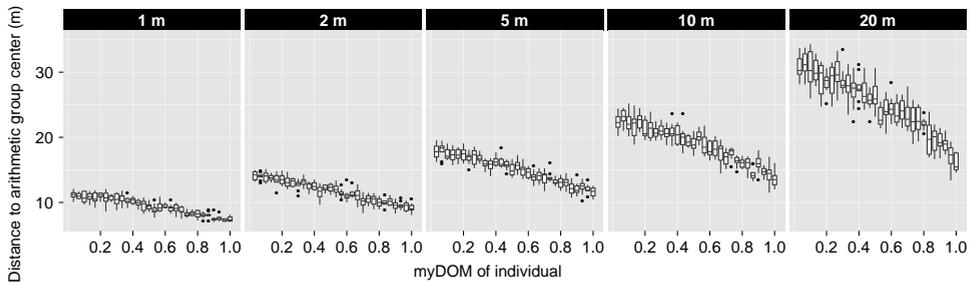


Figure S1.12: Centrality of dominants in the fleeing model with different values for fleeing distance. This graph shows the relationship between an individual's dominance strength (myDOM) and its centrality (distance to the arithmetic center of the group in meters) for the fleeing model with different values of *FleeD* (horizontally, 1 - 20 m). Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper, centrality of dominants is more pronounced. For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend. Boxplots show values of 10 simulation runs, averaged over time.

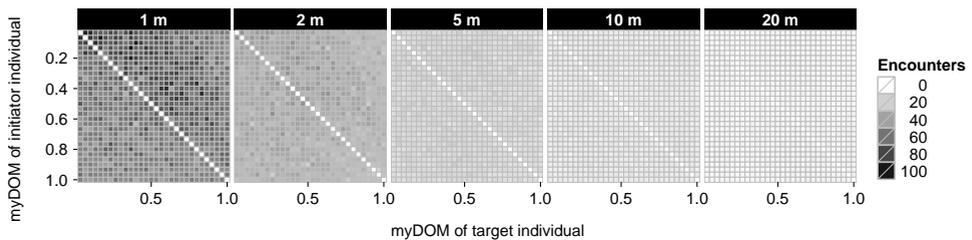


Figure S1.13: Encounter structure in the fleeing model with different values for fleeing distance. This figure shows the distribution and direction of encounters among the individuals of a group for the fleeing model with different values of *FleeD* (horizontally, 1 - 20 m). Encounters are directed from initiators (y-axis) to targets (x-axis), both are ordered by dominance strength (myDOM). For further implications of an individual's dominance strength depending on the model, see the Figure 1.4 legend. Plots show the mean values of 10 simulation runs. Dark shades represent frequent encounters. Values at the diagonal are by default not applicable.



Look before you leap - Individual variation in social vigilance shapes socio-spatial group properties in an agent-based model

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ABSTRACT

Next to predator detection, primate vigilance also serves to keep track of relevant conspecifics. The degree of vigilance towards group members often reflects the dominance rank of an individual: subordinates pay attention to dominants. Although it has been suggested that subordinates' vigilance may result in spatial centrality of dominants, this has not been addressed in either empirical or modeling studies. Using agent-based models, we determined how social vigilance affects socio-spatial properties of primate groups. A basic model without social vigilance, where individuals avoid potential aggressors (*avoidance model*), was contrasted with two models that each additionally included a different type of social vigilance: a) monitoring a specific potential aggressor to remain informed on its whereabouts (*monitoring model*) or b) scanning the whole group to detect potential aggressors (*scanning model*). Adding monitoring or scanning behavior to the avoidance model reinforced spatial centrality of dominants, a pattern often observed in primates, and resulted in more spread out groups. Moreover, variation in scanning tendency alone was already sufficient to generate spatial centrality of dominants: frequently scanning subordinates could move further away from the group center than dominants, before losing sight of group members. In the *monitoring model*, two mechanisms caused decreased encounter frequencies among subordinates: a) increased inter-individual distances, and b) frequent monitoring of central dominants. In the *scanning model*, encounters among subordinates decreased due to increased inter-individual distances. This agent-based model study provides a clear indication that individual variation in social vigilance may be an important structuring feature of primate social groups.

INTRODUCTION

Group-living animals can afford to spend less time on vigilance behavior towards potential predators than solitary animals (the *many eyes effect*: Pulliam, 1973; Powell, 1974). However, time spent on vigilance actually increases with group size in many group-living primates (Elgar, 1989; Roberts, 1996), revealing that vigilance behavior may not only be directed at external

threats, but also at conspecifics (Treves, 2000; Hirsch, 2002). Primates use social vigilance, or *social attention*, to track the whereabouts and the behavior of relevant conspecifics, such as offspring, potential mates or potentially aggressive group members (Keverne et al., 1978; Altman, 1980; Caine and Marra, 1988; Maestriperi, 1993; Watts, 1998; Cowlshaw, 1998; Kutsukake, 2006). Information gained by social vigilance may affect social and spatial group patterns. In this paper we use agent-based models to study the effect of employing social vigilance on spatial group patterns and the distribution of encounters among group members.

More than 40 years ago, Chance (1956) and Chance and Jolly (1970) proposed the importance of a *social attention structure*, a property of the whole group which is evident in who attends to whom (Immelmann and Beer, 1989; Barrows, 2001). More recently, researchers have found that many primate species show individual variation in the direction and frequency of social vigilance. Often, social vigilance is employed more frequently by subordinates than by dominants and is directed up the dominance hierarchy (e.g. in macaques: Haude et al., 1976; Deaner et al., 2005, baboons: Alberts, 1994, capuchins: Pannozzo et al., 2007, patas monkeys: McNelis and Boatright-Horowitz, 1998, talapoin: Keverne et al., 1978, squirrel monkeys: Caine and Marra, 1988, and preschool children: La Freniere and Charlesworth, 1983, but see also Torres de Assumpcao and Deag, 1979). This relation between dominance and social vigilance suggests that prevention of aggressive encounters is an important function of within-group vigilance. Thus, social vigilance may be used by subordinates to proactively seek information on the whereabouts of potential aggressors, which then allows for distance regulation towards these individuals (Chance, 1967; Rowell and Olson, 1983; Caine and Marra, 1988; Alberts, 1994; McNelis and Boatright-Horowitz, 1998; Watts, 1998; Blois-Heulin, 1999; Treves, 2000). This urge to detect, avoid and remain informed about potential aggressors is considered especially important in aggressive, intolerant species and/or species that lack the ability of communicating formal submission signals, such as patas monkeys (Rowell and Olson, 1983; Caine and Marra, 1988; Isbell and Pruettz, 1998; Thierry et al., 2008; see also Evers et al., 2011 for more references).

In this context of aggressor avoidance, in line with Chance (1967) we can distinguish between two different forms of social vigilance: First, an individual may selectively monitor a particular, potentially dangerous group member by remaining visually oriented towards this animal to keep track of its further actions. Second, individuals may actively scan the whole social environment for nearby potential attackers. In this way, potential aggressors are detected in time and can then be avoided. Both monitoring and scanning behavior have been observed in several primate species (e.g. in macaques: Pitcairn, 1976; Haude et al., 1976; Deaner et al., 2005, baboons: Alberts, 1994, capuchins: Pannozzo et al., 2007, patas monkeys: Rowell and Olson, 1983; McNelis and Boatright-Horowitz, 1998, talapoin: Keverne et al., 1978, squirrel monkeys: Caine and Marra, 1988, preschool children: La Freniere and Charlesworth, 1983, mangabeys: Blois-Heulin, 1999; Blois-Heulin and Girona, 1999 and gorillas: Watts, 1998). Note that authors of previous studies on primate social vigilance have used various definitions and terms for scanning and monitoring. Throughout this paper, we will utilize the definitions given above.

Individual variation in social vigilance has been suggested to result in dominants ending up at the “center of attention”, as well as at the spatial center of the group (Chance, 1967; Chance and Jolly, 1970). Chance (1967) proposed that “spatial features [of a primate group] are the outcome of subordinates behavior and of the attention to the dominant animal.” Unfortunately, these authors did not formulate a specific (testable) hypothesis about how exactly social vigilance may contribute to the spatial group structure. Nevertheless, there is some evidence that this relationship may exist (Table 2.1): in many primate species, where social vigilance is

dominance-related, also a central-peripheral spatial group structure, with central dominants and more peripheral subordinates, is found. However, this link is weak, since it concerns only a concurring of described features. To our knowledge, no direct evidence for a causal link between social vigilance and socio-spatial group structure is available. Thus, it is yet unclear how this interrelationship may come about. Social vigilance, a socio-cognitive feature, crucial for distance regulation within the group, has also not yet been studied in simulation models. Based on the suggestions by Chance (1967) and on what has since then become known about primate social vigilance, we hypothesize that a central-peripheral group structure is reinforced by and arises from dominance related variation in social vigilance. More specifically, we hypothesize that individual variation in monitoring and scanning behavior causes spatial centrality of dominants. To find out how exactly this group pattern will arise from individual variation in monitoring and scanning behavior we implemented these behaviors in a simulation model, allowing us to test our hypothesis.

Species	Dominance-related social vigilance structure	Dominance-related spatial structure
<i>Macaca mulatta</i>	Haude et al. (1976); Deaner et al. (2005)	Southwick et al. (1965); Kaufmann (1967)
<i>Macaca fuscata</i>		Itani (1954); Imanishi (1960); Yamada (1966); Sugiyama and Ohsawa (1982); Wada and Matsuzawa (1986)
<i>Macaca nemestrina</i>		Jensen and Tokuda (1974)
<i>Macaca arctoides</i>		Lopez-Lujan et al. (1989); Rasmussen and Farrington (1994)
<i>Papio cynocephalus</i>	Alberts (1994)	Washburn and DeVore (1961); Hall and DeVore (1965)
<i>Papio ursinus</i>		Busse (1984)
<i>Cebus apella</i>	PannoZZo et al. (2007)	Janson (1990)
<i>Cebus nigrivittatus</i>		Robinson (1981)
<i>Cebus capucinus</i>		Hall and Fedigan (1997)
<i>Erythrocebus patas</i>	McNelis and Boatright-Horowitz (1998)	
<i>Miopithecus talapoin</i>	Keverne et al. (1978)	
<i>Saimiri sciureus</i>	Caine and Marra (1988)	
<i>Homo sapiens</i>	La Freniere and Charlesworth (1983)	

Table 2.1: Overview of several primate species and the specific group properties that have been reported for them.

To investigate the mutual links between individual properties and group-level patterns (Hinde, 1976), we use agent-based models. Agent-based models (ABMs, also called individual-based models or IBMs) are a well-established tool to systematically study and understand structuring mechanisms in a complex system of moving and interacting entities (Hogeweg and Hesper, 1979; Bryson et al., 2007). Using a spatially explicit and individual-oriented model formalism allowed us to investigate how individual variation in behavioral, social and spatial properties may relate to each other. ABMs have been studied to understand how socio-spatial group

patterns may emerge from interactions between individuals in primates and other species (Hemelrijk, 2000; Bryson et al., 2007; Sellers et al., 2007; Rands et al., 2008; Sueur et al., 2011a; see also Evers et al., 2011 for additional references). For instance, several ABM studies have demonstrated that spatial centrality of dominants may emerge in the absence of predation and spatial preferences, simply as a side effect of dominance relations and resulting differential movement (Hemelrijk, 1998b; Evers et al., 2011). This offered a parsimonious alternative to Hamilton's *selfish herd theory* (Hamilton, 1971).

In the current study, we set out to explore if and how variation in social vigilance may affect socio-spatial patterns in primate groups. Since monitoring and scanning may primarily serve more effective aggressor avoidance, we investigated both in this specific context. We first constructed a model of a group of primates, where individuals employ grouping behavior, dominance interactions and spatial avoidance of potential aggressors (cf. the *avoidance model* in Evers et al., 2011). We contrast this *avoidance model*, which lacks any social vigilance behavior with two models that each additionally include one of the two types of social vigilance, reported in the primate literature: a) monitoring a specific potential aggressor to remain informed on its whereabouts (*monitoring model*) or b) scanning the whole group to detect potential aggressors (*scanning model*). In these three models, individual variation in fleeing tendency and avoidance tendency is present, which is known to affect the socio-spatial group structure (Hemelrijk, 1998b; Evers et al., 2011). Therefore, to assess the isolated effect of social vigilance (specifically scanning), we implemented a fourth model (scanning control model), where we eliminated the structuring effect of individual variation in fleeing and avoidance. This way we were able to test whether individual variation in social vigilance (i.e. scanning) alone is already sufficient to generate a central-peripheral group pattern.

METHODS

Simulations were run using NetLogo 4.0.3 (Wilenski, 2007). The program code of all models is available on the website of the first author¹. Definitions and values of the model parameters can be found in Table 2.2. Below, we describe our models according to the updated ODD protocol (Grimm et al., 2010).

Overview

Purpose

The models described in this paper serve two main purposes. First, we wanted to assess whether and how individual variation in primate social vigilance (monitoring or scanning) can affect or enhance certain properties at the group level, such as spatial centrality of dominants and relative encounter rates. Second, we wanted to explore whether and how individual variation in social vigilance alone may already be sufficient to result in spatial centrality of dominants, a pattern that has been reported for several primate species. The experimental set-up is explained in the section Simulation experiments and summarized in Table 2.3.

¹<https://sites.google.com/site/elleneversutrecht/models>

Parameter	Description	Value
General parameters		
D	Grid unit	1 m
T	Time step	1 s
$FIELD_SIZE$	Field size	300×300 m
N	Number of individuals in group	30
$PERS_DIST$	Maximum distance, within which others can be encountered	4 m
$NEAR_DIST$	Maximum preferred distance to the group	20 m
MAX_DIST	Maximum distance monkeys are able to see	50 m
FAR_DIST	Maximum preferred distance to the furthest group member	$NEAR_DIST * \sqrt{N} \approx 110m$
MIN_OTHERS	Minimum preferred number of conspecifics within $NEAR_DIST$	3
MAX_DOM	Maximum dominance strength	1.0
$myDOM_i$	Dominance strength of individual i	$(i * MAX_DOM)/N$
$VIEW_ANGLE$	Default view angle	120°
$ChaseD$	Distance the winner of a fight chases the loser	1 m
$FleeD$	Distance the loser of a fight flees from winner	2 m
$WalkD$	Default distance an individual walks	1 m
Avoidance parameters		
$AvoidD$	Distance an individual moves away from <i>avoider</i>	2 m
AV_DOM_DIFF	Avoidance dominance difference; difference in strength, above which an agent is considered a potential aggressor and consequently avoided	0.4
AV_DIST	Avoidance distance; spatial distance within which potential aggressors are avoided	15 m
Scanning parameters		
MAX_ANGLE	View angle when scanning	360°
$myVIEW_ANGLE$	View angle employed by individual i , depending on whether i employs scanning at this moment	$VIEW_ANGLE$ or MAX_ANGLE
$P(scan_i)$	Scanning tendency of individual i	$(MAX_DOM/2N) + MAX_DOM - myDOM - i$

Table 2.2: Parameters, definitions and values of the avoidance, monitoring and scanning model.

Factor:	Fleeing frequency	Avoidance tendency	Monitoring tendency	Scanning tendency
Avoidance model	Variable	Variable	Not employed	Not employed
Monitoring model	Variable	Variable	Variable	Not employed
Scanning model	Variable	Variable	Not employed	Variable
Scanning control model	Equal	Not employed	Not employed	Variable

Table 2.3: Experimental set-up and characteristics of the compared models.

Entities, state variables and scales

We model the interactions and movements of 30 individuals. These individuals are characterized by their dominance strength (*myDOM*), which ranges from *MAX_DOM/N* (for the lowest-ranking individual) to *MAX_DOM* (highest-ranking). Dominance strength does not change in time or after interactions (cf. the model in the appendix of Bryson et al., 2007). When scanning behavior is included in the model, individuals are also characterized by their scanning tendency, which is inversely related to dominance strength and thus also constant over time.

Furthermore, individuals are characterized by their spatial coordinates, these may change during the whole simulation run. The modeled environment is a continuous two-dimensional grid (300 × 300 grid units) with a torus shape to exclude disturbing border effects. One grid unit resembles 1 “meter”. We did not explicitly implement ecological features of the environment; in the model an individual’s environment is purely social. This also implies that the model individuals do not engage in foraging behavior. Thus, we model a group that is not traveling. One time step in the simulation resembles 1 “second” and simulations were run for 72 000 time steps (resembling 20 observation “hours”).

Process overview and scheduling

Our model is event-driven. During a simulation run, individuals’ activations are regulated by a timing regime. Agents are activated in a cyclic, asynchronous way. Each time, the agent with the lowest schedule time is activated first. After activation, this agent’s next activation is scheduled. The remaining time until its next scheduled activation is randomly drawn from a negative exponential distribution with a mean of 10 time steps. In other words, events are randomly distributed in time. Scheduled times are on a continuous range. If an action involves other individuals as well, each participant gets scheduled anew for its next action.

On activation, individuals execute an action-selection protocol (Figure 2.1). This protocol goes through a number of decisions to produce the behavior appropriate to the social situation. The decision procedure is structured hierarchically: interactions have priority over grouping, grouping has priority over avoidance and avoidance has priority over moving within the group.

The action-selection protocol starts with ego perceiving the configuration of the social environment. Right upon perception, ego checks whether another individual is encountered, which will lead to an agonistic interaction (see submodel Agonistic interactions below). If no one was encountered, ego turns and moves towards the group if necessary (see submodel Grouping below). If grouping is not necessary, ego may chose to avoid potential aggressors at a distance (see submodel Avoidance below). If none of the above actions were selected, ego simply moves randomly through the group (see design concept Stochasticity below).

When monitoring behavior was included in the model, avoidance of a specific individual was immediately followed by monitoring this individual (see submodel Monitoring below). When scanning behavior was included in the model, the action-selection protocol was preceded by, and thus started with the decision of ego, whether to employ scanning behavior or not (see submodel Scanning below).

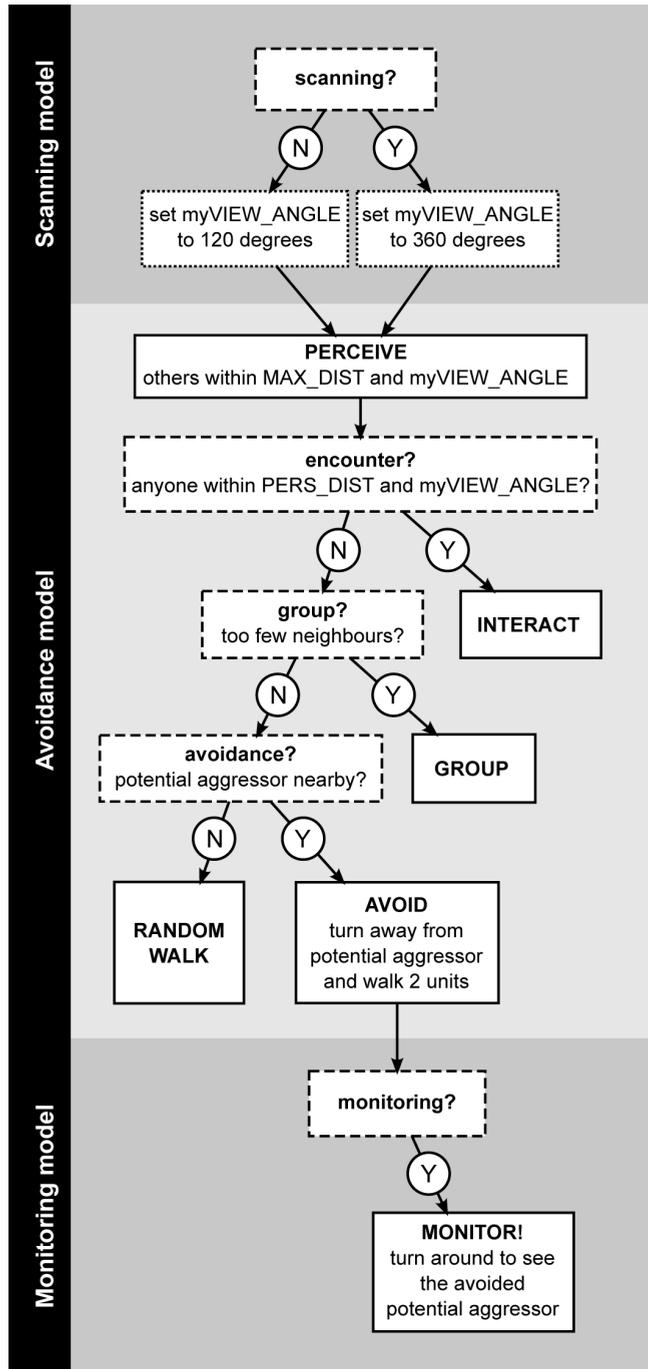


Figure 2.1: Interaction rules. Model individuals execute a hierarchical behavioral script. The script is starting at the top and ending in one of four or five (depending on the model) possible end states.

Design concepts

Emergence

In the models, individuals have a preference to stay near the group. However, individuals do not have any preference for a specific spatial location within the group (e.g. the group center). Any structure or pattern in the spatial configuration of the group is thus not imposed by the model rules, but arises purely from the interactions between the individuals and the resulting movements. Which individuals will encounter each other regularly (i.e. the encounter structure), will arise as a result of the emergent spatial structure in combination with the behavioral rules of the specific model.

Sensing

Individuals in the models are capable of perceiving the spatial distance and the dominance strength of others that are dwelling within a view angle of 120 degrees and a maximum perceivable distance of 50 m (VIEW_ANGLE and MAX_DIST in Figure 2.2). Note that when scanning behavior is included in the model, whenever an individual is scanning, its view angle is 360 degrees (see submodel Scanning below).

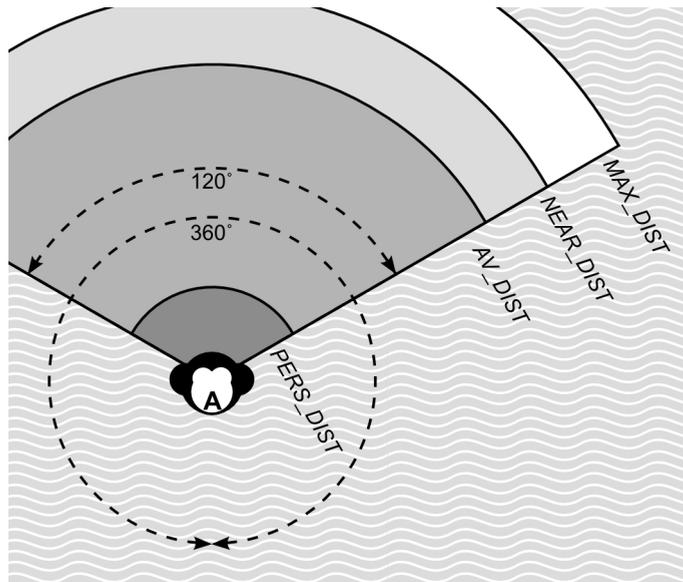


Figure 2.2: Perception. Model individuals perceive other group members within a default view angle of 120 degrees. When scanning, individuals perceive others within an angle of 360 degrees. The maximum distance within which another can be seen is MAX_DIST. Distances in the Figure are not to scale.

Interaction

Social interactions between individuals in the model may take place in several ways. Group members that were perceived within PERS_DIST may be chosen by ego as agonistic interaction partner (see submodel Agonistic interactions for more details). An agonistic interaction may then result in distance regulation by the lower-ranking individual, i.e. subordinate moving away from the dominant. If the dominance interaction escalates into a fight, the winner of the fight may chase the loser. Furthermore, potential aggressors that were perceived within AV_DIST may be avoided. Group members that were perceived within MAX_DIST may be approached by ego when grouping.

Stochasticity

In our model, when two individuals engage in a fight, the winner is stochastically determined: individual A wins from B, depending on its win chance, w_{AB} (cf. Evers et al., 2011). A higher difference in dominance strength results in a higher win chance for the dominant individual. When executing a random walk, individuals simply move forward (for WalkD = 1 m) and with a chance of 0.5, they then turn randomly up to 180 degrees to the right or left. In the scanning model, individuals may employ scanning. Prior to each activation, ego decides whether to employ scanning during the next action-selection cycle, depending on its scanning tendency.

Observation

To assess socio-spatial group properties within each model, we used several measures. We recorded each individual's distance to the centroid of the group (cf. Evers et al., 2011).

To calculate spatial group spread, we recorded the furthest neighbor distance within the group (the distance between the two individuals in the group that are furthest away from each other).

We assessed how dyadic distances and the number of encounters were distributed among all possible dyads. The spatial dyadic distances were simply recorded over time. To measure the total number and direction of encounters per simulation run (the encounter structure), we recorded the identity of the group members that ego had selected as interaction partner.

We recorded how perception was distributed and directed among group members (the perception structure). For each individual, we scored which other individuals it perceived within MAX_DIST and its employed view angle at the time of measuring. This was recorded several times per run (see below), using the *one-zero* sampling technique. Thus per dyad, possible scores were 1 (perceived) or 0 (not perceived) per sample. Note that depending on whether an individual was scanning or not, its employed view angle was either 360 or 120 degrees.

We only recorded data during the last 10 "hours" of each simulation run, to avoid transient spatial and social group effects due to the initial random placement. All measures of the socio-spatial structure of the group (distance to centroid of the group, spatial group spread, dyadic distances, encounter structure and perception structure) were recorded every 900 time steps, which was equivalent to 15 "minutes". All measures, except the number of encounters per dyad, were averaged over time for each simulation run. For the number of encounters per dyad all occurrences were recorded per simulation run. Per model, 50 independent simulations were run.

Details

Initialization

At the initialization of each simulation run, the x-coordinates and the y-coordinates of all individuals are drawn from a normal distribution around an arbitrarily chosen position on the spatial grid (standard deviation = 10 grid units), independent of an individual's dominance strength. Their initial heading was set to a random number between 1 and 360 degrees. Furthermore, the initial schedule time for each individual is randomly drawn from a negative exponential distribution with a mean of 10 time steps. Lastly, individuals get assigned their dominance strength (*myDOM*), which ranges from *MAX_DOM/N* (for the lowest-ranking individual) to *MAX_DOM* (highest-ranking) and which stays constant over the course of the simulation.

Submodels

This section describes each process that is executed by the model entities in more detail. Moreover, how each process is modeled and parameterized is explained.

Movement Movement of the model individuals may either be motivated by explicit social factors, such as grouping, fleeing, chasing or avoidance, where movement is directed away from or towards one specific individual, or is else implemented as a random walk of *WalkD* = 1m (see also design concept: Stochasticity). Parameter values concerning the random walk were kept the same as in our earlier model (*avoidance model* cf. Evers et al., 2011), where *WalkD* was adapted from the *DomWorld* model by Hemelrijk (1998b, 2000), while values for the other parameters were chosen arbitrarily.

Grouping To stay relatively close to other group members, ego checks whether at least three group members (*MIN_OTHERS*) are situated within a distance of 20 m (*NEAR_DIST*) within its employed view angle. If not enough group members were perceived, ego tries to find another group member within the maximum distance they can see (*MAX_DIST* = 50 m), or else within a broader view angle (360 degrees) by looking around (Figure 2.2). Of the perceived individuals, one is selected randomly and approached by 1 m (*WalkD*). Additionally, individuals are not allowed to increase the distance towards the furthest individual more than a certain distance (*FAR_DIST*). This procedure ensures a coherent group, which does not split up (see Evers et al., 2011).

Parameters concerning the grouping behavior of the model individuals were kept the same as in our earlier model (*avoidance model* cf. Evers et al., 2011), where *MAX_DIST*, *VIEW_ANGLE* and *WalkD* were adapted from the *DomWorld* model by Hemelrijk (1998b, 2000), *NEAR_DIST* was adapted from an earlier reimplementation of the *DomWorld* model Bryson et al. (2007) and *MIN_OTHERS* was adapted from van der Post et al. (2009).

Agonistic interactions When one or more group members are perceived within a personal distance of 4 m, ego chooses the nearest individual as an interaction partner. In our models interactions are always dyadic. For each interaction, this partner choice is recorded and scored as an encounter. Thus, encounters are directed from one individual (ego, who perceived the other first) to another (chosen partner).

Ego may either challenge its interaction partner or flee from it for 2 m. This decision depends on the chance of winning a fight with the opponent (de Vries, 2009; Evers et al., 2011). As a response to a challenge, the opponent may either reject or agree to engage in a fight, depending on its own expected win chance (cf. Evers et al., 2011). If one of the opponents declines and flees away, the conflict is settled. Only if both individuals agree to a fight does an actual fight take place. The winner of a fight is stochastically determined and depends on both individuals' win chance. Subsequent to a fight, the loser flees from the winner for 2 m (FleeD), while the winner chases the loser by running after him for 1 m (ChaseD).

The agonistic interaction procedure described above results in low-ranking individuals losing and fleeing more often than high-ranking ones. When controlling for individual differences in fleeing rate we simply assigned a win chance of 0.5 to each individual, independent of its actual dominance strength. In this way, fleeing rates were equal among individuals, while e.g. scanning frequency did still differ. Parameters concerning the dominance interactions of the model individuals were kept the same as in our earlier model (*avoidance model* cf. Evers et al., 2011), where PERS_DIST, ChaseD and FleeD were adapted from the DomWorld model by Hemelrijk (1998b, 2000).

Avoidance The model individuals are capable of avoiding potential aggressors at a distance. Whether ego may avoid another individual depends on the difference between both individuals' dominance strength (AV_DOM_DIFF) and on the spatial distance to that specific animal (AV_DIST). Whenever other group members have a larger dominance strength than the sum of ego's dominance strength and AV_DOM_DIFF and whenever such individuals (potential aggressors) are closer to ego than AV_DIST, ego may avoid them. If these conditions are true for several group members, ego chooses to avoid the nearest of these individuals. Therefore, by definition avoidance behavior is more frequently employed by lower-ranking individuals.

The actual avoidance behavior is implemented in the following way. If potential aggressors are detected, the nearest one is selected and avoided: ego turns away from this individual (180 degrees) and walks away for 2 m (AvoidD). Avoidance can either be a stand-alone reactive action on the perception of a potential aggressor, or it can be accompanied by additional mechanisms to prevent close proximity to potential aggressors in the first place by employing proactive (in contrast to reactive) detection of potential aggressors, namely monitoring and scanning.

Note, that extreme conditions for aggressor avoidance (namely avoidance of many dominants even when they were still at a large distance, i.e. small AV_DOM_DIFF and large AV_DIST) have been shown to result in subgroup formation in our model, even within the maximum allowed group spread (FAR_DIST) (Evers et al., 2011). In the current paper, we chose conditions (intermediate AV_DOM_DIFF and AV_DIST) that resulted in coherent groups that lacked any subgroup formation.

Monitoring Individuals may employ monitoring behavior to stay informed about the actions of a particular potential aggressor. Monitoring behavior is exclusively directed at potential

aggressors, i.e. the few highest-ranking individuals, and is only executed in conjunction with avoidance behavior. Avoiding a potential aggressor, i.e. moving away from it, results in a larger distance to the avoided individual and thus in a smaller aggression risk. Monitoring is employed right after detection and avoidance of a potential aggressor. From a larger distance, ego turns around towards the potential aggressor, to check whether it is now at a large enough distance (*AV_DIST*) from this specific individual or whether avoidance should be employed once more. As monitoring is in our model connected to avoidance behavior, it is (just like avoidance behavior itself) inversely related to dominance strength: low-ranking individuals frequently employ monitoring behavior.

Scanning Individuals may frequently scan their surrounding environment (within *MAX_DIST*) to detect known potential aggressors. When employing scanning behavior, an individual is turning its head right and left, thus expanding its view angle to 360 degrees (instead of the default view angle of 120 degrees). Individuals with low dominance strength (*myDOM*) have a higher chance to employ scanning. Scanning tendency is thus inversely related to dominance strength and is calculated as follows (for individual A):

$$P(\text{scan}_A) = \frac{\text{MAX_DOM}}{2N} + \text{MAX_DOM} - \text{myDOM}_A, \quad (2.1)$$

where *MAX_DOM* is 1.0 and *N* is the group size. Prior to the behavioral script, ego decides whether to employ scanning, during the next action-selection cycle. When scanning, also individuals outside of the default view angle (120 degrees) may be detected and avoided. As scanning for potential aggressors occurs indivisibly with scanning for conspecifics in general, the additional social information perceived through scanning is not exclusively used for avoidance behavior, but is also used when employing grouping behavior or when encountering others.

Simulation experiments

To investigate the implications of monitoring and scanning on the socio-spatial properties of primate groups, we compared a basic model where individuals avoid potential aggressors, but do not employ monitoring or scanning (*avoidance model*), to two models that additionally include either monitoring (*monitoring model*) or scanning (*scanning model*). As basic model, we used the *avoidance model* with parameter settings that result in a coherent group that does not split up (Evers et al., 2011). In this *avoidance model*, individuals follow a set of rules, inspired by real primates: (1) Individuals prefer to have at least three other group members in sight. (2) Individuals avoid potentially aggressive group members. (3) Individuals move within the group. (4) Individuals may engage in agonistic interactions.

In the *monitoring model*, individuals follow the same rules as the *avoidance model*, yet additionally individuals employ monitoring behavior. Thus, after detection and avoidance of a specific potential aggressor, the avoider may monitor this specific aggressor to stay informed about its further actions.

In the *scanning model*, individuals follow the same rules as in the *avoidance model*, yet additionally individuals employ scanning behavior. Thus, individuals may regularly scan their entire social environment to detect potential aggressors more efficiently.

Individual variation in social vigilance may also arise in contexts other than aggressor avoidance (e.g. due to maternal care or mate guarding). To check whether individual variation in social vigilance alone may be sufficient to generate socio-spatial group patterns, we investigated the properties of an additional model, where individuals merely differ in their scanning tendency (*scanning control model*). In this model, individuals do not differ in their fleeing frequency and do not employ any avoidance. Thus, in the *scanning control model*, the structuring effect of avoidance and variation in fleeing frequency (as found in Evers et al., 2011) was removed. Note that the isolated effect of monitoring has not been assessed, because employing monitoring behavior without avoidance behavior is not possible in our model: Avoiding a potential aggressor implies orienting (and moving) away from it. Subsequent monitoring enables the individual to visually orient back towards the potential aggressor. However, when no avoidance has been employed (yet), the individual would still be oriented towards the perceived potential aggressor.

Statistical analysis

To measure how individual differences in monitoring tendency and scanning frequency were related to the individuals' spatial position within the group, a regression line was fit to assess the relation between an individual's centrality (distance to the centroid of the group) and the individual's dominance strength (myDOM) per simulation run. The steeper this regression line, the more pronounced the relation between centrality and dominance strength was. A Wilcoxon rank sum test with continuity correction was used to assess whether monitoring or scanning affected the relation between centrality and dominance strength, i.e. the slope of the regression line. The two extended models (monitoring model and scanning model) were compared to the basic model (avoidance model). A t test was used to demonstrate a relation between spatial centrality and dominance strength in the scanning control model. The slope of the regression line in the scanning control model was compared to zero. Normality assumptions were checked using Shapiro-Wilk tests. Statistical analyses were performed in R 2.10.1 (R Core Team, 2012).

RESULTS

Avoidance

A detailed description and examination of the properties of the avoidance model can be found elsewhere (Evers et al., 2011). For the parameter settings chosen here, variation in fleeing frequency combined with variation in avoidance behavior (both due to differences in dominance strength) resulted in a clear central-peripheral group pattern (Figure 2.3a): subordinates (avoiders) populated the group periphery, as they frequently avoided and fled from central dominants (avoidees). Avoidance behavior resulted in fairly spread out groups (Figure 2.4): the average furthest neighbor distance was 67.4 ± 1.9 m (mean \pm standard deviation, $N = 50$ simulation runs). Dyadic distances among dominants (avoidees) were smaller compared to distances among subordinates (avoiders) and compared to distances between subordinates (avoiders) and dominants (avoidees) (Figure 2.5a). More encounters took place among individuals of the same subgroup, most of them among avoiders (Figure 2.6a). We also measured who is perceived by whom how often. In the avoidance model there was no noticeable variation within this perception structure and perception was almost equally distributed among all individuals (Figure 2.7a).

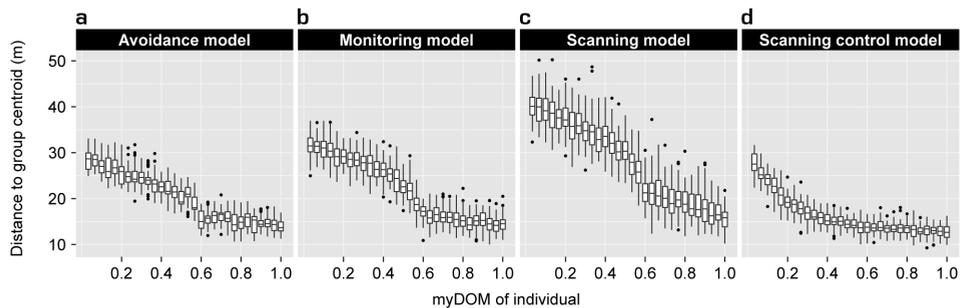


Figure 2.3: Centrality of dominants. This graph shows the relationship between an individual’s dominance strength (myDOM) and its centrality (distance to the centroid of the group in meters) for different models. **a:** Avoidance model. **b:** Monitoring model. **c:** Scanning model. **d:** Scanning control model. Small distances to the arithmetic group center indicate more central positions. When the relation between dominance strength and centrality is steeper (b and c), centrality of dominants is more pronounced. Depending on the model, a low dominance strength further implies low win chance and thus frequently employed fleeing behavior (avoidance, monitoring and scanning model), frequently employed avoidance behavior (avoidance, monitoring and scanning model), frequently employed monitoring behavior (monitoring model) and frequently employed scanning behavior (scanning and scanning control model). Boxplots show 50 simulation runs, averaged over time.

Monitoring

The central-peripheral structure in the monitoring model was slightly more pronounced compared to the avoidance model: individual differences in the distance to the centroid of the group were higher in the monitoring model (Figure 2.3b). This was also apparent in the slope of the regression line, which was significantly steeper in the monitoring model than in the avoidance model (Wilcoxon rank sum test: $W = 2438$, $P < 0.001$; mean slopes \pm standard deviation = -0.71 ± 0.056 and -0.55 ± 0.050 , respectively). Furthermore, groups in the monitoring model were significantly more spread out compared to groups in the avoidance model (Wilcoxon rank sum test: $W = 21$, $P < 0.001$; mean average furthest neighbor distance \pm standard deviation = 75.0 ± 2.6 m and 67.4 ± 1.9 m, respectively; Figure 2.4). This can be explained as follows. By employing monitoring, individuals remained informed on their distance towards central *avoidees*. This allowed them to constantly adjust their spatial distance towards these animals. More frequently employed avoidance behavior then resulted in more spread out groups.

Higher group spread in the monitoring model was also reflected in the dyadic spatial distances among group members (Figure 2.5b). Dyadic distances increased not only between monitoring subordinates and central dominants, but, as a side effect, also among subordinates.

In the monitoring model, encounters among individuals were less frequent than in the avoidance model, especially among subordinates (Figure 2.6b). However, spatial distances among subordinates only partly explain the decrease in encounters. An additional underlying mechanism concerns the visual orientation of subordinates. Subordinates frequently oriented towards central dominants in the monitoring model (Figure 2.7b). This “selective attention” towards dominants “distracted” subordinates from other peripheral subordinates and, thereby, lowered the chance of encountering them.

Scanning

The central-peripheral structure in the scanning model was clearly more pronounced than in the avoidance model, since individual distances to the centroid of the group were most

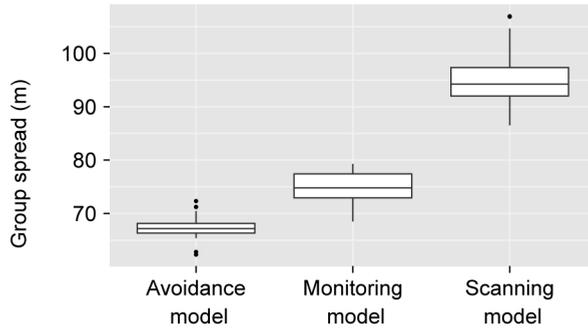


Figure 2.4: Group spread. This graph shows the groups spread (spatial group diameter in meters) for the different models avoidance model, monitoring model and scanning model. Boxplots show values of 50 simulation runs, averaged over time.

differentiated (Figure 2.3c). This was also apparent in the slope of the regression line, which was significantly steeper in the scanning model than in the avoidance model (Wilcoxon rank sum test: $W = 2500$, $P < 0.001$; mean slopes \pm standard deviation = -0.95 ± 0.059 and -0.55 ± 0.050 , respectively). Therefore, individual variation in scanning tendency reinforced the already existing spatial structure, which emerged from individual variation in fleeing frequency and avoidance behavior (Evers et al., 2011).

This raises the question whether individual variation in scanning tendency alone may already generate a central-peripheral structure. To test this, we implemented the scanning control model, in which we excluded the structuring effects of variation in fleeing frequency and avoidance behavior by setting all win chances to 0.5 and by excluding avoidance behavior. Surprisingly, a central-peripheral group structure still emerged (Figure 2.3d) and the slope of the regression line was significantly different from zero (t test: $t = -94.558$, $P < 0.001$; mean slope \pm standard deviation = -0.40 ± 0.030). This came about as follows. Frequently scanning individuals moved further away from the group, because they could still perceive enough group members, even when being oriented away from the group. In contrast, rarely scanning individuals had to turn around, and thus moved back to the group immediately, when approaching the periphery resulted in too few perceived group members. Differential perception resulted in differential grouping behavior and thereby in a central-peripheral group structure with frequent scanners at the periphery and infrequent scanners at the group center. We do not describe any further characteristics of the scanning control model, as this model only served to show the structuring effect of individual variation in scanning tendency.

In the scanning model, groups were significantly more spread out compared to the avoidance model (Wilcoxon rank sum test: $W = 0$, $P < 0.001$; mean average furthest neighbor distance \pm standard deviation = 95.0 ± 4.6 m and 67.4 ± 1.9 m, respectively; Figure 2.4). There are two ways to explain this pattern. First, subordinate individuals were occupying peripheral positions in the group. Frequent scanning allowed these individuals to move even further away from the group, while still perceiving the required number of other group members. Second, frequently scanning the group allowed individuals to avoid potential aggressors (central dominant individuals) more often. More frequent avoidance caused subordinates to move further

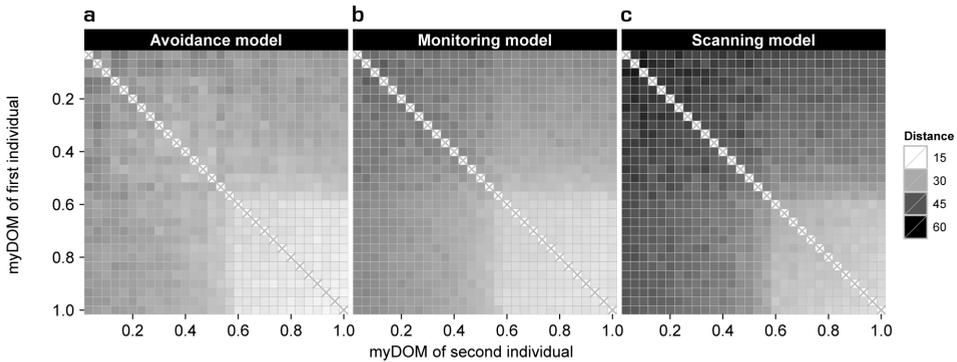


Figure 2.5: Spatial structure. This graph shows the distribution of dyadic distances (in meters) among the individuals of a group for different models. **a:** Avoidance model. **b:** Monitoring model. **c:** Scanning model. The x-axis shows the dominance strength of the first individual and the y-axis the dominance strength of the second individual per dyad. For further implications of an individual's dominance strength depending on the model, see the Figure 2.3 legend. Plots show the mean values of 50 simulation runs, averaged over time. Darker shades represent larger dyadic distances. Values at the diagonal (x) are by default not applicable. Note that the distance matrices are by definition symmetrical.

away from central aggressors and resulted in higher group spread. That groups were more spread out in the scanning model was also reflected in the dyadic distances among the group members (Figure 2.5c). Especially distances among frequently scanning subordinates and between subordinates and dominants were increased relative to the avoidance model.

In the scanning model, encounters among individuals were less frequent than in the avoidance model, especially among subordinates (Figure 2.6c). Frequent scanning of subordinates enabled enhanced perception of other group members (Figure 2.7c). As a result, a higher encounter rate for subordinates would be expected, as they may also encounter individuals outside of the default view angle of 120 degrees. However, the perceptive *advantage* of scanning was counteracted by the large dyadic distances and ultimately resulted in decreased encounter rates.

DISCUSSION

We presented a number of models, investigating how individual variation in social vigilance (monitoring or scanning) in the context of spatial avoidance of aggressors affect group-level properties (the socio-spatial structure). Our results showed that individual variation in social vigilance resulted in more spread out groups, decreased encounter rates between subordinates and reinforced the existing central-peripheral spatial structure of the group. Moreover, such a central-peripheral group structure may also emerge from individual variation in scanning tendency alone.

Emergence of a central-peripheral group structure

In the basic avoidance model, a central-peripheral group structure emerged from individual variation in fleeing and avoidance behavior (Evers et al., 2011). When individual variation in

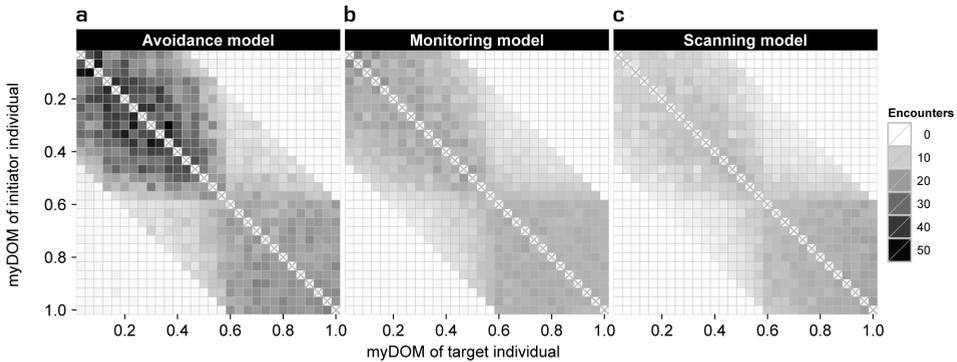


Figure 2.6: Encounter structure. This Figure shows the distribution and direction of encounters among the individuals of a group for different models. **a:** Avoidance model. **b:** Monitoring model. **c:** Scanning model. Encounters are directed from initiators (y-axis) to targets (x-axis), both are ordered by dominance strength (myDOM). For further implications of an individual's dominance strength depending on the model, see the Figure 2.3 legend. Plots show the mean values of 50 simulation runs. Dark shades represent frequent encounters. Values at the diagonal (x) are by default not applicable.

monitoring or scanning was added to the model, this spatial structure was reinforced by monitoring and, to a higher degree, by scanning behavior. The last result suggested that, besides reinforcing an existent group-structure, individual variation in social vigilance alone may even be sufficient to result in a central-peripheral group structure. This was explored in the scanning control model, which did not include any dominance-related variation in avoidance or fleeing rates. The individual variation in scanning tendency within the group indeed was sufficient to generate a central-peripheral group pattern. Frequently scanning individuals occupied more peripheral spatial positions in the group, even when the other structuring factors (variation in fleeing frequency and avoidance behavior) were excluded. Chance (1967) suggested that variation in frequency and direction of social vigilance might put dominant individuals into the spatial center of the group, but to our knowledge this has never been measured or tested. Our model shows indeed such a spatial pattern and explains how this pattern may arise purely as a side effect of individual differences in social vigilance. In contrast to the less frequently scanning dominants, frequently scanning subordinates often perceived group members outside of the default view angle. Therefore, frequent scanning allowed subordinates to employ grouping behavior less often compared to dominants. As a consequence, scanners occupied more peripheral positions. Of course, our results are relying on a number of specific assumptions we made in the model (e.g. the grouping rules), and the validity of these assumptions remains to be investigated empirically. We believe that one of the main advantages of agent-based modeling is that it may help to discover plausible behavioral rules to be verified empirically. Thus, ABMs allows for a strong interplay between constructing an explanatory model and obtaining empirical data (de Vries and Biesmeijer, 1998).

In animals, vigilance is not only directed at conspecifics, but, more commonly, also at predators. Hamilton (1971) tried to link within-group variation in predator vigilance to spatial positions within the group. He hypothesized that the higher predation risk at the periphery of the group should result in more frequently employed vigilance at these spatial positions (“edge effect”). Since then, a correlation between higher degree of vigilance and peripheral positions within a group is usually attributed to higher predation risk at the group periphery, in primates (Robinson, 1981; van Schaik and Noordwijk, 1989), birds (Inglis and Lazarus, 1981; Keys and

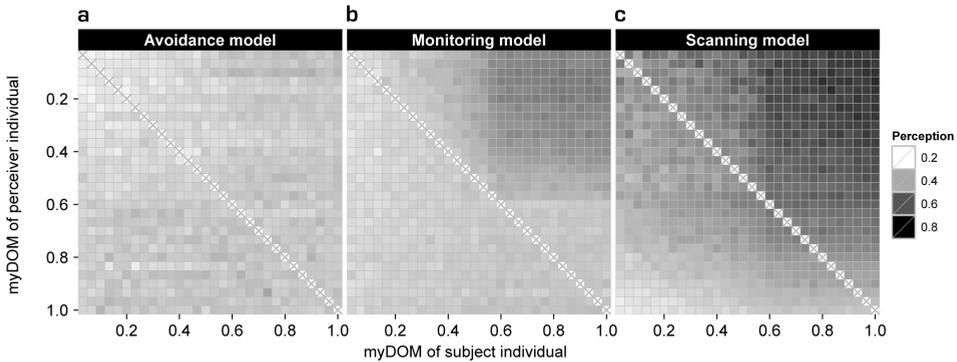


Figure 2.7: Perception structure. This Figure shows the distribution and direction of perception among the individuals of a group for the different models. **a:** Avoidance model. **b:** Monitoring model. **c:** Scanning model. Perception is directed from perceivers (y-axis) to subjects (x-axis), both are ordered by dominance strength (myDOM). For further implications of an individual's dominance strength depending on the model, see the Figure 2.3 legend. Plots show the mean values of 50 simulation runs. Dark shades represent frequent perception. Values at the diagonal (x) are by default not applicable.

Dugatkin, 1990; Black et al., 1992) and other species (see Table 5.3 in Caro, 2005). However, individual variation in vigilance may also originate from factors other than differential predation risk, for instance due to social factors, such as variation in risk of aggression (Chance and Jolly, 1970), infanticide (Steenbeek et al., 1999) or competition for mates or resources (Caraco, 1979; Cowlshaw, 1998). Our scanning control model predicts that whenever variation in vigilance (in our case scanning frequency) is present in a group, frequently vigilant individuals may end up at the group periphery automatically, even in the absence of any predator or any other structuring factors such as aggressor avoidance or dominance interactions. Thus, when peripheral group members employ vigilance behavior more frequently, a premature conclusion about a possible adaptation to differential predation risk is best avoided. The actual underlying mechanism should be evaluated carefully per species and environment.

In a former study (Evers et al., 2011), we investigated how individual variation in movement properties may shape socio-spatial properties within a group. Three factors driving the emergence of a central-peripheral group structure have been identified, namely individual variation in fleeing frequency, avoidance behavior and average velocity (Evers et al., 2011). In the current paper, we identified another factor that may contribute to the centrality of dominants typically reported in primate studies: individual variation in scanning tendency. We conclude that individual variation in different types of behavior (fleeing, velocity, avoidance and scanning) can generate a central-peripheral spatial pattern in primate groups. High fleeing frequency, frequent avoidance behavior, high average velocity and high scanning tendency are all properties that are often found in subordinate members of primate groups (Chance, 1956; Keverne et al., 1978; McNelis and Boatright-Horowitz, 1998; Pannoza et al., 2007; see Evers et al., 2011 for additional references). Disentangling this set of inter-related factors within a simulation model showed how each property independently may result in peripheral spatial positions of certain individuals within a group. We conclude that individual variation in different types of behavior (fleeing, velocity, avoidance and scanning) can generate a central-peripheral spatial pattern in primate groups. A central-peripheral group structure is, thus, a robust pattern, which may be driven by several independent mechanisms, commonly found in primate groups simultaneously.

Spatial structure, encounter structure and social vigilance

While in all three models, the avoidance, monitoring and scanning model, a central-peripheral structure emerged; group spread was highest in the monitoring and scanning model. Interestingly, the causes of high group spread differed for the monitoring and the scanning model. Monitoring potential aggressors resulted in more effective avoidance behavior and therefore in more spread out groups. Scanning, however, not only allowed for more effective avoidance of potential aggressors, but also gave rise to less frequent grouping behavior as a side effect. Both of these effects caused the group in the scanning model to be the most spread out.

In the monitoring and in the scanning model, the encounter structure (the frequency and direction of encounters) was affected by both the spatial group structure and the variation in social vigilance. In the monitoring model the rate of encounters was decreased due to larger dyadic distances and additionally to the subordinates' monitoring of central dominants. Subordinates mainly focused their vigilance on perceiving and avoiding dominants, thereby "losing sight" of other potential interaction partners (subordinates) at the periphery. In the scanning model, encounter frequencies among subordinates were also decreased due to large dyadic distances among peripheral individuals. Although scanning individuals had a higher chance to perceive and eventually encounter other group members, this was counteracted by the large inter-individual distances.

These results reveal that social group properties, such as encounter structure, are affected by, but not deducible from the average spatial distances alone. To reveal the underlying processes of socio-spatial group structure, spatial data of real primate groups are best analyzed in combination with data on social vigilance within a group.

Further directions

Our model predicts that monitoring and scanning behavior reduces encounter rates and, therefore, aggression. It would be interesting to test our findings and compare encounter structures between species or groups that differ in the amount of social vigilance employed. In gorillas, females have been shown to attend differentially towards kin, mates or recent immigrants (Watts, 1998). Similarly, chimpanzees adjust their level of social vigilance depending on their relationship quality with associates (Kutsukake, 2006). Whether such variation in social vigilance is related to encounter rates could be investigated in differently composed groups.

Furthermore, in social groups monitoring behavior may provide cues to group members. Individuals may be able to use the direction of monitoring (the gaze direction of other individuals) to infer information about the location of potential aggressors and possibly also about the attentive and emotional state of the monitoring animal (Goossens et al., 2008; Teufel et al., 2010). Thus, while monitoring is used to obtain social information by the monitoring animal, the behavior itself may provide social information to others and thereby reinforce social group structure (Coussi-Korbel and Fragaszy, 1995; Pannozzo et al., 2007). This opens up new research topics to investigate how social vigilance, and other ways of acquiring information from conspecifics (Bonnie and Earley, 2007), may affect group-level properties in primates and other social animals.

In our model, social vigilance was directed at feared individuals. Of course, real primates may employ social attention also to detect preferred individuals, such as kin, mates or allies, and seek their proximity. For example, monitoring may help to stay informed about the spatial position of affiliates while moving into a different direction (a so-called "secondary referent" cf. Emory, 1976; see also Virgo and Waterhouse, 1969), and scanning might be used to quickly find and recruit potential coalition partners.

Conclusion

By investigating the link between individual variation in social vigilance and socio-spatial group structure in an agent-based model, we offer a new perspective on the causal relations between different group-level patterns. Our model yields another possible explanation for one of the main questions in the primate literature: what causes centrality, in the light of a specific primate behavior: namely social vigilance. In line with the suggestion of Chance (1967), this agent-based model study provides a clear indication that variation in social vigilance may be an important structuring feature of primate social groups.

Acknowledgments

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The EMO-Model: An agent-based model of primate social behavior regulated by two emotional dimensions, anxiety-FEAR and satisfaction-LIKE

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ABSTRACT

Agent-based models provide a promising tool to investigate the relationship between individuals' behavior and emerging group-level patterns. An individual's behavior may be regulated by its emotional state and its interaction history with specific individuals. Emotional bookkeeping is a candidate mechanism to keep track of received benefits from specific individuals without requiring high cognitive abilities. However, how this mechanism may work is difficult to study in real animals, due to the complexity of primate social life. To explore this theoretically, we introduce an agent-based model, dubbed EMO-model, in which we implemented emotional bookkeeping. In this model the social behaviors of primate-like individuals are regulated by emotional processes along two dimensions. An individual's emotional state is described by an aversive and a pleasant dimension (anxiety and satisfaction) and by its activating quality (arousal). Social behaviors affect the individuals' emotional state. To implement emotional bookkeeping, the receiver of grooming assigns an accumulated affiliative attitude (LIKE) to the groomer. Fixed partner-specific agonistic attitudes (FEAR) reflect the stable dominance relations between group members. While the emotional state affects an individual's general probability of executing certain behaviors, LIKE and FEAR affect the individual's partner-specific behavioral probabilities. In this way, emotional processes regulate both, spontaneous behaviors and appropriate responses to received behaviors, while emotional bookkeeping via LIKE attitudes regulates the development and maintenance of affiliative relations. Using an array of empirical data, the model processes were substantiated and the emerging model patterns were partially validated. The EMO-model offers a framework to investigate the emotional bookkeeping hypothesis theoretically and pinpoints gaps that need to be investigated empirically.

INTRODUCTION

Many studies on animal behavior have contributed to a comprehensive body of knowledge concerning specific emotions (such as anxiety) and the relation between the underlying neurobiology and behavior. Yet, our understanding of how emotional processes within individuals regulate their behavior and how this in turn may result in group-level patterns, such as partner-specific reciprocity or the development and maintenance of affiliative relationships, is poor. To empirically study this, i.e. by manipulating distinctive factors within one or a few group members and assessing the resulting group-level changes, is methodologically difficult. Such invasive experiments may affect also other behaviors and regulatory processes and, furthermore, may disturb the complex relations and behavioral processes within the group. Observational studies of naturally occurring stressful events (Wittig et al., 2008) may give valuable insights. Yet, it remains difficult to untangle the exact causalities underlying the observed changes at the group level, as social behavior comprises many interactions of many individuals. Here, we present an agent-based model (ABM), providing a (biologically relevant) alternative tool to allow exploratory research on the patterns of social relationships and the necessary, underlying requirements. We developed our model, dubbed the EMO-model, using empirical data to substantiate the implemented emotional processes and behavioral rules. In this introduction, we first review the empirical and theoretical background on emotional processes and their role in regulating social behavior, specifically in macaques. We continue with the theoretical background on emotional bookkeeping and, finally, we describe the status quo of our specific contribution to agent-based models of social species, such as macaques.

Two dimensions of the emotional state: anxiety and satisfaction

Emotional processes are considered a prompt response to a (social) event preparing an individual to quickly react in a certain direction. The response consists of activating a concerted set of actions at the physiological (peripheral and central) and behavioral level (Paul et al., 2005), comprising the interface between perception, a first fast analysis of sensory input, and subsequent behavioral reaction (Aureli and Whiten, 2003). Emotional processes motivate an individual to conduct a certain behavior efficiently adapted to meet challenges of the (social) environment (Panksepp, 1998; Rolls, 1999). In this paper, we refer to emotional processes and emotional states without implying accompanying conscious, subjective states that are inaccessible to measurement in non-human animals (Paul et al., 2005; Panksepp, 1998; LeDoux, 1999; Berridge and Winkielman, 2003).

The quality component of an individual's emotional state, often referred to as valence or appraisal, has been proposed to comprise an aversive and a pleasant dimension (Watson and Tellegen, 1985; Watson et al., 1999). Social behavior of group living animals may also be described in terms of this dichotomy, encompassing an agonistic and affiliative dimension, which relate to different aspects of social organization, such as dominance hierarchies and affiliative bonds. Moreover, emotional processes employ different underlying mechanisms, as aversive emotional responses (e.g. anxiety, stress) are more associated with the amygdala and the HPA axis (Davis, 1992; Tsigos and Chrousos, 2002), while pleasant emotional responses employ the reward system consisting mainly of the ventral tegmental area (VTA), the opioid-dopamine system and oxytocin (Boissy et al., 2007). This suggests that social behavior may be regulated via two underlying emotional dimensions that relate to agonistic and affiliative behavior, respectively. These two emotional dimensions are, hereafter, referred to as *anxiety* (aversive) and *satisfaction* (pleasant). Anxiety and satisfaction are assumed to be independently regulated, e.g. a decrease in anxiety does not automatically result in increased satisfaction.

Anxiety can be defined as a state of apprehension or uneasiness that stems from (anticipation of) danger (APA, 2000). In contrast to fear, which is directed at a specific stimulus (object or subject, Lang et al., 2000), anxiety may be seen as a state of general *fearfulness*, in response to negative stimuli within the recent and current (social) environment as perceived by the individual. In parallel, satisfaction may be defined as a state of general *contentedness*, in response to positive stimuli within the recent and current (social) environment as perceived by the individual.

Emotional processes have been proposed to mediate between social interactions and the behavioral and physiological response (Aureli and Whiten, 2003; Aureli and Schino, 2004; Aureli and Smucny, 2000; Aureli and Schaffner, 2002; Aureli, 1997). For example in macaques, upon aggression, the recipient as well as the aggressor will show increased levels of anxiety (Aureli, 1997; Aureli and van Schaik, 1991; Schino et al., 2007b), which may enhance the individuals' tendency to affiliate (Aureli, 1997). Affiliation will in turn decrease anxiety (Aureli and van Schaik, 1991) and may increase satisfaction. In macaques and other primates, it has been shown, that grooming is pleasant for the receiver, but also the actor (Spruijt et al., 1992; Boccia et al., 1989; Shutt et al., 2007).

Moreover, primates use communicative signals (i.e. facial expressions) to express their behavioral intentions towards group members, thereby affecting the behavior of (potential) interaction partners. For instance in macaques, affiliative and submissive signals (such as *lip-smacking* or *bared-teeth*) are thought to appease the receiver of the signal, thereby reducing the risk of aggression or facilitating affiliation (Maestripietri, 1996a,b; Maestripietri and Wallen, 1997), while aggressive signals (such as *open-mouth threat*) may result in avoidance or counter-aggression (Angst, 1974; Goossens et al., 2008). As such, the expression and perception of communicative signals may also employ underlying emotional processes (Kuraoka and Nakamura, 2011). In this way, emotional processes may be involved in a homeostatic mechanism regulating spontaneous behaviors as well as appropriate responses to received behaviors on a short-term basis.

Activating quality of the emotional state: arousal

An individual's emotional state cannot only be characterized by its valence (anxiety and satisfaction), but also by its arousal (Paul et al., 2005; Lang et al., 2000; Barrett, 1998). Arousal refers to the intensity of an emotional state or its activating quality (Paul et al., 2005; Rendall, 2003), which may depend on the salience or relevance of the stimulus that elicited the specific emotional state. Arousal has been defined as an individual's level of sensory-motor responsiveness, its (physiological) activity or its motivational state (Jones, 2003; Winslow et al., 1989; Mason, 1973). In ethological research, several physiological parameters and displacement behaviors (e.g. heart rate and self-scratching, as put forward by Maestripietri et al., 1992) are commonly used as indicators of emotional arousal in primates (macaques: Aureli et al., 1999; Maestripietri, 2010; Schino et al., 1996, squirrel monkeys: Winslow et al., 1989, capuchins: Manson and Perry, 2000, baboons: Castles et al., 1999, chimpanzees: Koski et al., 2007b, and also in greylag geese Wascher et al., 2009). For instance in macaques, scratching and heart rate have been observed to increase quickly upon stressful (social) events, such as (the risk of) aggression (Aureli and Smucny, 2000; Schino et al., 2007b; Aureli et al., 1999; Pavani et al., 1991) and to decrease afterwards within several minutes (Kutsukake and Castles, 2001; Boccia et al., 1989). Positive (social) events, such as grooming, have been shown to facilitate an even faster decrease of these measures (Boccia et al., 1989; Pavani et al., 1991). Thus, arousal levels may change in response to (social) stimuli and correspond with the individual's state of responsiveness, activity or inclination to act. In macaques, increased vigilance

behavior and motor activity are commonly associated with increased arousal (Winslow et al., 1989). As high arousal levels are often caused by received aggression, the resulting increase of (social) vigilance may serve to avoid further potential aggression or to find potential affiliation partners.

Emotional bookkeeping via partner-specific emotional attitudes

Emotional processes have also been proposed to mediate the development, maintenance and assessment of social relations (Aureli and Schino, 2004; Aureli and Smucny, 2000; Aureli and Schaffner, 2002; Schino and Aureli, 2009). Aureli and colleagues have developed a hypothetical framework of emotional bookkeeping as a mediator of primate social relationships (Aureli and Schino, 2004; Aureli and Schaffner, 2002; Schino and Aureli, 2009). While recent social interactions affect an individual's (general) emotional state and, thus, its general behavior, individuals may also integrate the emotional states that accompanied earlier social interactions into an emotional attitude that is associated with each respective interaction partner. This partner-specific emotional attitude may in turn affect an individual's subsequent behavior towards the respective partner. In this way, fleeting emotional responses may be accumulated using a simple partner-specific bookkeeping mechanism, similar to that underlying de Waal's concept of *attitudinal reciprocity* (de Waal, 2000). In contrast to *attitudinal reciprocity* (de Waal, 2000) and the individual's general emotional state, both of which are assumed to work on a short-term scale, emotional bookkeeping has been proposed to integrate information over longer periods and, thus, to affect partner-specific behavior on a longer term (Schino and Aureli, 2009).

Since an individual's general emotional state is not specific to interaction partners, it constitutes a cognitively simpler mechanism than emotional bookkeeping, which is based on the rate and intensity of the emotional responses to the interactions with a particular individual and, thus, does require individual recognition. However, emotional bookkeeping does not require a specific memory of who did what and when (*episodic-like memory*, Crystal, 2009), due to the conversion of earlier interactions into a common currency, i.e. the partner-specific emotional attitude (Schino and Aureli, 2009). In other words, different types of social interactions (e.g. affiliation and support) with different partners may result in qualitatively similar partner-specific attitudes, resulting in qualitatively similar behavioral responses. However, the emotional attitudes assigned to several partners may differ quantitatively, for example between a frequent and an occasional groomer. As such, emotional bookkeeping may allow for differentiated valuation of partners dependent on quality and quantity of earlier interactions with these partners.

In line with the two dimensions of the general emotional state, anxiety and satisfaction, we here propose that a partner-specific emotional attitude also comprises an agonism-related and an affiliation-related dimension. Hereafter, these will be referred to as FEAR and LIKE attitude, respectively.

In the EMO-model, LIKE attitudes are implemented as the partner-specific equivalent of satisfaction. While an individual's satisfaction describes its general *contentedness*, LIKE attitudes reflect an individual's differential valuation of each group member, concerning the received affiliation over a certain timeframe. In turn, the LIKE attitude that an individual associates with a certain group member affects its probability to direct affiliative behavior towards this group member. In this way, LIKE attitudes may regulate the development and maintenance of partner-specific affiliative relations.

FEAR attitudes are implemented in the EMO-model as the partner-specific equivalent of anxiety and describe the agonistic relationships between an individual and each other group member, as perceived by the individual. Group members from whom an individual receives a lot of aggression cause high anxiety levels in this individual. Thus, the individual is expected to assign high FEAR attitudes to such group members. In this way, FEAR attitudes can be seen as an internal representation of the dominance relations with the group members. Such partner-specific bookkeeping of dominance outcomes has previously been proposed and implemented in agent-based models (Hogeweg and Hesper, 1985; Hemelrijk, 2000). However, in many primates, dominance hierarchies are stable over long periods of time (up to several years, macaques: Bernstein, 1969; Rhine et al., 1989; Ostner et al., 2008; Silk, 1988, gorilla: Robbins et al., 2005, baboons: Samuels et al., 1987; Hausfater et al., 1982, capuchins: Bergstrom and Fedigan, 2010, vervets: Bramblett et al., 1982). As we do not aim to study the development of a dominance hierarchy, but want to focus on the development and specifically the maintenance of affiliative relationships, we assume that in our model group a dominance hierarchy has been already established and does not change over the timeframe of two years in our model simulation. Therefore, FEAR attitudes in the EMO-model do not change dynamically over time and simply resemble the fixed rank distance between two individuals. In turn, FEAR attitudes affect the probability to direct submissive or aggressive behavior towards this partner. Assuming a fixed hierarchy and fixed FEAR attitudes, while studying dynamic LIKE attitudes seems reasonable as a starting point. In a study on macaques, where unfamiliar individuals were paired, unresolved dominance relations prevented engagement in affiliation (Schino et al., 1990), and thus also the potential development of LIKE attitudes.

Additions to existing ABM of primate social behavior

ABMs are a powerful tool to study social behavior, as they can reveal the potential for self-organization in social systems, showing that simple behavioral rules may lead to complex patterns at the group level, in primates (te Boekhorst and Hogeweg, 1994; Hemelrijk, 1998b, 1999b, 2000; van der Post and Hogeweg, 2004; Sueur et al., 2009; Puga-Gonzalez et al., 2009; Evers et al., 2011, 2012; Hemelrijk and Puga-Gonzalez, 2012) and other species (birds: Hildenbrandt et al., 2010, fish: Hemelrijk et al., 2010; Viscido et al., 2005; Oosten et al., 2010; Couzin et al., 2002, insects: Hogeweg and Hesper, 1983; de Vries and Biesmeijer, 1998, 2002; Johnson, 2009; Becher et al., 2010). For instance, ABM studies have demonstrated that spatial centrality of dominants may emerge from minimalistic behavioral rules concerning dominance interactions (Hogeweg and Hesper, 1983; Hemelrijk, 2000). In one of these models, DomWorld (Hemelrijk, 2000), the most extensively published ABM on primate behavior, low-ranking individuals typically lose dominance interactions and subsequently flee from their opponent. The resulting spatial group structure in turn results in differentiated interaction frequencies between different group members, potentially regulating social group properties (such as the dominance hierarchy). These outcomes indicate the potential of self-organization in real animals. However, the full validity of DomWorld has been questioned (Bryson et al., 2007), since real primates also employ other behaviors to regulate aggression, e.g. avoidance of the aggressor or monitoring its behavior and location. Implementing such alternative behavioral rules in an ABM, we have demonstrated elsewhere that different sets of behavioral rules concerning movement and perception may result in a similar spatial group structure, but may differ in other properties, such as the frequencies and patterns of interactions (Evers et al., 2011, 2012). This stressed the importance of implementing multiple levels of a system into a model of this system (Hogeweg and Hesper, 1990) to subsequently substantiate and validate patterns on multiple levels of the system (Grimm, 2005).

Most ABMs on primate behavior mentioned above did not include an emotional valuation of social behavior and only concerned one dimension of social behavior, i.e. aggression-submission. More recently, in the GrooFiWorld model, an extended version of the DomWorld model, also affiliative behavior (grooming) has been implemented (Puga-Gonzalez et al., 2009; Hemelrijk and Puga-Gonzalez, 2012). Moreover, a first attempt has been made to complement the behavioral rules with an underlying emotional component, namely anxiety. This model generates interesting behavioral patterns, such as reconciliation, grooming after a fight, grooming up the hierarchy and coalitions.

Here, we present a new ABM, the *EMO-model*, in which we explicitly incorporated the interrelation between social behavior and emotional states of primates along two dimensions (see above). The agonism-related dimension concerns agonistic behavior and anxiety and shares many features with previous models. The affiliation-related dimension concerns grooming and satisfaction. For the agonism-related dimension, many general features of our model resemble the GrooFiWorld model. In both models, aggression increases anxiety, which subsequently enhances the tendency to groom and in turn decreases anxiety. However, in the GrooFiWorld model emotional processes only involve anxiety. For instance, lack of grooming was implemented to result in high anxiety, subsequently enhancing the tendency to groom. In contrast, our EMO-model distinguishes between anxiety, satisfaction and arousal, backed by empirical data. Here, lack of grooming was implemented to result in low satisfaction levels and slightly increased arousal. As a result, the tendency to groom and the tendency to engage in active behavior as opposed to resting are enhanced. So, grooming tendency is enhanced through high anxiety levels (due to aggression) and low satisfaction levels (due to lack of grooming). The effect of satisfaction on grooming constitutes the affiliation-related dimension.

Furthermore, aggressive behavior in both models is risk-sensitive. However, while this risk-sensitivity only depends on the dominance relation between two opponents in GrooFiWorld, it is additionally dependent on the actor's anxiety levels in the EMO-model. Moreover, to our knowledge our model is the first agent-based model of primates that also implements partner-specific emotional attitudes along two dimensions, i.e. not only FEAR but also LIKE attitudes. Thus, this paper presents a first attempt to explicitly implement the process of emotional bookkeeping into an agent-based model of primate social behavior.

In contrast to many earlier models on primate social behavior (Hemelrijk, 2000; Puga-Gonzalez et al., 2009; Hemelrijk and Puga-Gonzalez, 2012), and building up on earlier attempts (Evers et al., 2011, 2012), here we explicitly define not only the aggressive, but also the submissive components of agonism, i.e. fleeing, submissive signaling and avoidance. While unidirectional signals of submission are not observed in very egalitarian species (Thierry, 2007; Thierry et al., 2008; Thierry, 2000), most macaque species direct submissive signals exclusively at higher-ranking individuals (de Waal and Luttrell, 1989; Berman et al., 2004; Cooper et al., 2005). For this reason, submissive signals are commonly used to determine the hierarchy within a group. In our model, submission was implemented such that it was exclusively directed at individuals that were higher in rank. Thus, we model a unidirectional, linear hierarchy. To our knowledge, this model is also the first agent-based model on primate social behavior that explicitly implemented communicative signaling. We implemented affiliative, submissive and aggressive signals that may represent *lip-smack*, *bared-teeth* and *open-mouth threat* in macaques. In the EMO-model, physical interactions, e.g. grooming and attacking, are only executed when in close proximity (1m) to the interaction partner. The choice of such a distance for physical interactions is logical, but in contrast to other ABM on primate behavior. For instance in GrooFiWorld, individuals can be groomed at a distance up to 8 units (Puga-Gonzalez et al., 2009). Furuichi (1983) found that in a troop of Japanese macaques, aggression occurred

mostly when the two opponents were closer to each other than 1m and only rarely when the distance was larger.

Agent-based modeling permits a stronger coupling between the two phases in scientific research: *obtaining empirical data* and *constructing an explanatory theoretical model* (de Vries and Biesmeijer, 1998), since ABM help to determine crucial parameters for explanatory models and reveal which empirical data are still missing. Accordingly, we aimed to choose the parameter settings of our model as realistic as possible, promoting the exchange between empirical data and models of behavior (Petit, 2011). To do this, we first surveyed empirical data of macaques to obtain an overview of realistic margins of general behavioral frequencies. We then tuned the general probabilities of executing these behaviors in our model, such that the resulting average behavioral frequencies were representing the empirical data well. Subsequently, to validate the EMO-model, we assessed whether our model was also able to reproduce patterns from empirical macaque data on a group or subgroup level. Such higher-level patterns are not explicitly implemented into the model, but emerge from the interactions of the model entities. This feature of ABM allows investigation of the link between emotional processes and patterns in social behavior at the group level.

In sum, we explicitly incorporated the proposed interrelations between primate social behavior and emotional processes, instead of modeling this as a black box. This way, the EMO-model serves as an explicitly formulated hypothesis, about how emotional processes may regulate primate social behavior and vice versa. Following Petit (2011), this model integrates several partial hypotheses (on emotional processes and emotional book-keeping in animals) and the current state of empirical data, which complement each other. We aimed to produce a representative model that may also generate structural properties at a group level. This model allows us to pinpoint gaps in the empirical data and in the theoretical understanding of the underlying mechanism. Our model serves as an initial attempt to study the emotional regulation of social processes and may offer a promising framework to study the complex dynamics of social relationships.

In this paper, we further describe the implementation of the model processes in detail, following the ODD protocol (Grimm et al., 2010). Next, we provide the validation of the EMO-model on multiple levels and present the general patterns that emerge in the model. Finally, we discuss the significance of the EMO-model to study complex behavioral patterns of social species such as macaques.

METHODS

Simulations were run using NetLogo 5.0.2 (Wilenski, 2007). The program code of all models will become available via the website of the first author¹. Below, we describe our models according to the updated ODD protocol (Grimm et al., 2010). This protocol is a standardized method of describing agent-based models, which ensures the model description to be more complete and better comparable to other models, allowing also reproducibility of the model. Following the ODD protocol (Overview, Design concepts, Details), this Methods section is structured as follows. The *Overview* part presents the general description of the model's 1) Purpose, its 2) Entities, state variables and scales and the 3) Process overview and scheduling. The *Design concepts* part describes ABM-specific characteristics and concepts of the model, namely 4) Basic principles, 5) Emergence, 6) Adaptation, 7) Learning, 8) Sensing, 9) Interactions, 10) Stochasticity and 11) Observation. The *Details* part covers the 12) Initialization of the

¹<https://sites.google.com/site/elleneversutrecht/models>

model, as well as the detailed implementation of parts and processes in the model, which are referred to as 13) Submodels. Additionally, this Methods section includes a subsection on the 14) Simulation experiments and the 15) Statistical analysis, which are not part of the ODD protocol.

Overview

Purpose

This model serves as an initial attempt of an explicitly formulated hypothesis, about how emotional processes may regulate primate social behavior and vice versa. We aimed to develop a model that a) reproduces general patterns of primate behavior and b) may also generate more complex patterns of behavior similar to those observed in primate groups. We analyze the effect of the degree to which emotional bookkeeping affects affiliative partner choice, on the general behavioral patterns within the model.

Entities, state variables and scales

We simulated the movements and interactions of 20 primate-like model individuals. These individuals are characterized by a number of state variables, which are summarized in Table S3.1 and described hereafter.

Individuals are characterized by their dominance strength (*myDOM*), which ranges from $1/N$ (for the lowest-ranking individual) to 1.0 (highest-ranking), where N describes the total number of animals in the group. Dominance strength does not change over time or after interactions (Evers et al., 2011, 2012; Bryson et al., 2007). Individuals also differ in their (current) schedule time, *myTIME*, which determines when the individual is activated anew. Furthermore, individuals differ in their (current) scanning probability, *myPscan*, and the related variable *myVIEW_ANGLE* (the current width of the view angle). The variables *myTIME*, *myPscan*, *myVIEW_ANGLE* and the spatial coordinates of the individuals change dynamically over the course of the whole simulation.

Next to these general state variables, our model entities are further described by their emotional state, consisting of an aversive and a pleasant dimension (*myANXIETY* and *mySATISFACTION*) and *myAROUSAL*, an individual's state of alertness or responsiveness to stimuli. While arousal affects an individual's general probability to engage in active behavior (in response to stimuli), both, anxiety and satisfaction enhance appropriate and inhibit inappropriate responses to stimuli. Arousal, anxiety and satisfaction may change dynamically over time depending on the social context of ego (i.e. a model entity). The current level of arousal, anxiety and satisfaction that is approached over time (*myAROUSAL_LIMIT*, *myANXIETY_LIMIT*, *mySATISFACTION_LIMIT*) depending on the currently experienced social context of the individual also changes dynamically over time. For instance during grooming satisfaction level slowly approaches 1.0, while in the absence of grooming it slowly approaches 0.0. Besides the general emotional state, individuals are also characterized by partner-specific emotional attitudes (*LIKE* and *FEAR*) they assign to each other group member. In our model *FEAR* attitudes are fixed, while *LIKE* attitudes are dynamically changing over time depending on earlier affiliative interactions.

General model parameters are summarized in Table S3.2 and described hereafter. The modeled environment is a continuous two-dimensional grid (300×300 grid units) with a torus shape

to exclude disturbing border effects. The length of one grid unit resembles one meter. We did not explicitly implement ecological features of the environment; in the model an individual's environment is purely social. This also implies that the model individuals do not engage in foraging behavior. Thus, we model a group that is not travelling.

One time step in the simulation resembles 1 MINUTE. One HOUR consists of 60 MINUTES and we defined 12 HOURS as one DAY, as this approximately resembles the active, non-sleeping part of the day for many primate species (Crowley et al., 1972). Furthermore, we defined 7 DAYS as 1 WEEK and 50 WEEKS were defined as 1 YEAR. Simulations were run for 504 000 time steps, i.e. 2 YEARS, plus a prior stabilization period of 21 600 time steps, i.e. ca. 4 WEEKS.

Process overview and scheduling

Our model is event-driven. While most social behaviors are discrete events in time, moving, resting and grooming are modeled as continuous duration behaviors. Therefore, time is modeled on a continuous scale. During a simulation run, individuals' activations are regulated by a timing regime. The general process overview and the timing regime are illustrated in Figure 3.1.

Each time, the agent with the lowest schedule time is activated first. Whenever an individual is activated, first all model entities update those state variables that may have increased or decreased over the time interval that has passed since the last activation of an entity (arousal, anxiety, satisfaction, LIKE attitudes) (see Submodels Arousal, Anxiety, Satisfaction and LIKE Attitudes below for more details). If the activated individual had scheduled a movement action, that action is executed (see Submodel Movement below). Else, ego checks the grouping criteria and employs grouping, if necessary (see Submodel Grouping below). If no grouping and no movement are to be performed, ego may select either a social behavior, or resting or random movement within the group. Which behavior (and which interaction partner) gets selected depends on ego's own emotional state and its arousal, as well as on its emotional attitudes towards the potential interaction partners (see Submodel Action Selection below). Moreover, the selected behavior may affect emotional attitudes of involved individuals. It may also affect the emotional state of ego and involved individuals (not depicted in Figure 3.1), as well as their schedule time (see Figure 3.1).

Thus, after activation, the next activation of ego, but also that of interaction partners or bystanders is scheduled anew. The exact time until an individual's next activation depends on the behavior performed, received or observed, respectively (see Design Concept: Stochasticity for the random drawing of the schedule times). Movement, resting and grooming are implemented as duration behaviors and are performed in bouts. Here, after starting a movement, resting or grooming bout, ego is activated after some time to decide whether the behavior is to be continued (Table S3.3). As social interactions may involve (and therefore activate) other group members, they may also interrupt a grooming or resting bout. As such, whenever ego receives an attack, it is immediately activated to respond with either fleeing or a counter-attack (Table S3.3). Whenever ego receives a communicative signal (e.g. an aggressive signal) or observes an attack nearby, a fast reaction is required and ego is activated shortly after to select an action (Table S3.3).

Design concepts

Basic principles

In our model, social behaviors affect the emotional states and attitudes of individuals. In turn, emotional state and attitudes affect the behavior of individuals. An overview of the interac-

tions between behavior, emotions and attitudes is given below and depicted in Figure 3.2. Receiving affiliative behavior increases satisfaction levels and decreases arousal and anxiety. While receiving submissive behaviors results in decreased arousal and anxiety, receiving aggressive behavior or observing (the risk of) aggression nearby results in increased levels of anxiety and arousal. Arousal affects ego's activity. Therefore increased arousal results in a

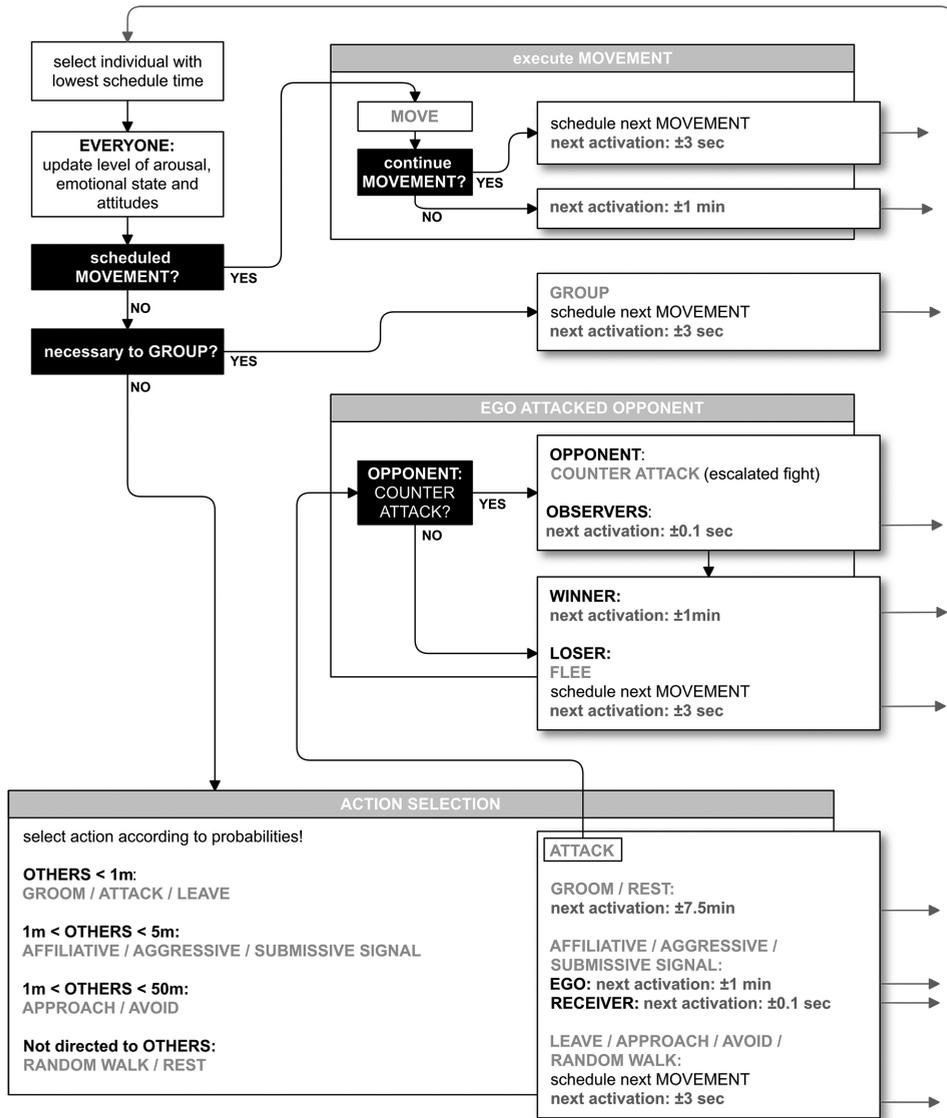


Figure 3.1: Process overview of the model. This figure illustrates the order of the processes executed by the model entities and their timing regime.

higher general probability for all social behaviors. High satisfaction levels decrease the probability of (further) affiliation. High anxiety levels result in increased probabilities for affiliative or submissive behavior and in more risk-sensitive aggression probabilities, i.e. the aggression probability decreases, but increases towards very low-ranking individuals. Receiving affiliation from a specific individual increases ego's LIKE attitude towards this individual. In turn, ego's probability to affiliate with this specific individual increases. Ego's FEAR attitude towards a specific individual represents the rank distance between ego and this individual. FEAR is not affected by behavior, but only regulates ego's agonistic behavior towards the specific individual: a high FEAR attitude results in high submission probabilities and low aggression probabilities. Finally, executing affiliative behavior (i.e. grooming) increases also ego's own satisfaction level and decreases ego's anxiety and arousal. On the other hand, executing aggressive behavior increases ego's own arousal. Depending on whether ego is the winner or loser of a fight, executing aggression may decrease or increase ego's own anxiety levels. In sum, the emotional state regulates appropriate behavior in response to received behaviors, while partner-specific emotional attitudes regulate appropriate behavior in response to specific individuals (see Figure 3.2).

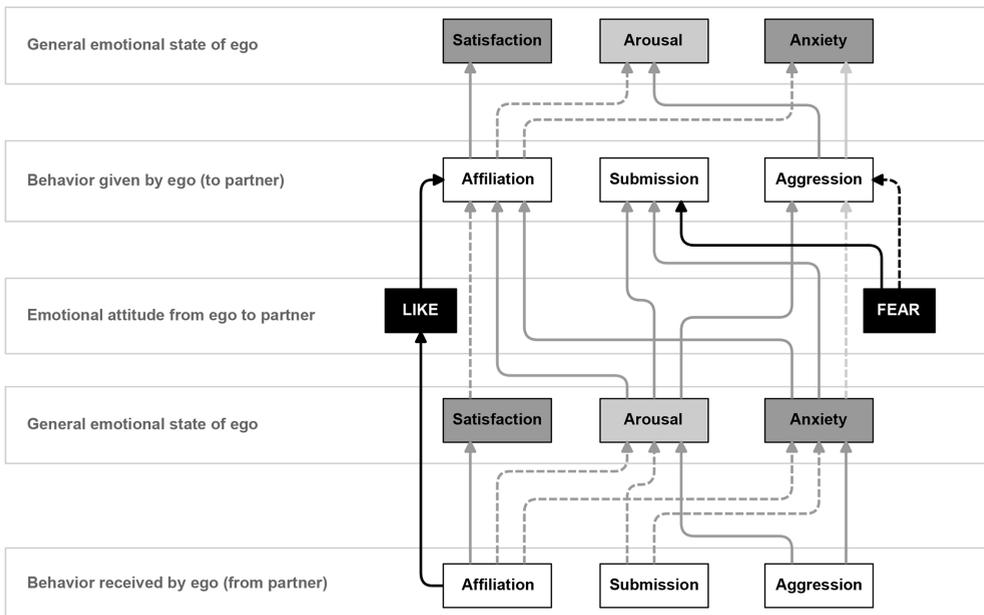


Figure 3.2: Interactions between behavior, emotional state and attitudes. This figure illustrates the effect of behavior on an individual's emotional state and its partner-specific attitudes towards others and vice versa. Solid arrows indicate an increasing effect, while dashed arrows indicate a decreasing effect. Partner-specific effects are depicted as black and general effects are depicted as grey arrows. Light grey arrows depict effects that also depend on other factors, such as the rank of the opponent or the outcome of a fight. See Subsection Basic Principles and the respective Submodels for more details.

Emergence

In agent-based models, group-level properties are usually not implemented explicitly into the model, but rather emerge from the interactions of the lower-level entities, i.e. the individuals. Individuals in our model prefer to stay near the group, but avoid proximity to those individuals that may pose a high risk of aggression. However, the probability of avoiding such a group member also depends on ego's own emotional state, which in turn depends on recent behaviors performed, received or observed by ego. Moreover, individuals in our model prefer to direct affiliative behavior to individuals towards whom they assign a high affiliative attitude (LIKE attitude), which in turn depends on earlier received affiliation from these individuals. Therefore, in our model, patterns of avoidance, approach and proximity are emergent properties arising from the interactions of the model entities. As social interactions depend on spatial proximity between interaction partners and also feed back on the spatial proximity, the patterns of those social interactions are also an emergent property in our model. LIKE attitudes in our model develop quickly, depending on earlier received affiliation from other individuals, but need to be maintained by affiliative behavior on a regular basis. LIKE attitudes affect affiliative partner choice and affiliative behaviors feed back on the level of LIKE attitudes. Therefore, in our model the structure of the network of LIKE attitudes and group level patterns such as reciprocity are emergent properties arising from the interrelation between LIKE attitudes and affiliative behavior. Thus, while individual behavior is explicitly implemented in the model rules, resulting group level patterns of proximity, behaviors and relations are emerging from the complex interactions between the model entities.

Adaptation

The model entities change their behavior in response to changes in their general emotional state (arousal, anxiety and satisfaction) and their partner-specific emotional attitudes towards others. We assume that individuals (implicitly) seek to increase satisfaction and to decrease anxiety. As appropriate behavior is mediated by emotional processes this yields a homeostatic regulation system. In this way, we aimed to produce adaptive (in the sense of flexible) behavior and emerging group properties that are representative of observed social behavior of real primates. Note however, that the model entities do not explicitly seek to increase certain fitness measures, but simply follow rules that are expected to result in adaptive behavior.

Learning

Some traits of our model entities change in response to earlier social interactions, i.e. the emotional state (arousal, anxiety and satisfaction) and LIKE attitudes. The change in LIKE attitudes, which are partner-specific, may be seen as a (basic) form of learning. Individuals in our model regularly update their LIKE attitudes to other group members, based on earlier grooming received from these individuals. When ego receives no affiliation from a certain group member over some time, its LIKE attitude towards this individual will slowly decrease, while it may increase again after episodes of received grooming. Moreover, the LIKE attitude integrates partner-specific information about the duration and frequency of recent and earlier received grooming. This mechanism of emotional bookkeeping provides individuals with summarized information on "valuable" affiliation partners, which may dynamically change over time according to these partners' behavior. In this way, individuals "learn" with which specific partners they should affiliate.

Sensing

Individuals in our model may perceive the location, certain behaviors and signals of other group members, but only locally within certain distances and within a specific view angle. The exact distances and view angles depend on the salience of the perceivable information, e.g. the presence of group members can be perceived at greater distance than the behavior of these individuals and nearby escalated fights can be perceived even when the opponents are located outside of the perceivers view angle (see Submodel Perception and Signaling for more details). Individuals “know”, are able to perceive, or are assumed to have learned the dominance strength of other group members. Perception of a group member elicits ego’s internal valuation of this group member, i.e. its FEAR and LIKE attitude that it assigned to this specific individual.

Interactions

Social interactions in our model can be categorized as affiliative (grooming, affiliative signaling and approaching), submissive (leaving, submissive signaling and avoiding) and aggressive (attacking and aggressive signaling) behaviors. Before deciding on which behavior to perform, the potential interaction partners, i.e. the 10 nearest recognizable individuals (within MAX_DIST and ego’s current view angle) are determined. If in total less than 10 recognizable individuals are perceived by ego, then only those group members are taken into account. The decision may further depend on ego’s attitude (FEAR and LIKE) towards these individuals and ego’s general emotional state (arousal, anxiety and satisfaction). The possible behaviors towards each of these 10 (or less) nearest neighbors are each assigned a probability and one behavior (towards one specific interaction partner) is chosen randomly, according to these probabilities (see Submodel Action Selection). Which social interactions can be performed towards a group member depends on the distance towards this individual (see Table S3.4 for an overview). Individuals within INTERACT_DIST (1m) can be groomed, left or attacked. Individuals within PERS_DIST (5m) can receive affiliative, submissive or aggressive signals. Individuals within MAX_DIST (50m) can be approached and individuals within PERS_DIST (5m) can be avoided. Note that individuals within a distance of 1m (INTERACT_DIST) are not approached anew, as they are already in close proximity. Individuals in our model are not able to perform grooming, attack or to send signals towards an individual that is currently executing any movement behavior. However, individuals are still able to move towards or away from such an individual.

Stochasticity

In our model, many processes are not implemented deterministically, but include some degree of stochasticity, to produce variability in those processes. When ego is to perform a behavior, each potential behavior is associated with a certain probability, depending on ego’s emotional state and its emotional attitudes towards the potential interaction partners. During action selection, one of the possible behaviors is randomly selected according to the probabilities. When two individuals engage in an escalated fight (i.e. an attack is followed by a counter-attack), the winner is stochastically determined, depending on its win chance w_{ij} (see Submodel Counter-attack and escalated fight). A higher difference in dominance strength results in a higher win chance for the dominant individual. When executing a random walk, an individual simply moves forward for one step. Before each subsequent step, either a new orientation is chosen randomly or the same orientation is kept. Both options have a probability of 0.5. When ego’s next activation is scheduled, the actual schedule time is drawn from a normal distribution around the appropriate mean value (depending on the context, see Table S3.3) with a standard deviation (SD) of 5%.

Observation

For the analysis of our model, we only used data that were recorded during the last 252 000 time steps of each simulation run, i.e. the last YEAR.

The individuals' level of arousal, anxiety and satisfaction, the level of the dyadic LIKE attitudes and the dyadic proximity scores, were sampled every 3.5 DAYS and then averaged (per individual or dyad, respectively) over one YEAR for each simulation run. The number or duration of dyadic behaviors was recorded per dyad per behavior over each recording interval of 3.5 DAYS and then divided by the duration of the recording interval to obtain average hourly behavioral rates.

The percentage of time spent grooming was recorded per individual and was defined as the total duration of an individual's grooming bouts divided by the total recording time, i.e. one YEAR. The exact durations of all grooming bouts were recorded per individual. The duration of a grooming bout was defined as the time interval an individual continuously engaged in grooming, i.e. gave and/or received grooming without any interruption. Thus, a grooming bout for individual i started whenever it started to groom another individual or started receiving grooming from another individual, given that individual i was not already engaging in grooming before. The grooming bout ended, whenever individual i neither received nor gave any grooming anymore.

Scanning and movement behavior was also executed in bouts, where a bout was defined as the duration of the time interval an individual continuously engaged in scanning or movement, respectively, without any interruption. The exact durations of all scanning and movement bouts were recorded per individual. The percentage of time an individual was employing scanning or movement behavior was then calculated as the total duration of an individual's scanning or movement bouts divided by the total recording time, i.e. one YEAR. The movement bout distance was defined as the distance (in meters) an individual moved during one movement bout. Per individual, all movement bout distances were recorded.

To assess the average dyadic proximity score, i.e. the average rate of being located in each other's proximity, we scored for each individual which other group members were found within close proximity (1m) at the time of sampling using the one-zero sampling technique. Thus per dyad, possible scores were 1 (in proximity) or 0 (not in proximity) per sample. Note, that the dyadic proximity score is by definition a symmetric measure. Per individual this translates into possible scores between 0 (no other group member was in proximity) and 19 (all other group members were in proximity).

Details

Initialization

At the initialization of each simulation run, the x-coordinates and the y-coordinates of the 20 individuals were drawn randomly from a predefined circular sphere with an arbitrary diameter of 50 m. Each individual's initial heading was set to a random orientation between 1° and 360° and the initial view angle was set to 120° for each individual. The dyadic affiliative attitudes (LIKE attitudes) from ego to all other group members were initialized at 0.0. Each individual's level of arousal was set to the default arousal level (0.09) and the level of anxiety and satisfaction was set to 0.0. Initially, the limit values of arousal, anxiety and satisfaction (i.e. the levels that arousal, anxiety or satisfaction will approach over time) were set to the

same values as the initial levels of arousal (0.09), anxiety (0.0) and satisfaction (0.0). However, individuals that perceived any higher-ranking group member, i.e. any group member towards whom they directed a FEAR attitude > 0 , within 5m (PERS_DIST), adjusted their limit values for arousal and anxiety, causing arousal and anxiety to increase over time (see Submodels Arousal and Anxiety for more details). Furthermore, the initial schedule time for each individual was drawn randomly from a normal distribution with a mean of 1 minute and a standard deviation of 0.05 minutes. Table S3.1 summarizes the initial settings.

Submodels

This section describes the main procedures of the EMO-model in more detail and covers the implementation of the emotional state (arousal, anxiety and satisfaction), the partner-specific emotional attitudes (LIKE and FEAR), action selection, perception and signaling, scanning, movement, grouping, resting, grooming and counter-attack and escalated fight.

Arousal In our model, an individual's arousal level, i.e. its responsiveness or activity, increases in response to receiving, executing or observing aggression or when in proximity of a dominant individual. On the other hand, arousal may decrease in response to receiving submissive or affiliative behavior and executing affiliative behavior (see Figure 3.2). To implement arousal in our model, we used an array of empirical heart rate and scratching rate data from different social contexts (e.g. baseline, post-conflict, grooming). This parameterization procedure is described in Text S3.1. In our model arousal level was scaled between 0 (inactive) and 1 (maximum stimulation).

We distinguished between point behaviors, which affect the arousal level instantly, and duration behaviors or social contexts, for which the effect on arousal depends on the duration of a behavior or context. Point behaviors that increase arousal in our model are *Escalated fight observed*, *Attack received*, *Attack given* and *Aggressive signal received*. Point behaviors that decrease arousal levels are *Submissive signal received* and *Affiliative signal received*. The extent of the arousal change depends on the impact of the stimulus (Table S3.5). For instance, receiving an aggressive signal or observing an escalated fight is less arousing than receiving an attack (i.e. contact aggression). Upon several aggressive events arousal gets increased per event and may build up quickly up to the maximum possible arousal level of 1.0 (MAX_AR_LIMIT). Submissive and affiliative signals may decrease increased arousal levels towards the baseline level of 0.09 (DEF_AR_LIMIT), but not below (see Table S3.5).

Duration behaviors that decrease arousal levels in our model are *Grooming received* and *Grooming given*, while *Perceived proximity of a dominant individual* is a social context that increases arousal levels. For the duration of such behaviors or contexts, arousal changes with a constant rate towards a context-specific maximum or minimum level, i.e. a limit value that is approached over time. Whenever such a behavior or context is ended, within a few minutes arousal quickly decreases or increases again back to the baseline level, with the default rate of 0.02/min. Thus, the rate of continuous arousal change and the level that is approached over time depends on the current social context (Table S3.5). For instance, during *Grooming received* arousal decreases faster and towards a lower level compared to the default arousal decrease over time.

Thus, arousal levels change in response to social interactions, which, in turn will affect the individual's state of responsiveness and activity. In this way, arousal regulates social behavior on a short-term timescale. In our model, higher arousal was implemented to result in an increased

probability of performing active behaviors (any behavior except resting) (see Submodel Action Selection) and in an increased probability to employ social vigilance, i.e. scanning behavior (see Submodel Scanning).

Anxiety In our model, anxiety level, i.e. an individual's general *fearfulness* in response to negative stimuli within the current social environment, was scaled between 0 (not anxious, DEF_ANXIETY) and 1 (anxious, MAX_ANXIETY). The level of anxiety in our model gets increased instantaneously in response to negative point behaviors, namely *Receiving* or *Giving an attack*, *Receiving an aggressive signal*, *Losing an (escalated) fight* or *Observing an escalated fight nearby*. The level of anxiety gets decreased instantaneously after positive point behaviors, namely upon *Receiving a submissive or affiliative signal* or after *Winning an (escalated) fight*. After an anxiety increase (e.g. due to received aggression) anxiety decreases again over time with a default linear rate of 0.002/min (DEF_ANX_DEC) towards baseline levels (DEF_ANXIETY). Thus, anxiety is assumed to decrease slower than arousal, i.e. within a few hours. Whenever ego engages in grooming, anxiety levels decrease with faster rates, namely 0.01/min for the groomer (GG_ANX_DEC) and 0.02/min (GR_ANX_DEC) for the groomed individual. Whenever grooming is ended, anxiety decreases with the default rate again. Thus, the extent and the rate of anxiety change depend on the current social context. The exact values and rates of anxiety increase and decrease in our model were chosen arbitrarily and are summarized in Table S3.5. The level of anxiety in turn affects ego's valuation of its own position and potential risk within the current social environment. Higher anxiety levels result in increased probabilities to execute affiliation and submission. Furthermore, aggression probability is generally decreased, but is increased towards much lower-ranking partners, resulting in aggression to be more conservative and risk-avoiding (see Submodel Action Selection for details).

Satisfaction In our model, satisfaction level, i.e. an individual's general *contentedness* in response to positive stimuli within the current social environment, was scaled between 0 (not satisfied, DEF_SATISFACTION) and 1 (satisfied, MAX_SATISFACTION). Whenever ego engages in grooming, satisfaction levels increase with linear rates, namely 0.05/min for the groomer (GG_SAT_INC) and 0.1/min (GR_SAT_INC) for the groomed individual. Whenever grooming had stopped, satisfaction decreases again to baseline level (DEF_SATISFACTION) with a default linear decrease rate of 0.02/min (DEF_SAT_DEC), i.e. within one hour. Thus, the extent and the rate of satisfaction change depend on the current social context. The rates of satisfaction increase and decrease in our model were chosen arbitrarily and are summarized in Table S3.5. The level of satisfaction in turn affects ego's valuation of its own affiliative motivation and need within the current social environment. In our model, higher satisfaction levels result in decreased probabilities of (further) affiliation (see Submodel Action Selection for details).

FEAR attitudes In our model, individuals assign a partner-specific FEAR attitude to each group member. The FEAR attitude resembles the difference in dominance strength between the individual and the respective group member. Although FEAR attitudes are fixed over the course of our simulation and are, thus, not affected by social interactions, they do affect the individual's valuation of its potential aggression risk related to the respective group member. A high FEAR attitude results in decreased probabilities of aggression (i.e. attack, aggressive signal) and increased probabilities of submission (i.e. leaving, submissive signal, avoidance) towards the respective group member (see Submodel Action Selection for details).

FEAR attitudes are calculated from the (known or perceivable) rank distance towards group members as $FEAR_{ij} = myDOM_j - myDOM_i$, where i is the owner of the FEAR attitude, j is the

subject the FEAR attitude is directed to and *myDOM* is the dominance strength of the respective individual. Thus, FEAR attitudes may have values ranging from -0.95 (directed from highest to lowest-ranking individual) to +0.95 (directed from lowest to highest-ranking individual). In other words, while positive FEAR attitudes (FEAR>0.0) are directed towards higher-ranking individuals and represent actual FEAR, negative FEAR attitudes (FEAR<0.0) are directed towards lower-ranking individuals and represent certain superiority. FEAR attitudes are, thus, directional and not symmetric.

LIKE attitudes In the EMO-model, LIKE attitudes are implemented as partner-specific satisfaction levels, as perceived by *ego*. LIKE attitudes are thus not necessarily symmetric between two individuals. LIKE attitudes are dynamic in our model. Upon receiving grooming, the level of an individual's LIKE attitude assigned to the groomer may increase quickly. Thus, $LIKE_{ij}$ reflects individual *i*'s valuation of individual *j*, concerning received affiliation. Several satisfaction responses, associated with several episodes of grooming, are integrated over a certain timeframe. LIKE attitudes slowly decrease over time (within days or weeks), depending on the current level of the LIKE attitude.

Ego has a higher probability to direct affiliative behaviors (i.e. grooming, affiliative signals, approach) towards individuals that it assigned a high LIKE attitude to (LIKEd individuals) than towards group members with low LIKE attitudes (less-LIKEd individuals) (see Submodel: Action Selection for details). In this way, LIKE attitudes may regulate the development and maintenance of partner-specific affiliative relations. In our model we implemented different settings of the degree to which *LIKEd* group members are preferred as affiliation partners over less-LIKEd ones (see Submodel: Action Selection for details).

LIKE attitudes may have values ranging from 0.0 (neutrally valued affiliation partner) to +1.0 (highly valued affiliation partner). The increase of $LIKE_{ij}$ depends on individual *i*'s current increase in satisfaction in response to grooming received exclusively from individual *j*, described by the partner-specific variable $PARTNER_SAT_{ij}$. When receiving grooming from individual *j* $PARTNER_SAT_{ij}$ increases with the same rate as the general satisfaction level is increasing (GR_SAT_INC). When the specific partner stopped grooming, $PARTNER_SAT_{ij}$ decreases with the same rate as the general satisfaction level is decreasing (DEF_SAT_DEC). Thus, $PARTNER_SAT_{ij}$ is by definition lower than or equal to the individual's general satisfaction level ($mySATISFACTION_i$). Whenever an individual is groomed by several partners simultaneously, the full increase in satisfaction level in response to this grooming is assigned to each groomer.

Partner-specific LIKE attitudes are then used to integrate earlier affiliation received from a partner, i.e. the changing level of $PARTNER_SAT_{ij}$ over time. In contrast to $PARTNER_SAT$, LIKE attitudes decrease slowly over time. In this way the emotional response to recent affiliation is "remembered" for a while and updated upon renewed affiliation. The LIKE attitudes are updated as follows:

$$LIKE_{ij}(t_n) = \max \left\{ \frac{LHW * LIKE_{ij}(t_{n-1}) + (t_n - t_{n-1}) * PARTNER_SAT_{ij}(t_n)}{LHW + (t_n - t_{n-1})}, PARTNER_SAT_{ij}(t_n) \right\} \quad (3.1)$$

Here, t_n is the current time, t_{n-1} is the time of the last update and $(t_n - t_{n-1})$ is the time since the last update (in MINUTES). $LIKE_{ij}(t_n)$ is the updated value of the LIKE attitude assigned from individual *i* to *j* and $LIKE_{ij}(t_{n-1})$ is the former level of LIKE to be updated. *LHW* (LIKE-HISTORY

WEIGHT) is a fixed parameter, which describes to which degree the updated LIKE attitude depends on earlier (emotional responses to) affiliation history as opposed to recent (emotional responses to) affiliation. $PARTNER_SAT_{ij}(t_n)$ is the current partner-specific satisfaction level (see above).

Thus, whenever the current level of $PARTNER_SAT_{ij}(t_n)$ exceeds that of $LIKE_{ij}(t_n)$, $LIKE_{ij}$ is instantaneously updated and increased to the same level. Otherwise, the updated level of $LIKE_{ij}(t_n)$ is a weighted combination of the former level of $LIKE_{ij}(t_{n-1})$ and the current level of $PARTNER_SAT_{ij}(t_n)$, where the former LIKE attitude is weighted stronger than the current $PARTNER_SAT$. This was done by setting LHW arbitrarily to 720 MINUTES (1 DAY), while $(t_n - t_{n-1})$ is usually only a few MINUTES. In this way, short-term fluctuations of $PARTNER_SAT$ will only have minor impacts on LIKE, while a certain regularity and quantity of affiliative interactions is necessary to maintain a high LIKE attitude on a more long-term basis.

When no affiliative behavior was received recently from the respective partner j , $PARTNER_SAT_{ij}$ is zero and $LIKE_{ij}$ will slowly decrease over time. Then LHW can be seen as the half-life of LIKE attitudes, which determines the time it takes before the LIKE attitude decreases to half its value. For instance, when individual i has developed a LIKE attitude of $LIKE=0.8$ towards individual j and is afterwards receiving no further affiliation from this individual, $LIKE_{ij}$ will decrease to 0.4 within 1 DAY (LHW=720 MINUTES=1 DAY). In sum, current affiliation received from a partner may quickly increase LIKE and/or maintain a high level of LIKE, while the lack of current affiliation will result in a slowly decreasing LIKE attitude.

Action selection In our model, activated individuals may select one of various possible actions. These actions may be directed to other individuals or may involve resting or random movement within the group.

The probability to execute a specific behavior towards another group member depends on a) the distance of the individual to ego, b) ego's emotional state (arousal, anxiety and satisfaction), c) ego's FEAR and LIKE attitudes directed to the individual and d) the parameter setting of LIKE-PARTNER SELECTIVITY (LPS), i.e. the degree to which LIKE attitudes are important during partner selection. The emotional state facilitates behavior that is appropriate to the individual's position and situation within the social group in general, while emotional attitudes facilitate behavior that is appropriate towards specific group members.

First, the 10 (or less) potential interaction partners are determined. Then the possible behaviors towards each of these individuals are determined dependent on their distance to ego. Finally, the probabilities for the possible behaviors towards each potential interaction partner are calculated. According to these probabilities, one of the possible behavior-partner combinations is randomly selected and executed. The details on the exact calculation of the probabilities for affiliation, aggression, submission and avoidance are described in Text S3.2 and summarized hereafter.

Ego's probability to direct affiliation, i.e. grooming, affiliative signaling and approaching, towards individual j increases with increased $LIKE_{ij}$ (given that $LPS > 0$) and with increased intrinsic affiliation motivation of ego (compare solid, dashed and dotted lines in Figure 3.3A). Ego's intrinsic affiliation motivation increases when satisfaction is low or anxiety is high. LPS is the degree to which LIKE attitudes are of importance for the affiliation probability. At $LPS=0$, the level of $LIKE_{ij}$ has no effect on the affiliation probability (see first panel of Figure 3.3A). The higher LPS, the more the affiliation probability depends on LIKE (see the steeper slopes of the lines at increased LPS in Figure 3.3A).

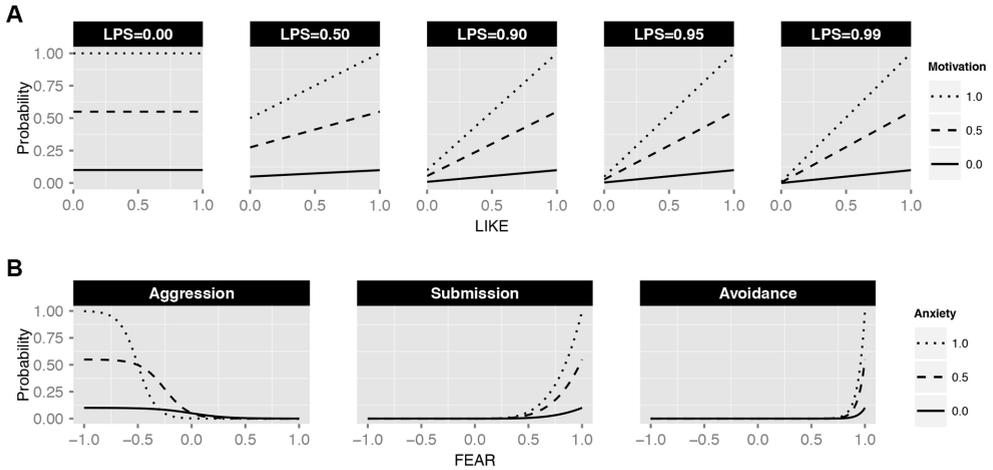


Figure 3.3: Behavioral probability functions. **A:** The upper part of this figure shows the general probability for affiliative behavior as a function of the LIKE attitude of ego towards the potential partner (x-axis), depending on the level of an individual’s intrinsic motivation to perform affiliative behavior (dotted line: high motivation, dashed line: intermediate motivation, solid line: no intrinsic motivation) and on the setting of LPS (see panels). The internal motivation is calculated based on ego’s level of anxiety and satisfaction (see text and equation for myAFF_MOT). Higher LPS results in lower affiliation probabilities for potential partners towards whom ego assigns a low LIKE attitude. Thus, with higher LPS ego becomes more selective and prefers high-LIKE partners relatively more than low-LIKE partners. **B:** The lower part of this figure shows the probability for agonistic behavior as a function of the FEAR attitude of ego towards the potential partner (x-axis), depending on the level of ego’s anxiety (dotted line: high anxiety, dashed line: intermediate anxiety, solid line: no anxiety). The panel shows the specific behavioral probabilities for aggression, submission and avoidance.

Ego’s probability to direct aggression, i.e. attacking and aggressive signaling, towards individual j decreases with increased $FEAR_j$ (see monotonously decreasing curves in the first panel of Figure 3.3B). Moreover, increased anxiety results in the aggression probability to be more conservative or risk avoiding. In other words, at increased anxiety levels, the sigmoid curve is steeper and shifted more to the left (compare solid, dashed and dotted lines in the first panel of Figure 3.3B), resulting in lower aggression probabilities towards high- and similar-ranking individuals, and in higher aggression probabilities towards very low-ranking opponents.

Ego’s probability to direct submission, i.e. leaving and submissive signaling, towards individual j increases with increased $FEAR_j$ and with increased anxiety (compare solid, dashed and dotted lines in the second panel of Figure 3.3B). Ego’s probability to direct avoidance towards individual i is very similar to the submission probability. However, avoidance is only directed towards individuals that are much higher in rank. Hence, the probability only increases when FEAR is very high (compare second and third panel of Figure 3.3B).

Perception and signaling Individuals in our model can individually recognize other group members within a maximum perceivable distance of 50 m (MAX_DIST) and within the currently employed view angle. The view angle is by default 120° (VIEW_ANGLE) or else 360° (MAX_ANGLE) when ego is scanning. Group members within 1m (INTERACT_DIST) are always perceived by ego, even when these individuals are located outside ego’s currently employed view angle.

Moreover, model entities can judge whether at least three other group members are present within 20 m (NEAR_DIST) and within the currently employed view angle. Furthermore, indi-

viduals in our model are capable to judge whether their distance to the furthest group member exceeds 100 m (FAR_DIST). The two latter criteria are used by ego to decide whether grouping behavior should be executed.

When an attack escalates into a fight (i.e. is followed by a counter-attack), other group members within 5 m (PERS_DIST) are able to perceive this behavior, even if this event took place outside of their currently employed view angle, since we assume that escalated fights are accompanied by a lot of noise.

Individuals can also perceive signals, which were (“intentionally”) directed at them from others within 5 m (PERS_DIST). In our model, individuals only direct signals towards others that are also oriented towards them and are thus able to receive the signal. Thus, a sender of a signal is always located within the signal receiver’s currently employed view angle.

Finally, whenever individuals interact with another individual, the visual orientation of the actor and the receiver are set towards each other. Similarly, whenever ego observes an escalated fight nearby, its visual orientation is set towards the salient stimulus, i.e. the counter-attacking individual. If ego (or one of the interacting individuals) was scanning, scanning behavior is stopped whenever attention is attracted by a salient stimulus, i.e. an interaction partner or a counter-attacking individual.

Parameter choices for VIEW_ANGLE, MAX_ANGLE, FAR_DIST, MAX_DIST, NEAR_DIST and PERS_DIST (see Table S3.2) were adapted from earlier ABM on primate social behavior (Hemelrijk, 1998b, 2000; Evers et al., 2011, 2012; Bryson et al., 2007).

Scanning When employing scanning behavior, an individual is turning its head right and left, thus expanding its view angle to 360° (MAX_ANGLE) instead of the default view angle of 120° (VIEW_ANGLE). Whenever a model individual executes movement or an interaction, we assume that its attention is focused on the movement or the interaction partner. Therefore, individuals in our model may not perform scanning behavior simultaneously with a movement or an interaction. Whenever a movement bout or a social interaction has ended, i.e. whenever ego selected resting, ego may decide to execute scanning behavior. Thus scanning may optionally accompany resting behavior. The probability to engage in scanning behavior increases with increased arousal (see Text S3.2 for more details). Moreover, in this model, we implemented scanning as duration behavior. Once ego selected scanning, it stays *in scanning mode* until its next activation.

Movement Concerning movement behavior, individuals in our model may either move towards (approaching, grouping) or away from (fleeing, leaving and avoiding) other group members or they may execute random movement within the group. Individuals in our model move with a constant speed of 0.6 m/s, which is reasonable for macaques (Beisner and Isbell, 2009). In contrast to earlier models (Evers et al., 2011, 2012), movement behavior in the EMO-model takes time and is implemented as movement bouts. After starting a movement bout ego is activated each 3 SECONDS to execute the last movement step and to decide whether movement is to be continued (see Text S3.3 for more technical details). After ending a movement bout ego always performs a proximity update. Ego checks whether any individuals towards which it assigned a positive FEAR attitude (i.e. higher-ranking group members) are now (or still) perceived within 5m (PERS_DIST), as this proximity of a potential aggressor has consequences for the level that ego’s arousal will approach over time (myAROUSAL_LIMIT). Additionally, also

other individuals who assigned a positive FEAR attitude towards ego are updated on ego's new spatial location, which includes potential updating of their myAROUSAL_LIMIT, if necessary.

Note, that in the EMO-model, fleeing, leaving and avoidance behavior are executed in the same way, i.e. ego moves away from a specific group member. What differs between these behaviors is the context in which they are executed. Leaving defines spontaneous movement away from another individual that is in close proximity, i.e. a potential aggressor. Avoiding defines movement away from another individual, i.e. a potential aggressor that is not (yet) in close proximity. Fleeing defines movement away from an opponent after an attack or an escalated fight. This allows us to implement different probabilities, depending on the specific social context.

Grouping Before selecting a social behavior, model entities always check whether grouping should be executed. Grouping will be selected if less than three (MIN_OTHERS) group members are located within 20 m (GROUP_DIST) and 360° (MAX_ANGLE) or whenever any group member is further away from ego than 100 m (FAR_DIST). When grouping is to be performed, ego simply approaches any randomly selected group member. Grouping was implemented in the model to prevent the group from splitting up into subgroups.

Resting In our model, resting behavior is implemented as a duration behavior, which is executed in bouts. When starting a resting bout, ego's next activation is scheduled several minutes later to choose its new behavior. Note, that the actual duration of the resting bout may be longer than this schedule time whenever ego selected to continue resting, and may be shorter, whenever ego got activated before it was scheduled (due to receiving an attack or a signal or due to observing an escalated fight nearby).

Grooming In our model, grooming behavior is implemented as a duration behavior, which is executed in bouts. When starting a grooming bout, ego's next activation is scheduled several minutes later to choose its new behavior. Note, that the actual duration of the grooming bout may be longer than this schedule time whenever ego selected to continue grooming the same individual subsequently. On the other hand the actual duration of the grooming bout may be shorter, whenever ego got activated before it was scheduled, due to receiving an attack or a signal or due to observing an escalated fight nearby. The average schedule time when grooming was set to 7.5 ± 0.375 min (mean \pm SD), which resulted in average grooming bout durations of around 6.6 min, which was reasonable for macaques (Adishesan et al., 2011). See Results: Model validation for more details.

In our model, receiving grooming was implemented to affect the arousal level and the emotional state of the groomed individual. Moreover, model individuals may receive grooming by two or more groomers simultaneously. For such a scenario, we assumed that the number of simultaneous groomers did not affect the impact of grooming on the arousal level and the emotional state of the groomed individual. In other words, whether ego receives a certain amount of grooming by a single or various groomers simultaneously this results in the same update for ego's arousal and emotional state. Grooming also affects the LIKE attitudes associated with other individuals. Here, we assumed that ego's LIKE attitude towards each of several simultaneous groomers is increased with an equal rate as its LIKE towards a single groomer.

Counter-attack and escalated fight Upon receiving an attack the respective model individual is immediately activated to respond with either fleeing or a counter-attack. Moreover, this initial attack immediately increases the anxiety level of the attacked individual. The probability to respond with a counter-attack is calculated using the general aggression probability, which is also used to calculate the probability of a spontaneous attack (see Text S3.3). Thus, due to ego's anxiety increase in response to the initial attack, ego's probability to execute a counter-attack is calculated more conservatively and risk-avoiding compared to ego's probability to attack the opponent without receiving an attack beforehand (see Text S3.3). In other words, an attack from a much lower-ranking opponent increases the probability to counter-attack, while an attack from similar- or higher-ranking opponents decreases the probability to counter-attack.

When a counter-attack was selected in response to an attack, we call this an escalated fight. The winner and loser of such an escalated fight are determined randomly according to the individuals' win chance w_{ij} (cf. Evers et al., 2011):

$$w_{ij} = \frac{1}{1 + e^{\eta * FEAR_{ij}}}. \quad (3.2)$$

When no counter-attack was selected in response to an attack, the attacked individual is defined as the loser and the attacker as the winner of this aggressive interaction. After an attack or an escalated fight, the loser flees from the winner, while the winner is scheduled anew shortly after.

Whenever an escalated fight takes place, individuals nearby get activated, their arousal level gets increased and their attention is focused at the escalated fight. Moreover, these individuals are activated shortly after to enable an appropriate response to the event. Note that besides avoiding the scene, this may also allow for reactions such as third-party affiliation, coalitionary support or contagion of aggression. However, this was not further studied in this paper.

Simulation experiments

In this paper we examined different settings for the parameter LIKE-PARTNER SELECTIVITY (LPS), i.e. the degree to which individuals prefer to affiliate with group members that they assign high LIKE attitudes to. LPS was set to 0.0, 0.5, 0.9, 0.95 or 0.99. LPS = 0.0 resembles a special null model setting. Here, individuals have no preference to select specific affiliation partners concerning LIKE attitudes whatsoever. In other words, individuals do not use LIKE attitudes during affiliative partner selection. Therefore, the null model setting serves as a control setting to assess the effect of the presence of any affiliative partner preference based on emotional bookkeeping. For each setting of LPS, 10 independent simulations were run, resulting in a total of 50 independent simulation runs.

Statistical analysis

We first explain how specific summarized measures were calculated from the recorded data, e.g. how data on dyad level were transformed to obtain measures on individual or (sub-)group level. We continue with the statistics that were used to compare the properties of different subgroups or individual categories. Finally, we explain how we calculated specific group properties, i.e. up/down index, reciprocity and Shannon index, which allowed for quantitative

comparison of our model to empirical data. All statistical analyses were performed in R 2.15.2 (R Core Team, 2012).

Individual proximity scores, strength of LIKE attitudes and behavioral rates were calculated as the sum of all dyadic proximity scores, LIKE attitudes or behavioral rates that an individual directed to others. Group means of behavioral rates were calculated as the mean of all individual behavioral rates. To calculate the mean proximity score, strength of LIKE attitude, emotional states and behavioral rates per rank category, we divided the 20 group members into 10 lower-ranking (subordinates) and 10 higher-ranking (dominants) individuals. We then averaged the individual proximity scores of subordinates or dominants, respectively. Similarly, we averaged the strength of dyadic LIKE attitudes that subordinates or dominants assigned to others, as well as the emotional states and the behavioral rates per subgroup. To calculate the average proximity scores, strength of LIKE attitudes and behavioral rates per rank-distance category, we divided all dyads into two similar-sized groups. Dyads, for which the absolute difference in dominance strength was less than 0.35 were defined as similar-ranking dyads (N=99 for symmetric measures and N=198 for directed measures). Dyads, for which the difference in dominance strength was more than or equal to 0.35 were defined as distant-ranking dyads (N=91 for symmetric measures and N=182 for directed measures). We then averaged the respective dyadic proximity scores, strength of LIKE attitudes and behavioral rates per subgroup.

To assess the effect of rank categories (subordinates and dominants) or rank-distance categories (similar- and distant-ranking dyads) on proximity scores, strength of LIKE attitudes, emotional states and behavioral rates, we compared the mean values per category over all simulation runs. Data were analyzed using paired t tests with the significance level set at 0.05. For instance the mean grooming rate of subordinates in run i was paired with the mean grooming rate of dominants in run i.

To compare our model to empirical data, we calculated the individual up/down index according to de Waal and Luttrell (1989) and Castles et al. (1996) as follows:

$$\text{Individual up/down index}_i = up_i / (up_i + down_i). \quad (3.3)$$

Here, up_i is individual i's rate of a behavior directed to higher-ranking group members, divided by the number of group members that are higher in rank than individual i, while $down_i$ is individual i's rate of a behavior directed to lower-ranking group members, divided by the number of group members that are lower in rank than individual i. This individual up/down index is calculated per individual, except for the lowest- and the highest-ranking group member, and then averaged over those individuals.

To assess the reciprocity of behaviors and LIKE attitudes at the group level we calculated the Kendall's tau row-wise matrix correlation between the dyadic interaction matrix (or the LIKE matrix) and its transposed (Hemelrijk, 1990; de Vries, 1993) using the R software package DyaDA (Leiva et al., 2010).

To assess how evenly individuals distributed their grooming among all potential partners, we calculated the Shannon index (H). This diversity measure has frequently been used in earlier primate research (Castles et al., 1996; Nakamichi and Shizawa, 2003). H of individual i was calculated as:

$$H_i = - \sum_j p_{ij} \log p_{ij}, \quad (3.4)$$

where i is the actor, j are all potential receivers and p_{ij} is the relative proportion of grooming given by the actor i to the j th receiver. We calculated H using the dyadic grooming rates averaged over one YEAR. To compensate for group size, an evenness index was applied to the Shannon index following Buzas and Gibson (1969) as:

$$H_i^* = \frac{e^{H_i}}{N - 1}, \quad (3.5)$$

where N is the group size. H^* describes whether grooming is directed equally often to all possible partners ($H^* = 1$) or only restricted to one partner (H^* approaches 0). H^* was calculated per individual and then averaged over the group.

RESULTS

Below we present the validation of the EMO-model, first describing the behavioral patterns that we aimed to reproduce in our model, and second, describing higher-level patterns that were not explicitly implemented but were emergent properties of our model. Third, we present further patterns that emerged in our model, but of which no empirical data are available yet. These patterns may offer new hypotheses that still have to be validated empirically. Finally, we explain the causation of the patterns in our model and explain the effect of partner selectivity (LPS) on some of these patterns.

Model validation

In Table 3.1, we give an overview of the surveyed empirical data of behavioral patterns, that we aimed to reproduce in our model by tuning a set of model parameters, i.e. the relative action selection probabilities (GG_PROB, AFS_PROB, APP_PROB, ATT_PROB, AGS_PROB, LE_PROB, SS_PROB, AV_PROB, RNDW_PROB and REST_PROB), schedule time when grooming and the chance to end a movement bout (STOP_CHANCE). These parameters were tuned such that the resulting behavioral patterns in our model deviated at most one standard deviation from the mean of the empirical data.

Whenever surveyed empirical data sets distinguished between different types of individuals or different conditions, we confined ourselves to those subsets of data that resembled free-living macaques best using the following criteria. Since relatedness is not implemented in our model, data from non-kin were preferred over data from groups with kin relations. Since we did not implement sex differences into our model, data from mixed-sex groups were preferred over data where only one sex was observed. To ensure a consistent way of data recording individual rates of behavior were preferred over dyad-specific data or data that controlled for the number of available partners. Old groups with stabilized relationships were preferred over recently established groups. Groups from vegetated enclosures or enclosures with grass substrate were preferred over groups from non-vegetated enclosures or enclosures with gravel substrate. If data were only presented for subordinates and dominants, we used the average of both groups to estimate a group mean.

Table 3.1 summarizes the empirical and model data and confirms that the compared measures in our model resemble the empirical data well.

Behavioral measure (Unit)	Empirical Mean \pm SD	Model mean				Species & references for empirical data	
		LPS=0.00	LPS=0.50	LPS=0.90	LPS=0.99		
Grooming given (min/h)	9.2 \pm 8.4	9.9	8.5	7.0	7.0	M. nemestrina (Castles et al., 1996), M. arctoides, M. mulatta (de Waal and Luttrell, 1989), M. fuscata (Majolo et al., 2009)	
Grooming received (min/h)	5.9 \pm 3.5	8.1	7.4	6.4	6.5	M. fascicularis (Shively, 1998)	
Time spent grooming GG+GR (% of time)	19.5 \pm 11.1	28.3	24.8	20.9	21.0	M. mulatta (Bernstein and Mason, 1963a; Southwick, 1967), M. fuscata (Jaman and Huffman, 2008; Maruhashi, 1981), M. fascicularis (Son, 2004), M. sylvanus (Came et al., 2011)	
Grooming bout duration GG+GR (min)	6.6 \pm 5.6	6.3	6.0	5.7	5.7	M. radiata (Adisheshan et al., 2011)	
Approach rate (1/h)	8.8 \pm 8.1	9.7	10.1	9.2	8.1	M. nemestrina (Castles et al., 1996), M. assamensis, M. mulatta (Cooper et al., 2005), M. arctoides, M. mulatta (de Waal and Luttrell, 1989), M. arctoides (Richter et al., 2009)	
Attack rate (1/h)	0.55 \pm 0.87	0.56	0.61	0.68	0.69	M. nemestrina (Castles et al., 1996), M. arctoides (de Waal and Luttrell, 1989; Richter et al., 2009), M. mulatta (de Waal and Luttrell, 1989; Southwick, 1967)	
Aggressive signal (1/h)	1.46 \pm 1.96	0.82	1.01	1.38	1.53	1.83	M. nemestrina (Castles et al., 1996), M. arctoides (de Waal and Luttrell, 1989; Richter et al., 2009), M. mulatta (de Waal and Luttrell, 1989; Southwick, 1967)
Movement bout distance (m)	6.5 \pm 3.5	6.0	5.9	6.1	6.2	6.7	M. mulatta (Beisner and Isbell, 2009)
Time spent scanning (% of time)	4.4 \pm 2.3	4.4	5.1	5.7	5.5	4.2	M. fuscata (Jaman and Huffman, 2008), M. fascicularis (Shively, 1998)
Time spent scanning - dominants (% of time)	2.76	2.34	2.72	3.02	2.98	2.34	M. fascicularis (Shively, 1998)
Time spent scanning - subordinates (% of time)	7.05	6.49	7.44	8.34	8.10	6.09	M. fascicularis (Shively, 1998)

Table 3.1: Model validation and tuned parameters.

Higher-level validation of the model

We investigated whether our model is able to reproduce higher-level patterns from empirical data.

First, we compared the differences in behavioral patterns between subordinates and dominants (for different settings of LPS) in our model with empirical data of macaques. The following differences between dominants and subordinates that have been shown in macaques were also emerging in our model (see Table 3.2 for an overview and references of the empirical studies). Subordinates gave less and received more aggression compared to dominants. Subordinates gave more and received less submission than dominants. Subordinates groomed others more often than dominants. Subordinates were more aroused than dominants and engaged more often in scanning and movement behavior. The only emergent pattern that was not fully consistent with empirical data was the amount of grooming received. While some empirical studies have reported that subordinates received less grooming compared to dominants, other studies have found no significant difference between the amount of received grooming of subordinates and dominants. In our model, low LPS resulted in subordinates receiving less grooming than dominants. However, at high LPS ($LPS \geq 0.9$), this pattern was reversed, as subordinates groomed especially other subordinates at these settings. The causation of this pattern in our model will be explained further below.

Second, we compared the differences in behavioral patterns between similar-ranking and distant-ranking dyads in our model (for different settings of LPS) with empirical data of macaques. The following patterns that have been documented for macaques (Table 3.3) were also emerging in our model. Submissive behaviors were more often directed to distant-ranking than to similar-ranking group members. Affiliative behaviors were more often directed to similar-ranking than to distant-ranking group members. However, note that some studies did not find a significant difference in grooming rates between similar and distant-ranking dyads. Similar-ranking dyads also have been shown to be more often in close proximity than distant-ranked dyads and to have stronger affiliative bonds (as was concluded from the composite sociality index, a measure that involves proximity and grooming rates). Similar-ranking dyads have also been shown to engage more often in aggression than distant-ranked dyads. Our model showed the same pattern considering attacks. However, aggressive signals were only more frequent among similar-ranked dyads than distant ranked dyads, when LPS was high ($LPS = 0.99$). Else the difference was reversed or not significant in our model. Note, that the difference in frequency of aggressive signals was significant, but only very small at low LPS.

Third, we compared some additional group patterns that emerged in our model with empirical data from macaques (Table 3.4). The individual up/down index (de Waal and Luttrell, 1989; Castles et al., 1996) of approach was close to 0.5 in our model as well as in empirical data, suggesting that individuals did not prefer to approach especially individuals higher or lower in rank. The individual up/down index of grooming suggested that grooming was slightly more directed up the hierarchy in the empirical data than in our model. The causation of this pattern in our model will be explained further below. However, the mean values of our model were still within one standard deviation of the mean of the empirical data.

Regarding the reciprocity of grooming at a group level, as measured by Kendall's τ_{uv} , we found that the range of values found in empirical matrices was quite comparable to our model, except when LPS was very high ($LPS = 0.99$). Lastly, the range of the Shannon index of grooming was only comparable to the empirical data when LPS was high enough ($LPS \geq 0.9$). Else the Shannon index of grooming suggested that individuals in our model were distributing grooming more equally compared to empirical data, as the Shannon index was higher in our model than

Behavioral measure	Empirical pattern	Model mean			Species & references for empirical data		
		LPS=0.00	LPS=0.50	LPS=0.90	LPS=0.95	Model mean	Model mean
Aggression							
Aggression given	S < D						M. fascicularis (Shively, 1998; Kaplan et al., 1982; Morgan et al., 2000)
Attacks given	S < D	S < D***	S < D***	S < D***	S < D***	S < D***	M. fascicularis (Kaplan et al., 1982)
Aggressive signal given	S < D	S < D***	S < D***	S < D***	S < D***	S < D***	M. fascicularis (Kaplan et al., 1982)
Aggression received	S > D						M. fascicularis (Shively, 1998; Morgan et al., 2000)
Attacks received		S > D***	S > D***	S > D***	S > D***	S > D***	
Aggressive signal received		S > D***	S > D***	S > D***	S > D***	S > D***	
Submission							
Submission given	S > D						M. fascicularis (Shively, 1998; Morgan et al., 2000)
Leaving given	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. fascicularis (Kaplan et al., 1982)
Submissive signal given	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. fascicularis (Kaplan et al., 1982)
Avoidance given	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. fascicularis (Kaplan et al., 1982)
Submission received	S < D						M. fascicularis (Morgan et al., 2000)
Leaving received		S < D***	S < D***	S < D***	S < D***	S < D***	
Submissive signal received		S < D***	S < D***	S < D***	S < D***	S < D***	
Avoidance received		S < D***	S < D***	S < D***	S < D***	S < D***	
Affiliation							
Grooming given	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. arctoides, M. fuscata (Estrada et al., 1977; Ventura et al., 2006)
Grooming received	S < D; NS	S < D***	S < D***	S > D**	S > D***	S > D***	S < D* : M. fascicularis, M. arctoides, M. fuscata (Estrada et al., 1977; Ventura et al., 2006); Morgan et al., 2000 NS : M. sylvanus, M. radiata, macaca fuscata (Carne et al., 2011; Takahashi and Furuichi, 1998; Sugiyama, 1971)
Other measures							
Arousal	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. fascicularis (Kaplan et al., 1990)
Movement	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. fascicularis (Morgan et al., 2000)
Scanning	S > D	S > D***	S > D***	S > D***	S > D***	S > D***	M. mulatta (Haude et al., 1976; Deaner et al., 2005)

Table 3.2: Differences between subordinates and dominants. This table summarizes the differences between subordinates (S) and dominants (D) documented in the literature, and compares the findings to the patterns emerging in our model at different settings for LPS. The differences between subordinates and dominants in our model were tested with a paired t-test (N=10 simulation runs), using significance levels of 0.05 (*), 0.01 (**) and 0.001 (***). The model findings in **bold** type are contrast to empirical findings.

Behavioral measure	Empirical pattern	Model mean LPS=0.00	Model mean LPS=0.50	Model mean LPS=0.90	Model mean LPS=0.95	Model mean LPS=0.99	Species & references for empirical data
Aggression							
Aggression	S > D	S > D***	<i>M. nigra</i> , <i>M. mulatta</i> (Reed et al., 1997; de Waal, 1991)				
Attacks		S > D***					
Aggressive signal		S < D***	S < D***	S < D***	S < D***	S > D***	
Submission							
Submission	S < D	S < D***	<i>M. mulatta</i> (Judge and de Waal, 1993)				
Leaving		S < D***					
Submissive signal		S < D***					
Avoidance		S < D***					
Affiliation							
Composite sociality index (grooming + proximity)	S > D	S > D***	<i>M. mulatta</i> (Schülke et al., 2013)				
LIKE		S > D***					
PROX	S > D	S > D***	<i>M. mulatta</i> (de Waal, 1991)				
Grooming	S > D; NS	S > D***	<i>S > D</i> : <i>M. mulatta</i> , <i>M. arctoides</i> , <i>M. fuscata</i> (Nakamichi and Shizawa, 2003; Estrada et al., 1977; de Waal and Luttrell, 1986)				
							NS : <i>M. arctoides</i> , <i>M. tonkeana</i> (Cooper et al., 2005; Thierry et al., 1990)
Affiliative signal		S > D***					
Approach	S > D	S > D***	<i>M. mulatta</i> (de Waal, 1991)				

Table 3.3: Differences between similar and distant-ranked dyads. This table summarizes the differences between similar (S) and distant-ranked dyads (D) documented in the literature, and compares the findings to the patterns emerging in our model at different settings for LPS (N=10 simulation runs), using significance levels of 0.05 (*), 0.01 (**), and 0.001 (***). The differences between similar and distant-ranked dyads in our model were tested with a paired t-test. The model findings in **bold** type are contrast to empirical findings.

in empirical data. Interestingly, in the model the τ_{uv} values and the Shannon index of grooming strongly depended on the LPS setting. This will be analyzed more thoroughly in a sequel paper.

Model-generated predictions

We present some additional group-level patterns and differences between dominants and subordinates that emerged in our model. To our knowledge, no empirical data are available yet of these patterns. Therefore, these results (presented in Table 3.5) may serve as predictions from our model and point out which empirical data are still needed to further validate our model.

Our model predicted that subordinates have generally higher levels of anxiety compared to dominants. Moreover, subordinates in our model executed and received approach and affiliative signals more frequently than dominants. Furthermore, individuals assigned higher or more frequent LIKE attitudes to subordinates than to dominants. These patterns are similar (and connected) to the pattern of grooming, another affiliative behavior, found in our model (compare Table 3.2).

For the level of LIKE attitudes that individuals directed to others, and the related level of satisfaction, both of which are affected by received grooming, our model predicted rank-differences that depended on the degree of partner selectivity (LPS). Low LPS resulted in higher LIKE attitudes towards others and higher satisfaction levels for dominants than for subordinates. At high LPS the pattern was reversed and subordinates assigned higher LIKE attitudes to others and had higher satisfaction levels than dominants.

In our model, attacks and aggressive signals were more often directed to lower- than to higher-ranking group members, while affiliative signals were equally often directed to lower- as to higher-ranking group members.

In our model, reciprocity of approaching, affiliative signals and LIKE attitudes strongly depended on the LPS setting, with increased LPS resulting in higher reciprocity. This will be analyzed more thoroughly in a sequel paper.

Causation of rank differences and the effect of partner selectivity

Here, we explain the causation of the patterns of the EMO-model concerning differences between dominants and subordinates in their emotional states (level of arousal, anxiety and satisfaction) and behavioral patterns. We explain the patterns for the null model setting (LPS=0), where LIKE attitudes do not affect the affiliative partner selection of individuals, and assess the effect of increased partner selectivity (LPS). Results are depicted in Figure 3.4, unless indicated otherwise. Note, that in the EMO-model levels of anxiety (and arousal) get increased upon giving, receiving or perceiving aggression, while they decrease upon receiving submissive signals or when engaging in affiliation. On the other hand, levels of satisfaction increase upon engaging in grooming.

LPS, i.e. partner selectivity, determined the degree to which individuals preferred to selectively affiliate with partners that were assigned a high LIKE attitude. In the null model setting (LPS=0), where individuals had no preference for specific affiliative partners, interaction patterns were mainly driven by the dominance relations in the group. Individuals avoided mainly distant-ranking group members (Table 3.3), resulting in higher proximity scores and affiliation

Behavioral measure	Empirical Mean \pm SD	Model mean					Species & references for empirical data
		LPS=0.00	LPS=0.50	LPS=0.90	LPS=0.95	LPS=0.99	
Individual up/down index							
Approach	0.44 \pm 0.11	0.49	0.45	0.44	0.44	0.45	<i>M. arctoides</i> , <i>M. mulatta</i> , <i>M. nemestrina</i> (de Waal and Luttrell, 1989; Castles et al., 1996; Richter et al., 2009)
Grooming	0.8 \pm 0.34	0.62	0.58	0.55	0.54	0.53	<i>M. arctoides</i> (Richter et al., 2009)
Reciprocity Kendall $\tau_{b,rs}$							
Grooming	0.41 \pm 0.23 (Range: -0.02 - 0.74)	-0.10	0.39	0.66	0.73	0.84	<i>M. fuscata</i> , <i>M. arctoides</i> , <i>M. fascicularis</i> (Estrada et al., 1977; Ventura et al., 2006; Mehlman and Chapais, 1988; Butovskaya et al., 1994, 1995)
Shannon index							
Grooming	0.52 \pm 0.19 (Range: 0.30 - 0.86)	0.96	0.91	0.80	0.73	0.51	<i>M. fuscata</i> , <i>M. mulatta</i> , <i>M. assamensis</i> , <i>M. nigra</i> , <i>M. thibetana</i> (Cooper et al., 2005; Nakamichi and Shizawa, 2003; Berman et al., 2008; Duboseq et al., 2013)

Table 3. 4: Group patterns. This table summarizes some additional group patterns documented in the literature, and compares the findings to the patterns emerging in our model at different settings for LPS. The model findings in **bold** type are contrast to empirical findings.

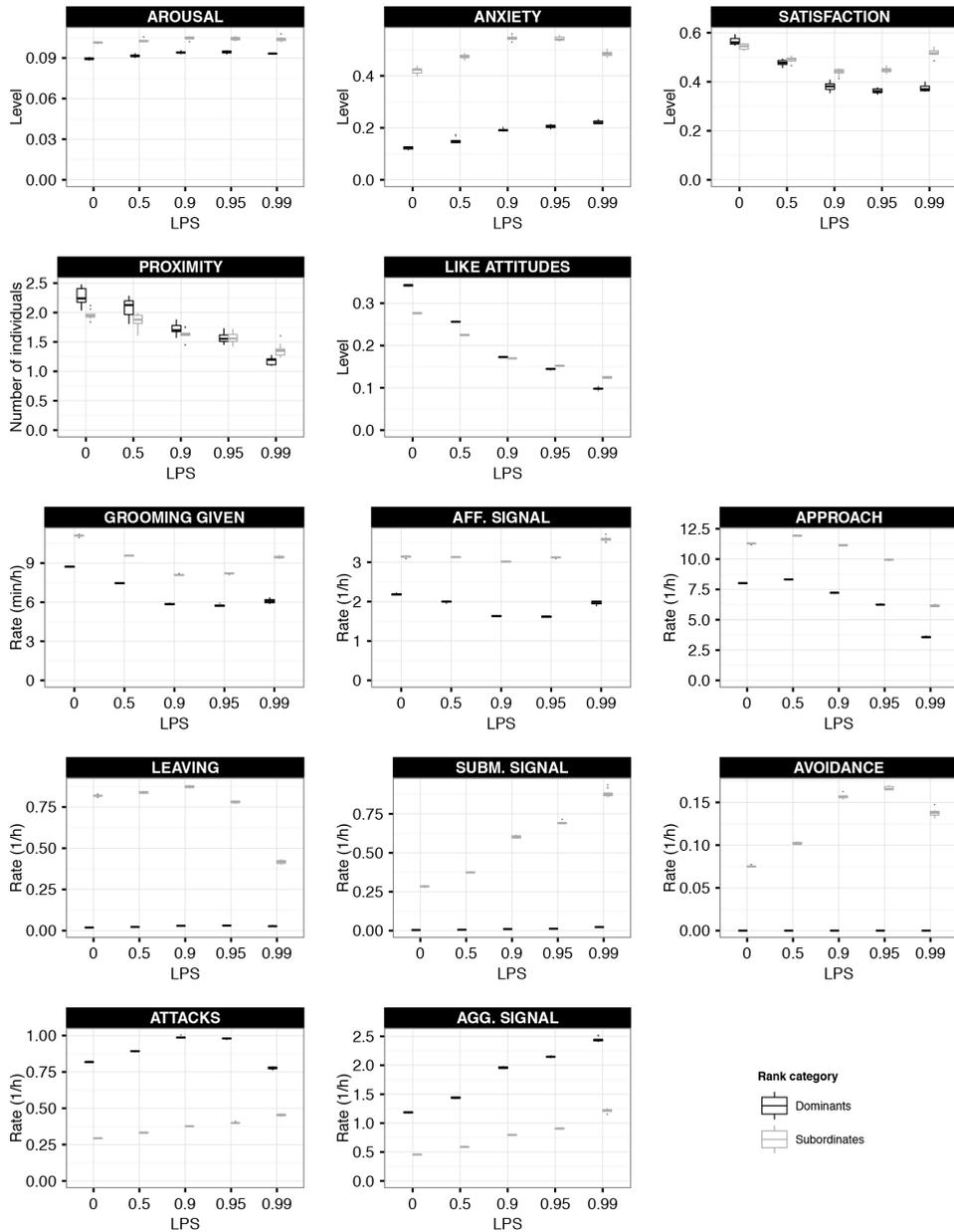


Figure 3.4: Emotional levels and behavioral rates per rank category. This figure shows the averaged levels of the emotional state and rates of behavior for dominants (black box-plots) and subordinates (grey box-plots) at different settings of selectivity (LPS). Proximity is measured as the average number of individuals in proximity. The LIKE attitudes were measured as the average level of all dyadic LIKE attitudes an (subordinate or dominant) individual directed to other group members. Grooming given is measured in MINUTES per HOUR per individual. Signals, approach, leaving, avoid and attacks are measured in occurrences per hour given per individual. Levels of arousal, anxiety and satisfaction levels were averaged per individual. The box-plots show the results of 10 simulation runs, averaged over 1 YEAR.

Behavioral measure	Model mean LPS=0.00	Model mean LPS=0.50	Model mean LPS=0.90	Model mean LPS=0.95	Model mean LPS=0.99
Differences between subordinates and dominants					
Affiliative signal given	Sub > Dom***				
Affiliative signal received	Sub > Dom***				
Approach given	Sub > Dom***				
Approach received	Sub > Dom***				
Anxiety	Sub > Dom***				
Satisfaction	Sub < Dom**	Sub > Dom*	Sub > Dom***	Sub > Dom***	Sub > Dom***
LIKE given	Sub < Dom***	Sub < Dom***	Sub < Dom***	Sub > Dom***	Sub > Dom***
LIKE received	Sub > Dom***				
Individual up/down index					
Attack	0.23	0.22	0.21	0.21	0.24
Aggressive signal	0.15	0.15	0.15	0.15	0.18
Affiliative signal	0.48	0.47	0.47	0.48	0.51
Reciprocity Kendall tau_{rw}					
Approach	0.48	0.68	0.83	0.87	0.90
Affiliative signal	0.35	0.55	0.70	0.76	0.84
LIKE	-0.10	0.43	0.71	0.79	0.90

Table 3.5: Predicted patterns emergent from our model. This table summarizes the emergent patterns from our model (for different settings of LPS), for which empirical data are still needed. The differences between subordinates (Sub) and dominants (Dom) in our model were tested with a paired t-test (N=10 simulation runs), using significance levels of 0.05 (*), 0.01 (**) and 0.001 (***).

rates among similar-ranked than among distant-ranked dyads (Table 3.3). At LPS>0, affiliation feeds back onto the LIKE attitudes. LIKE attitudes decrease towards partners that do not groom an individual regularly enough (i.e. distant-ranking group members), while they are maintained towards regular groomers (i.e. similar-ranking group members). At increased LPS, this differentiation in LIKE attitudes gets reinforced, as individuals almost exclusively groom regular groomers. This is also reflected in the Shannon index of grooming, which decreases at increased LPS (Table 3.4).

In our model, subordinates always had higher levels of arousal and anxiety than dominants, independently of the setting of LPS. Lower win chances of subordinates were explicitly implemented in our model. As a result, subordinates received aggression more frequently than dominants. At increased LPS, anxiety levels, and to a smaller extent also arousal levels, were generally increased for both, subordinates and dominants. This was mostly a result of generally increased aggression rates (see also below). Only at high LPS (LPS>0.9), subordinates' levels of anxiety decreased again due to increased rates of affiliation in these settings (see also below). In the null model setting (LPS=0), dominants had slightly higher satisfaction levels than subordinates, as they received more grooming than subordinates (see Table 3.2). At increased LPS, satisfaction levels first decreased (due to more selective affiliation at high LPS), and this decrease was stronger for dominants than for subordinates. At high LPS (LPS>0.9) subordinates' satisfaction levels increased again. This is explained below.

Proximity indices and the values of LIKE attitudes were always quite similar for dominants

and subordinates and they generally decreased at increased LPS due to more selective, i.e. decreased, affiliation. While at low LPS ($LPS \leq 0.5$) dominants had slightly higher proximity scores and directed higher average LIKE attitudes to others than subordinates, this was reversed at maximum LPS ($LPS = 0.99$). Note, that in the null model setting we measured the (hypothetical) LIKE attitudes resulting from received affiliation. However, individuals did not use this information in this setting. Hence, LIKE attitudes (i.e. emotional bookkeeping) had no effect on any of the behavioral patterns in the null model setting.

At low LPS, affiliative behaviors were slightly more directed up the hierarchy (Table 3.4) resulting in dominants receiving more affiliation than subordinates (Table 3.2) and therefore directing higher LIKE attitudes to others and being more often in proximity to others compared to subordinates. At increased LPS, affiliative behaviors were more reciprocated and more restricted to fewer (similar-ranking) individuals (Table 3.4 and 3.5). Additionally, subordinates still had higher anxiety levels than dominants. The resulting higher affiliation rates of subordinates were almost exclusively directed at other subordinates at high LPS, causing subordinates to have slightly higher proximity values, to direct slightly higher LIKE attitudes to other (mostly also subordinate) group members and to have higher satisfaction levels than dominants.

As subordinates always had higher anxiety levels than dominants, they always engaged more frequently in affiliative behaviors (grooming, affiliative signals, approach) than dominants, independently of the setting of LPS. At increased LPS, approach rates generally decreased for all individuals due to more selective affiliative partner choice, which also affected whom to approach. Also, grooming and affiliative signals first decreased for all individuals (due to more selective partner choice), but increased again at high LPS ($LPS \geq 0.9$). Only at high LPS, the affiliative partner selectivity was strong enough for individuals to develop and maintain LIKE attitudes towards a few preferred partners that were high enough to increase affiliation rates such that the decrease of affiliation due to selectivity was counteracted. The decrease of affiliation at increased LPS and the increase at still higher LPS was also reflected in the satisfaction levels. Moreover, the more frequent affiliation among subordinates than dominants at high LPS was also reflected in the decrease in anxiety levels for subordinates.

Dominants always engaged more often in aggressive behaviors (attack, aggressive signals) than subordinates, independently of the setting of LPS, due to their higher rank and thus their higher chance of winning. At increased LPS, aggression rates for both, subordinates and dominants, generally increased, except for the dominants at maximum LPS ($LPS = 0.99$). This was a result of more selective affiliation at increased LPS, which resulted in decreased affiliation rates, increased anxiety levels and individuals being more often in proximity of similar-ranking than distant-ranking individuals. Moreover, the probability to direct aggression towards similar-ranking is usually higher than towards distant-ranking individuals, except when ego itself was very high-ranking. Therefore, at maximum LPS ($LPS = 0.99$) attack rates decreased again for dominants, as their opponents were now more similar-ranking, which resulted in lower win chances and, thus, lower probabilities to attack.

Submissive behaviors (leaving, submissive signals, avoidance) were almost exclusively executed by subordinates, as these behaviors were implemented as strictly unidirectional behaviors in our model. Additionally, this was a result of subordinates having generally higher levels of anxiety due to their losing of fights and receiving of aggressive signals. At increased LPS, rates of submissive signals and avoidance increased for subordinates due to their increased levels of anxiety. At maximum LPS ($LPS = 0.99$) avoidance rates decreased again for subordinates due to selective proximity towards similar-ranking individuals. Similarly, rates of leaving decreased at high LPS ($LPS > 0.9$) due to selective proximity towards similar-ranking individuals.

DISCUSSION

In this paper, we presented the EMO-model, i.e. the first agent-based model that explicitly incorporates the interrelations between primate social behavior, emotional processes and emotional bookkeeping of affiliative relationships. We integrated an array of empirical data and several partial hypotheses (on general macaque behavior, animal emotions, the two-dimensionality of the emotional system and emotional book-keeping), to obtain an explicitly formulated hypothesis, about how emotional processes may regulate primate social behavior and mediate affiliative relationships (Aureli and Schino, 2004; Aureli and Schaffner, 2002). We succeeded in producing a representative model that also generated many structural properties of real macaque groups on multiple levels. While general behavioral frequencies in the model were tuned to empirical data, group-level patterns arose as a result from the incorporated underlying processes without being explicitly implemented into the model. This multi-level validity of our model suggests that the implemented causal relations between processes are plausible (Grimm, 2005).

Substantiation of the model

While developing the EMO-model we aimed to base each emotional and behavioral process implemented in the model on empirical data. In many respects we succeeded in doing so, but not in all. Yet, to be of value to empirical research, simulation models should be well grounded in empirical data.

We were able to use empirical data on macaques to determine an array of parameter settings of the model entities, such as the active (non-sleeping) time of a day, the distance at which individuals may interact physically, the percentage of time spent grooming or scanning, the duration (minutes) of grooming bouts, the movement bout distance (in meters) and the speed with which individuals move. Based on empirical data, we assumed a stable hierarchy. Moreover, we were able to construct an arousal measure and its dynamics from empirical heart rate and scratching data. However, more data, ideally measured simultaneously during a specific social context, would allow a more reliable comparison and transformation between heart rate and scratching rate data. Ample knowledge was acquired about how arousal levels may differentially increase or decrease in response to received, given or observed behaviors, such as aggression, grooming and perceiving a dominant individual in proximity, as well as how arousal may decrease over time accompanied by affiliation or not. Based on empirical data, we assumed that increased arousal level results in increased social vigilance (scanning) and activity. However, more quantitative data in macaques are needed to substantiate this.

For some parts of our model, parameter settings and processes were based on an educated guess or adapted from comparable modeling studies, since we were unable to find relevant empirical studies. This concerned settings for some general parameters, such as the width of the default field of view of macaques, quantitative activation or reaction times in specific contexts, the number of potential interaction partners taken into account during action selection and the distances at which group members may be perceived, recognized, avoided or signaled to. This also concerned the implemented order of decisions in the decision tree during action selection, grouping criteria and the implementation of the win chance. Moreover, no empirical data were available to validate the unidirectionality of avoidance or leaving. However, as submissive signals were found to be unidirectional, this seemed a plausible assumption.

Quantitative data on how arousal levels may differentially increase or decrease in response to particular received, given or observed behaviors are still needed to further substantiate

our EMO-model. This concerns the qualitative impact on arousal of observing aggression and receiving submissive or affiliative signals, as well as the quantitative increase or decrease specific to the social behavior and context, how it depends on the intensity and frequency of the behaviors and the question whether there are indeed context-specific minima/maxima of arousal level.

A few behavioral or physiological traits have been defined as immediate and quantitative markers of negative or positive emotional state (anxiety/satisfaction). However, a positive emotional state is often measured rather in terms of the absence or decrease of negative measures, e.g. stress indicators (Boissy et al., 2007; Held and Tpinka, 2011) and measures of a negative emotional state, such as heart rate and scratching rate, often primarily reflect arousal instead of valence (Boissy et al., 2007). Quantitative measures of the emotional state, which can be distinguished from arousal, would allow a more quantitative substantiation of our model concerning the dynamics of anxiety and satisfaction in response to (social) behavior.

Specifically, the importance of anxiety and satisfaction with respect to the affiliation motivation is yet unclear. In our model, anxiety determines affiliation motivation to a stronger degree than satisfaction. This seemed a reasonable assumption, as we assumed that to decrease anxiety (e.g. in response to received aggression) should have a higher priority than to increase satisfaction (in response to the lack of recent grooming). This anxiety-driven grooming in our model leads to extensive grooming among subordinates and much less grooming in dominants.

Validation of the model

Our model represents a plausible framework of emotional regulation of social behavior and affiliative relationships in macaques. While we tuned our model to reproduce general behavioral frequencies that match empirical data of macaques, the model also yielded higher-level patterns similar to macaque groups without explicitly implementing them. Higher-level patterns that match the empirical data strengthen the validity of our model, as those patterns were not intended to be reproduced by the model, but emerged from the complex interactions of the model entities.

In total, we have compared an array of 30 emergent model properties, i.e. differences between subordinates and dominants, differences between similar and distant-ranked dyads and some additional group-level properties, to empirical data. Most of the model patterns were consistent with empirical data. Four of the 30 behavioral patterns in our model were only partially validated and depended on the specific parameter setting of LPS (LIKE-PARTNER SELECTIVITY), i.e. the degree of the preference for *LIKEd* affiliation partners. This concerned differences in aggressive signaling between similar and distant-ranked dyads, rank differences in received grooming, as well as reciprocity and distribution of grooming.

However, inconsistent differences in aggressive signaling between similar and distant-ranked dyads were only very small in these settings and the causality of the unsupported rank differences in received grooming could be explained within our model (see Results). The strong dependence of reciprocity and distribution of grooming on the LPS parameter will be analyzed further in a sequel paper.

In sum, most of the emergent behavioral patterns in our model are consistent with empirical data. While we did not achieve a complete validation of all model patterns, we succeeded in developing a model implementation of emotional bookkeeping, which reproduces social

behavioral patterns of macaques sufficiently and specifically allows us to understand how these patterns are affected by the degree of LPS.

Moreover, some additional behavioral patterns were not available from empirical data, but are consistent with measures of related phenomena. The individual up/down indices in our model suggest that attacks and aggressive signals are more often directed to lower- than to higher-ranking group members. This seems consistent with empirical data that suggest higher aggression rates for similar-ranking dyads compared to distant-ranking ones. Furthermore, approaching was very symmetric in our model. This seems consistent with the individual up/down index found in empirical data.

One may criticize our choice to ignore sex differences and to use data of various macaque species for the validation of our EMO-model. Sex ratio within a group may affect the group dynamics and we are aware of the fact that different macaque species show considerable behavioral diversity, for instance concerning the steepness of their hierarchy. There has been already a lot of effort to study this theoretically (Hemelrijk, 1999a; Puga-Gonzalez et al., 2009; Hemelrijk et al., 2008). We consider these topics outside of the scope of the current study, yet they are worth to be addressed in the future. We do not pursue to fit our model to one specific macaque species. Instead, we aimed to produce a qualitative model, inspired by macaques, to understand the emotional regulation of behavior and emotional bookkeeping. Since the general mechanisms underlying the emotional framework are not expected to differ considerably between macaque species or sexes, we deem our approach valid.

Model-based predictions

Our model yielded results that may pinpoint gaps in the empirical data and in the theoretical understanding of the underlying mechanisms. All model-based predictions, i.e. rank-differences in anxiety, satisfaction, giving and receiving of approach, affiliative signals, LIKE attitudes, the direction of attacks, aggressive and affiliative signals and the reciprocity of approach, affiliative signals and LIKE attitudes are connected to patterns of grooming and aggression found in our model and are consistent with these dynamics within our model. Yet, empirical data are still needed to verify these patterns.

Interestingly, our model predicted that the reciprocity of LIKE attitudes and affiliative behaviors, i.e. grooming, affiliative signals and approach, was enhanced at increased partner selectivity. This suggests that emotional bookkeeping may affect reciprocal affiliative relationships to a great degree. This will be explored more thoroughly in our model in a sequel paper. LIKE attitudes, i.e. the internal representation of the differential valuation of grooming partners, cannot easily be assessed quantitatively in real animals. Similarly, the degree of affiliative partner selectivity (LPS), and thus its effect on reciprocity of LIKE attitudes, is a theoretical construct that is tied to the concept of LIKE attitudes, which makes it difficult to assess this in real animals.

Further directions

As our model presents an initial attempt to integrate emotional processes and primate social behavior, several processes of the emotional dynamics implemented in this model may be subject to refinement or improvement.

For instance, in the current EMO-model LIKE attitudes quickly increase in response to grooming, and slowly decrease, integrating the recent history of LIKE (and thus earlier grooming). However, the updating of LIKE attitudes may also be directly dependent on the current level of the LIKE attitudes. Some researchers recently have reported long-term, but not necessarily short-term, reciprocity in primates (Jaeggi et al., 2013; Schino et al., 2007a). Thus, in established relationships (internally represented by high LIKE attitudes), renewed grooming, or especially the lack of it, may have less impact compared to newly developing relationships (internally represented by low LIKE attitudes). On the other hand, in recent research on chimpanzees, higher oxytocin levels have been found after grooming with bond partners than after grooming with non-bond partners (Crockford et al., 2013). Thus, in contrast to the first suggestion, grooming with established bond partners (assigned a high LIKE attitude) might be more rewarding than grooming with non-bond partners.

Given that empirical data are not consistent with the rank-dependent patterns of received affiliation in our model, the model may be partially adjusted to represent the empirical data better. We suggest that a possible starting point might be to more carefully study the importance of anxiety and satisfaction with respect to the affiliation motivation. This should be done empirically, but further exploration of our model with adjusted settings also promises to yield valuable insights. In the current EMO-model, anxiety determines affiliation motivation to a stronger degree than satisfaction, i.e. anxiety is weighted nine times higher than satisfaction. Exploring our model with more similar weighting factors for anxiety and satisfaction in the calculation of the affiliation motivation may yield more plausible simulation results.

Moreover, our model may be extended by further mechanisms. For instance, in the current model, the hierarchy and the FEAR attitudes were fixed and assumed to be stable. An earlier model, GrooFiWorld (Puga-Gonzalez et al., 2009), implemented a dynamic dominance hierarchy, as well as agonistic and affiliative behavior. Interestingly, this model generated similar emergent patterns, whether the dominance hierarchy was dynamic or stable. Yet, the GrooFiWorld model did not implement LIKE attitudes or any emotional regulation of dynamic dominance ranks. In our EMO-model, FEAR attitudes may be implemented in a dynamic way by integrating the anxiety that was caused by aggression received from a specific group member or by fights that were lost from that individual. As FEAR attitudes in turn affect the future agonistic behavior, this is expected to reinforce the differentiation in FEAR attitudes. How dynamic FEAR attitudes may affect the development and maintenance of LIKE attitudes and vice versa, is interesting to study and may offer new hypotheses for the relation between affiliative and agonistic relationships in macaques. For instance, it is still unclear whether agonistic relationships restrict affiliative relationships, or whether the same partner may for example be assigned a high LIKE and a FEAR attitude simultaneously.

A limitation of the current model is that LIKE attitudes are only affected by grooming. A central aspect of the emotional bookkeeping hypothesis and of general research on emotional processes is that different social interactions may be integrated into a common currency. Our model may be extended by the possibility that also agonistic interactions, such as agonistic support, may affect LIKE. This may result in LIKE attitudes (and resulting grooming) that are directed up the hierarchy, a pattern that is still problematic in the current model, and in an exchange of grooming and support. Nonetheless, the model presented in this paper serves as a starting point to study the emotional regulation of social processes theoretically and may offer a promising framework to study the complex dynamics of social relationships. The model allows the exploration of how affiliative relationships may be developed and maintained. It will be interesting to study the differentiation and structure of affiliative relationships within the group, and how these patterns depend on certain crucial parameters. Lastly, this model

allows the exploration of emotional bookkeeping and its consequences for the duration and stability of social bonds. For instance, it has been proposed that emotional bookkeeping, which integrates earlier partner-specific episodes over a long term, may result in long-term but not necessarily short-term reciprocity of affiliative behavior (Jaeggi et al., 2013; Schino et al., 2007a). Moreover, complex behavioral patterns such as reconciliation, redirection, reciprocity, behavioral contagion or coalitions may emerge in our model and may be explained in terms of the underlying emotional regulation.

The EMO-model will be used in future studies to investigate the effect of two key parameters, LHW (LIKE-HISTORY WEIGHT) and LPS (LIKE-PARTNER SELECTIVITY) on affiliation patterns. LHW determines the extent to which earlier, as opposed to recent, affiliative episodes are integrated into the valuation of affiliation partners via LIKE attitudes. LPS determines the degree to which “valuable” affiliative partners, i.e. partners that are assigned high LIKE attitudes, are preferred as affiliation partners. Exploring the EMO-model for different settings of LHW and LPS will give further insights on the plausible timeframe of emotional bookkeeping and the degree of partner selectivity, necessary for the emergence of long-term reciprocal, individual-specific affiliative relationships.

Conclusion

The EMO-model assumes that patterns in social behavior may result from two emotional dimensions, anxiety and satisfaction, that form an individual’s current emotional state, in combination with individual-specific FEAR and LIKE attitudes stored in the individual’s social memory due to earlier interactions. Modeling two emotional dimensions mimics at least part of the empirical complexity and these particular emotional dimensions represent two fundamentally different and important emotions. By modeling two emotional dimensions, we chose not to search for the simplest rules generating social complexity, but chose to explore realistic rules and their interactive effects on social patterns. The EMO-model generates several emergent patterns at group level that are consistent with empirical data, in particular in macaques, and some new patterns. This suggests that a (more) realistic representation with emotions of different valence guiding social interactions can yield emergent patterns in behavior. This research tool will allow the disentangling of the organizing effects of the two different emotions anxiety-FEAR and satisfaction-LIKE on sociality.

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SUPPLEMENTARY MATERIAL

State Variable Name	Description	(Initial) Value	Possible Range or Values	Fixed/ Dynamic
General state variables				
<i>myTIME</i>	Waiting time until next scheduled activation	1 ± 0.05 min (mean \pm SD)	May range between 0.0 (attack received) and 7.5 ± 0.375 min (rest/groom) (depending on the social context)	Dynamic
<i>myDOM</i>	Dominance strength	Between $1/N$ and 1.0	Scaled between $1/N$ (lowest-ranking) and 1.0 (highest-ranking)	Fixed
<i>mySCAN_PROB</i>	Probability of employing scanning	Depends on arousal and current behavior	May range between 0.0 and 1.0 (depending on arousal and current behavior)	Dynamic
<i>myVIEW_ANGLE</i>	Width of currently employed view angle	120°	May be either 120° (not scanning) or 360° (scanning)	Dynamic
Emotional state variables				
<i>myAROUSAL</i>	Arousal state	0.09	May range between 0.0 (inactive) and 1.0 (aroused)	Dynamic
<i>mySATISFACTION</i>	Affiliation-related emotional state	0	May range between 0.0 (unsatisfied) and 1.0 (satisfied)	Dynamic
<i>myANXIETY</i>	Agonism-related emotional state	0	May range between 0 (not anxious) and 1 (anxious)	Dynamic
<i>myAROUSAL_LIMIT</i>	Arousal level that is approached over time	0.09	May be 0.03 (grooming received), 0.04 (grooming given), 0.09 (default), 0.12 (dominant perceived), 1.0 (aggression)	Dynamic
<i>myANXIETY_LIMIT</i>	Anxiety level that is approached over time	0	May be 0.0 (not anxious) or 1.0 (anxious)	Dynamic
<i>mySATISFACTION_LIMIT</i>	Satisfaction level that is approached over time	0	May be 0.0 (not satisfied) or 1.0 (satisfied)	Dynamic
Emotional attitude variables				
<i>FEAR_{ij}</i>	Agonism-related emotional attitude from individual <i>i</i> to <i>j</i>	$myDOM_j - myDOM_i$	$myDOM_j - myDOM_i$	Fixed
<i>LIKE_{ij}</i>	Affiliation-related emotional attitude from individual <i>i</i> to <i>j</i>	0	May range between 0 (neutral) and 1 (preferred affiliation partner)	Dynamic

Table S3.1: Individual-specific state variables of the model entities.

Parameter	Description	Value
General parameters		
<i>N</i>	Number of individuals in the group	20
<i>D</i>	Grid unit	1 m
<i>FIELD_SIZE</i>	Field size	300 x 300 m
<i>MINUTE</i>	Time step	1 min
<i>HOUR</i>	1 hour	60 MINUTES
<i>DAY</i>	1 day	12 HOURS
<i>WEEK</i>	1 week	7 DAYS
<i>YEAR</i>	1 year	50 WEEKS
Sensing parameters		
<i>VIEW_ANGLE</i>	Default view angle	120°
<i>MAX_ANGLE</i>	View angle when scanning	360°
<i>FAR_DIST</i>	Maximum tolerated distance to furthest group member	100 m
<i>MAX_DIST</i>	Maximum distance to individually recognize group members	50 m
<i>NEAR_DIST</i>	Maximum preferred distance to the group	20 m
<i>PERS_DIST</i>	Maximum distance to perceive signals or escalated fights	5 m
<i>INTERACT_DIST</i>	Maximum distance to physically interact with others	1 m
<i>MIN_OTHERS</i>	Minimum preferred number of conspecifics within <i>NEAR_DIST</i>	3
Movement parameters		
<i>SPEED</i>	Movement speed	0.6 m/s
<i>STOP_CHANCE</i>	Probability of ending the current movement bout	0.1

Table S3.2: General model parameters.

Behavior	Schedule time (mean ± SD)
ATTACK received	0.0 sec
Escalated FIGHT observed / SIGNAL received	0.1 ± 0.005 sec
Movement (LEAVE, FLEE, AVOID, APPROACH, RANDOM WALK)	3 sec
FIGHT won / ATTACK given / SIGNAL given	1 ± 0.05 min
GROOMING given / REST	7.5 ± 0.375 min

Table S3.3: Schedule times depending on performed, received or observed behavior.

Interaction category	< 1m	< 5m	> 1m
Affiliation	GROOM	AFFILIATIVE SIGNAL	APPROACH (< 50m)
Submission	LEAVE	SUBMISSIVE SIGNAL	AVOID (< 5m)
Aggression	ATTACK	AGGRESSIVE SIGNAL	

Table S3.4: Experimental set-up and characteristics of the compared models.

Behavior	Change of arousal, anxiety or satisfaction level in the model	Parameter name
Behaviors affecting arousal level		
Escalated fight observed	+ 0.04	<i>EFO_AR_INC</i>
Aggressive signal received	+ 0.04	<i>ASR_AR_INC</i>
Attack given	+ 0.04	<i>AG_AR_INC</i>
Attack received	+ 0.08	<i>AR_AR_INC</i>
Affiliative signal received	- 0.04	<i>AS_AR_DEC</i>
Submissive signal received	- 0.04	<i>SS_AR_DEC</i>
Default decrease	- 0.02 / min	<i>DEF_AR_DEC</i>
Default increase	+ 0.02 / min	<i>DEF_AR_INC</i>
Proximity of dominant	+ 0.02 / min	<i>PD_AR_INC</i>
Grooming given	- 0.02 / min	<i>GG_AR_DEC</i>
Grooming received	- 0.04 / min	<i>GR_AR_DEC</i>
Behaviors affecting anxiety level		
Escalated fight observed	+ 0.2	<i>EFO_ANX_INC</i>
Aggressive signal received	+ 0.2	<i>ASR_ANX_INC</i>
Attack given	+ 0.2	<i>AG_ANX_INC</i>
Attack received	+ 0.4	<i>AR_ANX_INC</i>
(Escalated) fight lost	+ 0.4	<i>EFL_ANX_INC</i>
Affiliative signal received	- 0.2	<i>ASR_ANX_DEC</i>
Submissive signal received	- 0.2	<i>SSR_ANX_DEC</i>
(Escalated) fight won	- 0.4	<i>EFW_ANX_DEC</i>
Default anxiety decrease rate	- 0.002/min	<i>DEF_ANX_DEC</i>
Anxiety decrease rate when giving grooming	- 0.01/min	<i>GG_ANX_DEC</i>
Anxiety decrease rate when receiving grooming	- 0.02/min	<i>GR_ANX_DEC</i>
Behaviors affecting satisfaction level		
Satisfaction increase rate when giving grooming	+ 0.05/min	<i>GG_SAT_INC</i>
Satisfaction increase rate when receiving grooming	+ 0.10/min	<i>GR_SAT_INC</i>
Default satisfaction decrease rate	- 0.02/min	<i>DEF_SAT_DEC</i>

Table S3.5: Effect of social behaviors on arousal, anxiety and satisfaction levels.

Text S3.1: Parameterization of arousal

To implement arousal in our model, we constructed a measure based on an array of empirical heart rate (HR) and scratching rate (SR) data from different social contexts (e.g. baseline, post-conflict, grooming). The average baseline HR in macaques described in the literature was 141.1 bpm (Boccia et al., 1989; Manuck et al., 1989, 1983; Watson et al., 1998) and the average baseline SR was 0.33 bouts/min (Aureli, 1997; Aureli and van Schaik, 1991; Schino et al., 2007b; Pavani et al., 1991; Kutsukake and Castles, 2001; Aureli et al., 1989; Aureli, 1992; Aureli and Yates, 2010). We further extracted from the empirical literature the average changes in HR and SR in different social contexts, as well as the maximum and minimum rates described in the literature on macaques. These are summarized in Table S3.6 (second and third column).

To transform these data into an arousal measure to be used in our model we first fitted a linear line through the heart rate (HR) and scratching rate (SR) data. For this, we used the average HR and SR of those social contexts for which both, HR and SR data were available, namely *Baseline*, *Proximity dominant* and *Post-conflict victim* (see contexts marked with * in Table S3.6). Fitting a linear regression model through the origin (minimum heart rate and scratching rate) yielded $HR = 127.8 + 38.19 * SR$. Using this linear model, we predicted the HR for those social contexts where only SR data were available (see measure indicated in bold type in Table S3.6). Finally, we converted the empirical and predicted HR data onto a scale ranging from 0 to 1 using the function $Arousal\ level = (HR - 127.8) / 149$ (5th column in Table S3.6). Predicted HR data were used whenever empirical HR data were lacking. Only for *Proximity dominant* we chose the maximum of predicted and empirical HR to define the maximum arousal increase in this social context (see below). The minimum SR was assumed to be 0.0. This scaled measure was then used as the level of arousal in our model. Thus, in our model arousal level was scaled between 0 (inactive) and 1 (maximum stimulation).

The instantaneous impact of *Attack received* and *Attack given* on arousal were based on empirical data (see Table S3.6). The impact of other point behaviors on arousal was chosen arbitrarily, assuming that receiving an attack has a higher impact than giving or perceiving an attack or receiving an aggressive signal. We assumed, that upon several aggressive events arousal gets increased per event and may build up quickly. We further assumed that aggressive behaviors may increase arousal levels up to the maximum possible arousal level of 1.0 (*MAX_AR_LIMIT*), while submissive and affiliative signals may decrease increased arousal levels towards the baseline level of 0.09 (*DEF_AR_LIMIT*), but not below (see Table S3.7).

The average default decrease rate of arousal was estimated using an array of time series data of heart rate and scratching rate after a conflict (without post-conflict grooming) (Aureli and Smucny, 2000; Boccia et al., 1989; Kutsukake and Castles, 2001; Aureli et al., 1989). After transforming these data to our model arousal measure (see above), we fitted a linear model through each of four datasets of time and (converted) arousal data and averaged the obtained arousal decrease rates. This average arousal decrease rate of 0.02/min was then used as default arousal decrease rate in our model (*DEF_AR_DEC*). We assumed that the default increase rate is similar to the default decrease rate and also set it to 0.02/min (*DEF_AR_INC*).

Whenever a dominant individual is perceived in proximity, arousal slowly increases up to a context-specific maximum arousal level (limit value) of 0.12 (*PD_AR_LIMIT*). The maximum arousal level for this social context was based on empirical data (see Table S3.6). As arousal increase rate for this social context we arbitrarily chose the same rate as for the default arousal increase rate of 0.02/min (*PD_AR_INC*). When grooming is given or received, arousal may

Social context	Change (and level) of heart rate in bpm	Change (and level) of scratching rate in bouts/min	Predicted change (and level) of heart rate in bpm	Arousal level in the model	Parameter name in the model	References empirical heart rate data	References empirical scratching rate data
Maximum arousal	+135.7 (276.8)			1.0	MAX_AR_LIMIT	(Manuck et al., 1989, 1983)	
Acute stress peak	+91.6 (232.7)			0.70 (+0.61)		(Manuck et al., 1989, 1983)	
Agonism	+25.7 (166.8)			0.26 (+0.27)		(Boccia et al., 1989)	
Post-conflict (victim)*	+12 (153.1)	+0.31 (0.64)		0.17 (+0.08)	AR_AR_INC	(Aureli and Smucny, 2000)	(Aureli and van Schaik, 1991; Schino et al., 2007b; Kutsukake and Castles, 2001; Aureli et al., 1989)
Post-conflict (aggressor)		+0.16 (0.49)	+5.4 (146.5)	0.13 (+0.04)	AG_AR_INC		(Aureli, 1997; Schino et al., 2007b)
Proximity dominant*	+3.4 (144.5)	+0.15 (0.48)	+5.0 (146.1)	0.12 (+0.03)	PD_AR_LIMIT	(Aureli et al., 1999)	(Pavani et al., 1991)
Baseline*	±0.0 (141.1)	± 0.0 (0.33)		0.09	DEF_AR_LIMIT	(Boccia et al., 1989; Manuck et al., 1989, 1983; Watson et al., 1998)	(Aureli, 1997; Aureli and van Schaik, 1991; Schino et al., 2007b; Pavani et al., 1991; Kutsukake and Castles, 2001; Aureli et al., 1989; Aureli, 1992; Aureli and Yates, 2010)
Physical contact (Grooming given)		-0.17 (0.16)	-7.2 (133.9)	0.04	GG_AR_LIMIT		(Pavani et al., 1991)
Grooming received	-9.5 (131.6)			0.03	GR_AR_LIMIT	(Boccia et al., 1989; Aureli et al., 1999)	
Minimum arousal level*	-13.3 (127.8)	-0.33 (0.00)		0.0		(Manuck et al., 1983)	

Table S3.6: Arousal levels in various social contexts. Column two and three summarize how heart and scratching rate differ from baseline levels in different social contexts (first column) reported in the literature (last two columns). In brackets, we also mention the respective expected level of heart and scratching rate assuming baseline levels of 141.1 bpm (heart rate) and 0.33 (scratching rate). Values of those social contexts where heart and scratching rate data were available (marked with *) were used to obtain a linear model to predict heart rate from scratching rate (third column). Those heart rate data (empirical or predicted) that were used to obtain the model arousal measure (4th column) are indicated in **bold** type.

Behavior	Change of arousal level in the model	Parameter name	Maximum / minimum arousal level caused by behavior	References empirical data
Point behaviors				
Escalated fight observed	+0.04	<i>EFO_AR_INC</i>	<i>MAX_AR_LIMIT</i>	
Aggressive signal received	+0.04	<i>ASR_AR_INC</i>	<i>MAX_AR_LIMIT</i>	
Attack given	+0.04	<i>AG_AR_INC</i>	<i>MAX_AR_LIMIT</i>	
Attack received	+0.08	<i>AR_AR_INC</i>	<i>MAX_AR_LIMIT</i>	
Affiliative signal received	-0.04	<i>AS_AR_DEC</i>	<i>DEF_AR_LIMIT</i>	
Submissive signal received	-0.04	<i>SS_AR_DEC</i>	<i>DEF_AR_LIMIT</i>	
Duration behaviors				
Default decrease	- 0.02 / min	<i>DEF_AR_DEC</i>	<i>DEF_AR_LIMIT</i>	(Aureli et al., 1989; Boccia et al., 1989; Aureli and Smucny, 2000; Kutsukake and Castles, 2001)
Default increase	+ 0.02 / min	<i>DEF_AR_INC</i>	<i>DEF_AR_LIMIT</i>	
Proximity of dominant	+ 0.02 / min	<i>PD_AR_INC</i>	<i>PD_AR_LIMIT</i>	
Grooming given	- 0.02 / min	<i>GG_AR_DEC</i>	<i>GG_AR_LIMIT</i>	
Grooming received	- 0.04 / min	<i>GR_AR_DEC</i>	<i>GR_AR_LIMIT</i>	(Aureli et al., 1989; Boccia et al., 1989; Aureli and Smucny, 2000)

Table S3.7: Effect of social behaviors on arousal levels.

decrease even below baseline levels down to context-specific minimum values (limit values) of 0.04 (*GG_AR_LIMIT*) or 0.03 (*GR_AR_LIMIT*), respectively, but not below.

GG_AR_LIMIT and *GR_AR_LIMIT* were based on empirical data (see Table S3.6). Note, that for *GG_AR_LIMIT* we assumed that giving grooming is similarly relaxing as contact sitting (see Table S3.6). When ego is giving grooming, we assumed that its arousal decreases with a rate similar to the default arousal decrease rate of 0.02/min (*GG_AR_DEC*). When receiving grooming, arousal is expected to decrease faster than the default arousal decrease rate. The arousal decrease rate during receiving grooming was estimated similarly to the default arousal decrease rate, using an array of time series data of heart rate and scratching rate after a conflict with post-conflict grooming (Aureli and Smucny, 2000; Boccia et al., 1989; Aureli et al., 1989). After transforming these data to our model arousal measure (see above), we fitted a linear model through each of three datasets of time and (converted) arousal data and averaged the obtained arousal decrease rates. This average arousal decrease rate of 0.04/min was then used as arousal decrease rate during receiving grooming in our model (*GR_AR_DEC*) (see Table S3.7).

Behavior	Probability
Affiliative behaviors towards individual j	
Grooming	$myAROUSAL_i * GG_PROB * myAFF_PROB_{ij}$
Affiliative signal	$myAROUSAL_i * AFS_PROB * myAFF_PROB_{ij}$
Approach	$myAROUSAL_i * APP_PROB * myAFF_PROB_{ij}$
Aggressive behavior towards individual j	
Attack	$myAROUSAL_i * ATT_PROB * myAGG_PROB_{ij}$
Aggressive signal	$myAROUSAL_i * AGS_PROB * myAGG_PROB_{ij}$
Submissive behavior towards individual j	
Leave	$myAROUSAL_i * LE_PROB * mySUB_PROB_{ij}$
Submissive signal	$myAROUSAL_i * SS_PROB * mySUB_PROB_{ij}$
Avoid	$myAROUSAL_i * AV_PROB * myAV_PROB_{ij}$
Non-directed behavior	
Random walk	$myAROUSAL_i * RNDW_PROB$
Rest	$REST_PROB$

Table S3.8: Behavioral probabilities for individual i.

Text S3.2: General behavioral probabilities

Ego's arousal level ($myAROUSAL$) positively affects the probabilities for active behaviors during action selection, i.e. any behavior except resting (see Table S3.8). The parameters GG_PROB , AFS_PROB , APP_PROB , ATT_PROB , AGS_PROB , LE_PROB , SS_PROB , AV_PROB , $RNDW_PROB$ and $REST_PROB$ are fixed and were used to tune the relative probabilities between all behaviors such that the resulting average behavioral frequencies represented empirical observations. The values for these parameters are given in Table S3.9.

The general affiliation probability ($myAFF_PROB_{ij}$), which affects the probabilities of grooming, affiliative signals and approach (see Table S3.8), is calculated as follows:

$$myAFF_PROB_{ij} = (AFF_0 + ((1 - AFF_0) * myAFF_MOT_i)) * ((1 - LPS) + LPS * LIKE_{ij}). \quad (S3.1)$$

Here, i is the actor and j is the (potential) receiver of the affiliative behavior and $LIKE_{ij}$ is the LIKE attitude directed from individual i to j . AFF_0 is a constant parameter, which determines the maximum probability to execute affiliative behavior when the actor has no intrinsic motivation to affiliate ($myAFF_MOT_i = 0$, see solid lines at $LIKE=1$ in Figure 3.3A). AFF_0 is set arbitrarily to 0.1. Increased intrinsic motivation to affiliate ($myAFF_MOT_i > 0$) may increase the affiliation probability up to 1.0 (see dashed and dotted lines at $LIKE=1$ in Figure 3.3A). LPS is the degree to which LIKE attitudes are of importance for the affiliation probability. At $LPS=0$, the level of $LIKE_{ij}$ has no effect on the affiliation probability (see first panel of Figure 3.3A). LPS describes the degree to which the maximum affiliation probability (at $LIKE=1$) decreases with decreasing $LIKE_{ij}$ (see steeper slopes of the lines at increased LPS in Figure 3.3A). Thus, in our model, $myAFF_PROB_{ij}$ increases with increased $LIKE_{ij}$ (given that $LPS > 0$) and with increased $myAFF_MOT_i$.

Action selection parameter name	Description	Value
AFF_0	Baseline affiliation probability when intrinsic affiliation motivation is 0	0.1
SW	Weight of satisfaction for intrinsic affiliation motivation	0.1
AW	Weight of anxiety for intrinsic affiliation motivation	0.9
AGG_0	Baseline maximum aggression probability when $FEAR_{ij} = -1$ and $myANXIETY_i = 0$	0.1
AGG_{IPD}	Maximum shift of inflection point of aggression probability	0.5
AGG_{SI}	Maximum increase of slope of aggression probability	1.0
η	Default slope of aggression probability and win chance w_{ij}	6
SUB_0	Baseline maximum submission or avoidance probability when $myANXIETY_i = 0$	0.1
SE	Parabolic effect of FEAR on submission probability	4
AE	Parabolic effect of FEAR on submission probability	16
GG_PROB	Relative probability factor for grooming	10
AFS_PROB	Relative probability factor for affiliative signal	50
APP_PROB	Relative probability factor for approach	100
ATT_PROB	Relative probability factor for attack	10
AGS_PROB	Relative probability factor for aggressive signal	50
LE_PROB	Relative probability factor for leaving	40
SS_PROB	Relative probability factor for submissive signal	50
AV_PROB	Relative probability factor for avoidance	100
RNDW_PROB	Relative probability factor for random walk	0.1
REST_PROB	Relative probability factor for resting	0.2

Table S3.9: Action selection parameters.

The intrinsic affiliation motivation of individual i depends on its satisfaction and anxiety and is calculated as follows:

$$myAFF_MOT_i = SW * (1 - mySATISFACTION_i) + AW * myANXIETY_i. \quad (S3.2)$$

Here, SW and AW are fixed weighting factors, which determine the relative importance of satisfaction and anxiety, respectively, for the intrinsic affiliation motivation. Intrinsic affiliation motivation is high when ego has a low level of satisfaction and a high level of anxiety. SW is set arbitrarily to 0.1 and AW is set arbitrarily to 0.9. Thus, we assumed, that high anxiety is affecting the intrinsic affiliation motivation to a higher degree than low satisfaction.

The general aggression probability ($myAGG_PROB_{ij}$), which affects the probabilities of attacking and aggressive signals (see Table S3.8), is calculated as follows:

$$myAGG_PROB_{ij} = \left(\frac{1}{1 + e^{myRISK_{ij}(FEAR_{ij}, myANXIETY_i)}} \right) * (AGG_0 + (1 - AGG_0) * myANXIETY_i) \quad (S3.3)$$

Here, i is the actor and j is the (potential) receiver of the aggressive behavior and $FEAR_{ij}$ is the FEAR attitude, i.e. the difference between the dominance strength of individual j and individual i . $myAGG_PROB_{ij}$ is a decreasing sigmoid function of $FEAR_{ij}$ (see first panel of Figure 3.3B). AGG_0 is a constant parameter, which determines the baseline maximum probability to execute aggressive behavior at minimum $FEAR_{ij}$ and minimum $myANXIETY_i$ (see solid line, $myANXIETY_i = 0$, in first panel of 3.3B at $FEAR_{ij} = -1$). AGG_0 is set arbitrarily to 0.1. The maximum probability to execute aggressive behavior at minimum $FEAR_{ij}$ ($FEAR_{ij} = -1$) is

increased with increased $myANXIETY_i$ (see dashed and dotted line at $FEAR_{ij} = -1$ in the first panel of Figure 3.3B). The slope and the location of the inflection point of the sigmoid function depend on the level of $myANXIETY_i$ and are determined, via the parameters AGG_{IPD} and AGG_{SI} , by the function $myRISK_{ij}(FEAR_{ij}, myANXIETY_i)$ as follows:

$$myRISK_{ij}(FEAR_{ij}, myANXIETY_i) = (FEAR_{ij} + AGG_{IPD} * myANXIETY_i) * \eta * (1 + AGG_{SI} * myANXIETY_i). \quad (S3.4)$$

Here, AGG_{IPD} is a fixed parameter, which describes the maximum decrease of the inflection point of the sigmoid function relative to the baseline sigmoid function at $myANXIETY_i = 0$. AGG_{IPD} is set arbitrarily to 0.5, thus at maximum $myANXIETY_i$ ($myANXIETY_i = 1$), the inflection point shifts from 0 to -0.5 (compare the inflection points of the solid and dotted line in the first panel of Figure 3.3B). The fixed parameter η describes the baseline slope of the sigmoid function and is set to 6. Note, that in the baseline situation ($myANXIETY_i = 0$), $myAGG_PROB_{ij}/AGG_0$ would actually describe individual i's chance of winning an escalated fight from individual j. Thus, η here is the same as in the win chance function w_{ij} . Finally, AGG_{SI} is a fixed parameter, which determines the maximum increase of the slope of the sigmoid function relative to the baseline sigmoid function at $myANXIETY_i = 0$. AGG_{SI} is set arbitrarily to 1. Note, that the slope of $myAGG_PROB_{ij}$ is also affected by $(AGG_0 + (1 - AGG_0) * myANXIETY_i)$. Taken together, this results in a slope of the sigmoid function at $myANXIETY_i = 1$, which is twenty times as steep compared to $myANXIETY_i = 0$ (compare slope of the solid and dotted line in the first panel of Figure 3.3B).

In sum, higher levels of anxiety result in a more conservative (or risk avoiding) probability of aggression concerning the FEAR attitudes directed to the potential receivers of aggression. On the one hand, when the FEAR attitude towards the opponent is very low (i.e. the opponent is much lower-ranking than ego) aggression probability increases with increased anxiety. On the other hand, the inflection point of the sigmoid function decreases. Thus, at low anxiety aggression probability changes from high to low around $FEAR=0$ (i.e. similar-ranking opponent), while at high anxiety it already changes from high to low around $FEAR=0.5$ (i.e. somewhat lower-ranking opponent)(compare solid, dashed and dotted line in the first panel of Figure 3.3B).

The general submission probability ($mySUB_PROB_{ij}$), which affects the probabilities of leaving and submissive signals (see Table S3.8), is calculated as follows:

$$mySUB_PROB_{ij} = \begin{cases} (FEAR_{ij})^{SE} * (SUB_0 + (1 - SUB_0) * myANXIETY_i) & FEAR_{ij} > 0 \\ 0 & else \end{cases} \quad (S3.5)$$

Here, SE is a fixed parameter, which increases the effect of FEAR at higher FEAR (see second panel in Figure 3.3B). SE was arbitrarily set to 4. SUB_0 is a fixed parameter, which describes the maximum submission probability when $myANXIETY_i = 0$ (see solid line at $FEAR=+1$ in the second panel in Figure 3.3B). SUB_0 was set arbitrarily to 0.1. The maximum submission probability at maximum $FEAR_{ij}$ is increased with increased $myANXIETY_i$ (see dashed and dotted line at $FEAR=+1$ in the second panel in Figure 3.3B). Moreover, submission was by definition only directed at individuals towards which ego directed a positive FEAR attitude, i.e. individuals that were higher in rank than ego.

The general avoidance probability ($myAV_PROB_{ij}$), which affects the probability of avoidance behavior (see Table S3.8), is calculated as follows:

$$myAV_PROB_{ij} = \begin{cases} (FEAR_{ij})^{AE} * (SUB_0 + (1 - SUB_0) * myANXIETY_t) & FEAR_{ij} > 0 \\ 0 & else \end{cases} \quad (S3.6)$$

Here, AE is a fixed parameter similarly to SE in the calculation of the submission probability above. However, AE was set to a higher value (AE=16), i.e. the effect of FEAR was even stronger depending on the value of FEAR. Thus, the avoidance probability was calculated very similarly to the submission probability, except that it only increased substantially at very high FEAR (see third panel in Figure 3.3B).

The probability to perform scanning behavior increases with the individual's current arousal level as follows:

$$mySCAN_PROB_{ij} = \begin{cases} 0 & myAROUSAL_t > SPO/SPS \\ 1 & myAROUSAL_t > (1 + SPO)/SPS \\ SPS * myAROUSAL_t - SPO & else \end{cases} \quad (S3.7)$$

Thus, highly aroused individuals employ scanning, while non-aroused individuals do not. For moderate arousal levels, just above the baseline arousal level and just below the increased arousal after *Receiving a (single) attack*, the scanning probability increases linearly with arousal (see Figure S3.1). SPS is a fixed parameter, which describes the slope with which scanning probability increases for moderate arousal levels. SPO is a fixed parameter, which describes the offset of the linear increasing scanning probability at moderate arousal levels. SPS was set to 18.0 and SPO was set to 1.8, which resulted in average percentages of time spent scanning that were reasonable for macaques.

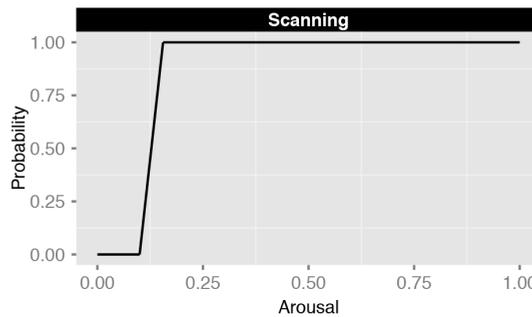


Figure S3.1: Scanning probability. This figure shows the probability to employ scanning behavior as a function of ego's arousal level (x-axis).

Text S3.3: Technical details on movement in bouts

Movement behavior in the EMO-model takes time and is implemented as movement bouts. Individuals in our model move with a constant speed of 0.6 m/s, which is reasonable for macaques (Beisner and Isbell, 2009). During such a movement bout, movement is executed step by step. After starting a movement bout, ego is activated each 3 SECONDS to execute the movement it was to perform during this time interval and to decide whether movement is to be continued. During such a movement *step* individuals move 1.8 m. Whenever ego had decided to move towards or away from a certain individual at the start of a movement bout, this goal stays consistent during the whole movement bout. Moreover, if ego approaches or avoids an individual that itself is moving, after each step ego adjusts its movement direction towards (or away from) the individual's updated position. This step-by-step implementation allows individuals to visually and physically "follow" another moving individual. The parameter STOP_CHANCE describes the probability to end the current movement bout. STOP_CHANCE was set to 0.1, which resulted in an average movement bout distance of around 6.5 m that are reasonable for macaques (Beisner and Isbell, 2009). Whenever an approached individual is reached, the movement bout is ended. An individual could be approached up to 0.5 m from the x-y coordinates that defined its spatial location, to account for the physical space an animal requires, i.e. individuals cannot be *on top of each other*, but move in a 2D-field and take up space. Whenever an individual that is to be approached is closer to ego than one movement step (1.8 m), ego moves only the actual distance towards the individual and then this movement step also takes only the respective amount of time.

4

Emotional bookkeeping and highly selective partner preference are necessary for the emergence of partner-specific reciprocal affiliation in an ABM of primate groups

A version of this chapter is submitted to publication.

ABSTRACT

Primate affiliative relationships are differentiated, individual-specific and often reciprocal. However, the underlying mechanism and the required cognitive abilities are still under debate. Recently, we introduced the *EMO-model*, in which two emotional dimensions regulate social behavior: anxiety-*FEAR* and satisfaction-*LIKE*. Emotional bookkeeping is modeled by providing each individual with partner-specific *LIKE* attitudes in which the emotional experiences of earlier affiliations with others are accumulated. Individuals also possess fixed partner-specific *FEAR* attitudes, reflecting the stable dominance hierarchy. In the current paper, we focus on one key parameter of the model, namely the degree of partner selectivity, i.e. the extent to which individuals rely on their *LIKE* attitudes when choosing affiliation partners. Studying the effect of partner selectivity on the emergent affiliative relationships, we found that at high selectivity, individuals restricted their affiliative behaviors more to similar-ranking individuals and that reciprocity of affiliation was enhanced. We compared the emotional bookkeeping model with a control model, in which individuals had fixed *LIKE* attitudes simply based on the (fixed) rank-distance, instead of dynamic *LIKE* attitudes based on earlier events. Results from the control model were very similar to the emotional bookkeeping model: high selectivity resulted in preference of similar-ranking partners and enhanced reciprocity. However, only in the emotional bookkeeping model did high selectivity result in the emergence of reciprocal affiliative relationships that were highly partner-specific. Moreover, in the emotional bookkeeping model, *LIKE* attitude predicted affiliative behavior better than rank-distance, especially at high selectivity. Our model suggests that emotional bookkeeping is a likely candidate mechanism to underlie partner-specific reciprocal affiliation.

INTRODUCTION

Observing social grooming in primates, it quickly becomes clear that grooming does not only serve a hygienic function of removing ectoparasites or dust particles from the other animal's skin (Barton, 1985; Zamma, 2002). The groomed animal, and, to a lesser degree, also the

grooming one becomes more relaxed (Terry, 1970; for the groomee: Schino et al., 1988; for the groomer: Aureli and Yates, 2010; Shutt et al., 2007) as indicated by the decrease of observable signs of distress such as self-scratching (Schino et al., 1988) and heart rate (Aureli et al., 1999; Boccia et al., 1989). Whether primates can integrate such pleasant grooming episodes in their socio-emotional memory and associate it later with former grooming partners is at present unknown, but not unlikely (Crockford et al., 2013; Curley and Keverne, 2005; Dunbar, 2010). The general significance of grooming in building and maintaining affiliative relationships in primates is widely accepted (Dunbar, 2010; Silk, 2002b).

As many primate studies have shown, grooming behavior is often reciprocated (Adishesan et al., 2011; Carne et al., 2011; Schino and Aureli, 2008). For the occurrence of reciprocal grooming between two individuals A and B, the following preconditions are often assumed to be necessary: (i) A and B should repeatedly encounter each other, (ii) they should be able to recognize each other, (iii) animal A should be able to memorize grooming it had received from B in order to return these, and (iv) animals should be able to select such grooming partners from which they had received grooming earlier. While there is no doubt about the necessity of the first condition, the necessity of the three cognitive abilities is debated (see further below). Group-living allows animals to interact repeatedly; however, encounter frequencies are not random and can even be zero for some dyads. Individual recognition is a cognitive ability possessed by many animal taxa, ranging from insects to primates (Tibbetts and Dale, 2007). Condition (i) and (ii) are, thus, easily met by social primates. Regarding condition (iii), it is unclear what aspects of the quality or quantity of earlier grooming acts should be memorized to allow for reciprocity. Similarly, regarding condition (iv), it is unknown how strict such partner selectivity should be when there are several interaction partners to choose from. In this paper we use a simulation model to explore these two uncertainties to illuminate the cognitive capacities that may be necessary for reciprocation of affiliative behavior among primates living in a social group.

Diurnal primates are group-living animals that are found to have reciprocal affiliative and supporting relationships (Carne et al., 2011). On the basis of variation in the rate of affiliation, proximity and support, social relationships with group members are considered to range from high to low quality (Aureli and Schaffner, 2002; Kummer, 1978; Massen et al., 2010a; Silk, 2002b). Individuals with high quality relationships typically exchange affiliative and support behavior (Schino and Aureli, 2010a). In primates, the presence of such high quality relationships has been related to different characteristics, such as kinship (Schülke et al., 2013), similarity in dominance rank (Seyfarth, 1977; de Waal, 1991; but see Leinfelder et al., 2001) and age-similarity (Widdig et al., 2001, but see Massen and Sterck, 2013). Yet, while these characteristics are often predictive of the quality of a dyadic relationship, they are statistical predictions and appreciable variation in the strength of the social bonds exists among dyads with similar characteristics (kinship: Nakamichi and Shizawa, 2003; Schino and Aureli, 2010b, dominance rank: Xia et al., 2013, age: Schaffner et al., 2012; for all three: Silk et al., 2010a, 2006b). For instance, the degree of grooming reciprocity varies substantially between dyads of the same dominance rank class in Tibetan macaques (see Figure 3 in Xia et al. 2013). In baboons Silk et al., 2010a, the strength of social bonds is correlated with rank distance, age proximity and kinship. However, a large degree of the variation in dyadic sociality is left unexplained by these factors. Apparently, reciprocal grooming relationships are not only determined by general dyadic characteristics such as kin, rank difference and age proximity, but can also be specific for the partners in the dyad. How this partner-specific reciprocity in affiliative relationships can arise in a social group of primates is one of the main questions addressed in this simulation study. Although variation in relationship quality is overwhelmingly present in primate groups, researchers disagree whether primates themselves regulate their behavior

on the basis of relationship quality. One line of thought argues that variation in relationship quality emerges from interaction patterns and the relationship of a dyad is an epiphenomenon recognized only by human observers, but not by the primates themselves (Barrett et al., 2007; Barrett and Henzi, 2002; Hemelrijk, 1999b). In this view, interactions are the short-term contingent responses to current needs, without memory of previous interactions or anticipation of future ones playing a role (Henzi and Barrett, 2007). In contrast, others argue that primates know their own relationships with group members and even relationships among others (Aureli and Schaffner, 2002; Bovet and Washburn, 2003). Some memory of past interactions signifies the quality of relationships with others and affects the selection of current interactions with them (Seyfarth and Cheney, 2012) mediated by current emotions and socio-emotional memory (Aureli et al., 2012). Complex cognitive capacities, such as anticipation of future needs or interactions, are not required (Seyfarth and Cheney, 2012). Consequently, several different underlying cognitive mechanisms have been proposed to regulate reciprocation of affiliative behavior, ranging from cognitively simple to complex.

A cognitively simple mechanism may suffice to generate reciprocation at a group level when there is a persistent pattern in spatial proximity among the group members (Puga-Gonzalez et al., 2009). This spatial pattern may result from structuring dominance interactions (Evers et al., 2012, 2011; Hemelrijk, 2000). Here, individual recognition is not required, since the selection of a behavior towards a group member nearby may only be influenced by the (observable) rank difference between individuals and the degree of tension of the actor, but not by earlier (affiliative) interactions with specific group members (Puga-Gonzalez et al., 2009). This mechanism does not require animals to keep track of interactions with others in the past, because only the currently perceivable state of affairs determines the behavior of each animal.

A more complex mechanism involves taking only a recent event into account, in which case one speaks of reciprocity through short-term temporal contingency (Schino and Aureli, 2010a) or attitudinal reciprocity (Brosnan and de Waal, 2002; de Waal, 2000). This requires individual recognition, unless the reciprocated behavior is always executed simultaneously with or immediately after the received behavior, as is the case in mutual grooming. However, while originally attitudinal reciprocity was conceived to act only in the short term, later definitions released this restriction (Schino and Aureli, 2010a), by which it became effectively equivalent to the concept of *emotional bookkeeping* (see below). The short-term temporal contingency mechanism and the short-term attitudinal reciprocity mechanism can in fact both be considered as specific cases of *emotional bookkeeping*, namely when only the most recent beneficial act is remembered for a (very) short while.

Taking the emotional experiences from past interactions with specific partners into account over a longer time span is called *emotional bookkeeping* (Aureli and Schaffner, 2002; Schino and Aureli, 2010a, 2009). Here, individuals assign and update long-lasting emotional attitudes towards specific partners based on earlier interactions, without remembering these events specifically. This mechanism evidently requires individual recognition. The cognitively most advanced mechanism is calculated reciprocity (Brosnan and de Waal, 2002), where an individual keeps track of past interactions with a partner and behavioral decisions are based on these memorized interactions such that received favours are equally returned.

Which cognitive process underlies reciprocity is still under debate. However, evidence is mounting that social behavior is mediated by emotional processes (Aureli and Schaffner, 2002; Dunbar, 2010; Massen et al., 2010a). Therefore, emotional bookkeeping has been proposed as a candidate mechanism to integrate positive emotions due to affiliative behavior without requiring high cognitive abilities of remembering exactly who did what to whom and when (i.e.

episodic-like memory, Clayton et al., 2003). Emotional bookkeeping involves tracking of the current valuation of group members based on previous affiliative interactions. Whether emotional bookkeeping constitutes the process of reciprocity is difficult to study in real animals, due to the complexity of primate social life, but its effects on patterns in social behavior can be studied theoretically in an agent-based model.

Besides socio-emotional memory, another factor influencing the emergence of reciprocal affiliative behavior is partner choice (Tiddi et al., 2011). Partner choice is often discussed in the context of the biological market approach (Noé, 2006). Depending on the supply and demand of different commodities, such as grooming and tolerance, and their relative values, an individual should select an interaction partner based on the availability of these commodities within the group for that individual. More specifically, when choosing a grooming partner the individual should take into account the probability of others to reciprocate grooming later on. This assessment of potential grooming partners may, at least partly, be based on the memory of received affiliation from those individuals so far. For instance, when grooming is assumed to be the only commodity, it is predicted that good reciprocators preferentially groom each other, which indeed has been found (Leinfelder et al., 2001). Thus, application of the biological market approach to “altruistic” acts such as grooming presupposes that selection of a grooming partner is, at least partly, based on memory of the amount of received grooming from others.

How strict this partner selection should be, that is, to what degree A's decision to groom B rather than C should depend on the (memorized) different amounts of grooming received from B and C in order for reciprocity of grooming to arise, is unknown. Moreover, it may well be that selection of specific partners is not really necessary. Dominance related behavior can give rise to spatial distribution patterns of the group, where nearby group members are often of similar dominance rank (as shown in several modelling studies by Hemelrijk, 2000 and Evers et al., 2011, 2012). In this way, suitable (similar-ranking) grooming partners may already automatically be in proximity. Reciprocal grooming at a group level can then result from randomly choosing an animal nearby as grooming partner whenever grooming motivation is high enough (Puga-Gonzalez et al., 2009). Neither specific selection of a partner nor any memory of earlier received grooming is necessary.

Agent-based models (ABM) formulate characteristics of interacting entities and study the group-level patterns that emerge from their interactions. Previous ABMs modelling the effect of social interactions among group living animals have investigated group level patterns like dominance relationships and spatial ordering (bumble bees: Hogeweg and Hesper, 1983; primates (macaques): Hemelrijk, 2000). The behavioral rules in these models regulate behavior on the basis of relative dominance position (the chance to win or lose a fight). Later versions also included an emotional reaction to aversive events (receiving aggression enhances anxiety) that in turn affect affiliative behavioral tendencies (i.e. grooming; Hemelrijk and Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). These models generate reciprocal patterns in grooming (Puga-Gonzalez et al., 2009). However, real animals do not only entertain negative emotions (anxiety), but also positive ones (Boissy et al., 2007).

To study the effect of both negative and positive emotions on patterns of social behavior, we developed the *EMO-model*. The *EMO-model* is a first attempt to model the social behavior of group living primates where the behavior of the individuals is regulated by two different emotional dimensions and the degree of their arousal. We took great care to ground all behavioral and emotional processes implemented in our model on empirical studies. Although we did not succeed fully in doing so, many simulation results corresponded with empirical data (Evers et al., 2014). The *EMO-model* assumes that anxiety and satisfaction are two important

emotional dimensions regulating different types of behavior. The model animals also have an arousal state. A high arousal state increases the probability to perform some active behavior and also increases the probability to scan the environment for group members.

Besides anxiety and satisfaction, which are influenced by behavior and affect general behavioral probabilities (independently of the interaction partner), we also provided each model animal with partner-specific emotional attitudes, i.e. LIKE and FEAR attitudes. The LIKE attitude towards an individual is dynamically updated after receiving affiliative behavior (i.e. grooming) from that specific individual. The update depends on the extent of the emotional response to received grooming, i.e. on the frequency and duration of grooming bouts. LIKE attitudes slowly decrease over time. When updating the LIKE attitude towards animal A, recently received grooming from A is weighted relative to the emotional memory of earlier received grooming from A. In this way, the model animals are provided an emotional bookkeeping mechanism.

In two recent ABM studies, reciprocity emerges from preferential approach of group members (Puga-Gonzalez, 2014), or from obligate cooperation (Campenni and Schino, 2014) with group members that have cooperated (i.e. groomed or benefited ego) most over the past. Partner choice based on benefits received may be regulated via emotional bookkeeping. In contrast to the EMO-model, neither emotional bookkeeping nor any emotional regulation processes are implemented explicitly in these two models.

As the current version of the EMO-model focuses on the effect of the dynamical LIKE attitudes, FEAR attitudes were kept fixed and purely dependent on the (fixed) rank distance between individuals. Previous models investigated the dynamics of dominance relations in relation to spatial structure (Hemelrijk, 2000). However, in primates, dominance hierarchies can be stable over several years. Moreover, similar spatial distribution patterns were found independent from modeling dominance relations as dynamic or fixed (Bryson et al., 2007; Evers et al., 2011). Thus, to keep things simple, we decided to model a primate group with a stable dominance hierarchy, where each individual had a fixed dominance strength.

In this paper we will use the EMO-model to investigate how and when affiliative relations a) emerge, b) are self-reinforcing, and c) are maintained. Moreover, we study how reciprocity in affiliative relations depends on one key parameter in the model, i.e. the degree of partner-selectivity. Lastly, we investigate whether emotional bookkeeping is necessary for reciprocal affiliative relationships to emerge. To do this, we study a control model with fixed instead of dynamic LIKE attitudes. In this cognitively simpler *fixed attitudes model* both, FEAR and LIKE attitudes, are based on the rank distance between individuals: individuals simply prefer grooming partners of similar rank. We explore the differences between the reciprocal affiliative relationships that emerge in the *fixed attitudes model* compared to the *dynamic attitudes model*.

METHODS

Simulations were run using NetLogo 5.0.2 (Wilenski, 2007). The program code of all models will become available via the website of the first author¹. Below, we describe our models according to the updated ODD protocol (Grimm et al., 2010), which is a standardized method of describing agent-based models. This ensures the model description to be more complete and better comparable to other models, allowing also reproducibility of the model. The ODD protocol contains an *Overview*, *Design concepts*, and *Details*. The detailed ODD protocol information on the EMO-model can be found elsewhere (Evers et al. 2014). Additionally, this methods section includes parts on the Simulation experiments and the Statistical analysis, which are not part of the ODD protocol.

¹<https://sites.google.com/site/elleneversutrecht/models>

Overview

Purpose

The purpose of the model described in this paper was to explore certain capacities of information integration that may be used in primates (e.g. macaques) to develop and maintain social relationships, and their effect on the emergent properties of affiliative relationships. We studied affiliative partner selectivity, i.e. the degree of exclusively preferring certain individuals as affiliation partners. Moreover, we compared the use of *dynamic* affiliative attitudes based on partner-specific affiliation history and emotional bookkeeping to *fixed* affiliative attitudes simply based on rank-distance.

Entities, state variables and scales

We modeled the movements and interactions of 20 individuals. The individuals are characterized by a number of state variables (Table S4.1 and see below). These state variables are identical to the ones used in the introductory paper on the EMO-model (Evers et al., 2014), with the exception of fixed LIKE attitudes we use here in a control model.

Individuals are characterized by their dominance strength (*myDOM*), which does not change over time or after interactions (Bryson et al., 2007; Evers et al., 2014, 2012, 2011). Individuals differ in their schedule time (*myTIME*), (current) scanning probability (*myPscan*) and in the current width of the view angle (*myVIEW_ANGLE*), which change dynamically over the course of the simulation.

Our model entities are further described by their emotional state, consisting of arousal, anxiety and satisfaction (*myAROUSAL*, *myANXIETY* and *mySATISFACTION*), i.e. an individual's state of alertness and an aversive and a pleasant dimension of the emotional state. Arousal, anxiety and satisfaction may change dynamically over time depending on the social context ego (i.e. a model entity) had experienced. The level of arousal, anxiety and satisfaction that is approached over time is described by the respective limit value (*myAROUSAL_LIMIT*, *myANXIETY_LIMIT*, *mySATISFACTION_LIMIT*). Model individuals are also characterized by partner-specific emotional attitudes (LIKE and FEAR), they assign to each other group member. In our model FEAR attitudes are fixed, while LIKE attitudes are dynamically changing over time depending on earlier affiliative interactions. Only in a control model, the fixed attitude model, LIKE attitudes were fixed.

General model parameters are identical to those used in the introductory paper on the EMO-model (Evers et al. 2014) and are summarized in Table ???. The modeled environment is a continuous two-dimensional grid (300 × 300 grid units) with a torus shape to exclude disturbing border effects. The length of one grid unit resembles 1 “meter”. We did not explicitly implement ecological features of the environment; in the model an individual's environment is purely social.

One time step in the simulation resembles 1 MINUTE. One HOUR consists of 60 MINUTES and we defined 12 HOURS as one DAY, 7 DAYS as 1 WEEK and 50 WEEKS as 1 YEAR. Simulations were run for 504 000 time steps, i.e. 2 YEARS, plus a prior stabilization period of 21 600 time steps, i.e. ca. 4 WEEKS.

Process overview and scheduling

Our model is event-driven. Most social behaviors are modeled as discrete events in time, except for moving, resting and grooming, which are modeled as continuous duration behaviors. Time is modeled on a continuous scale and during a simulation run individuals' activations are regulated by a timing regime. The general process overview and the scheduling are identical to those used in the introductory paper on the EMO-model (Evers et al., 2014, see also Figure 3.1 in Chapter 3).

Each time, the agent with the lowest schedule time is activated first. Whenever an individual is activated, first all model entities update those state variables that may have increased or decreased over the time interval that has passed since the last activation of an entity (arousal, anxiety, satisfaction, LIKE attitudes). If the activated individual had scheduled a movement action, that action is executed; else, ego checks the grouping criteria and employs grouping, if necessary. If no grouping and no movement are to be performed, ego may select a social behavior, resting or random movement within the group. Which behavior (and which interaction partner) gets selected depends on ego's own emotional state, as well as on its emotional attitudes towards the potential interaction partners. Subsequently, the selected behavior may affect emotional attitudes of involved individuals, as it may affect the emotional state of ego, of receivers and observers of the behavior. As a consequence, ego, receivers and observers may be activated sooner or later, depending on the behavior executed.

Thus, after activation, the next activation of ego, but also that of interaction partners or bystanders is scheduled anew. The exact time until an individual's next activation depends on the behavior performed, received or observed, respectively. As movement, resting and grooming are implemented as duration behaviors, they are performed in bouts. After starting a movement bout ego is activated each 3 seconds to execute the last movement "step" and to decide whether movement is to be continued. After starting a grooming or resting bout ego is activated anew after 7.5 ± 0.375 min (mean \pm SD). Social interactions may involve (and therefore activate) other group members and may also interrupt a grooming or resting bout. Whenever ego receives an attack, it is immediately activated to respond with either fleeing or a counter attack. Whenever ego receives a signal or observes an attack nearby, a fast reaction is required and ego is activated 0.1 ± 0.005 sec (mean \pm SD) later to select an action.

Design concepts

Basic principles

In our model, given, received and observed behaviors may affect the general emotional state (arousal, anxiety and satisfaction) of individuals. In turn, an individual's emotional state affects its general short-term probability of executing certain behaviors. In this way, emotions regulate spontaneous behaviors as well as appropriate responses to received behaviors.

More specifically, receiving and executing affiliative behavior increases satisfaction levels and decreases arousal and anxiety. While receiving submissive behaviors results in decreased arousal and anxiety, receiving aggressive behavior or perceiving aggression nearby results in increased levels of anxiety and arousal. Executing aggressive behavior increases ego's own arousal, while ego's own anxiety level decreases or increases depending on the outcome of the conflict. In turn, high arousal levels result in a higher general probability for all active behaviors, high satisfaction levels decrease the probability of (further) affiliation and high

anxiety levels result in increased probabilities for affiliative or submissive behavior and in more risk-sensitive aggression probabilities.

In the dynamic attitude model, partner-specific LIKE attitudes summarize earlier received affiliation from specific individuals on a longer-term and in turn affect the probability of affiliating with these individuals. In this way, LIKE attitudes regulate the development and maintenance of affiliative relations. More specifically, receiving affiliation from a specific individual increases ego's LIKE attitude towards this individual. In turn, ego's probability to affiliate with this specific individual increases. In a control model, the fixed attitude model, the feedback regulation between affiliation and LIKE attitudes is absent and LIKE attitudes are fixed, i.e. they depend on similarity of dominance and are not affected by behavior.

In sum, the emotional state regulates appropriate behavior in response to received behaviors, while partner-specific emotional attitudes regulate appropriate behavior in response to specific individuals. A more detailed description of the regulation of behavior via emotions and dynamic LIKE attitudes can be found elsewhere (Evers et al., 2014).

Emergence

In agent-based models, individual behavior is imposed by the model rules, while group-level properties are usually not implemented explicitly into the model, but rather emerge from the interactions of the lower-level entities, i.e. the individuals. In our model, behavioral patterns, e.g. affiliation, aggression and proximity, are emergent properties arising from the interactions of the model entities. The structure of the network of LIKE attitudes and group level properties such as reciprocity and partner-specificity are an emergent property arising from the interrelation between emotional attitudes and affiliative behavior.

Adaptation

The model entities change their behavior in response to changes in their general emotional state and their emotional attitudes towards others and individuals (implicitly) seek to increase satisfaction and to decrease anxiety. As appropriate behavior is mediated by emotional processes this yields a homeostatic regulation system. In this way, we aimed to produce adaptive (in the sense of flexible) behavior and emerging group properties that are representative of observations of the social behavior of real primates.

Learning

Individuals in the dynamic attitude model regularly update their partner-specific LIKE attitudes assigned to other group members, based on earlier grooming received from these individuals. This may be seen as a (basic) form of "learning". Emotional bookkeeping provides individuals with summarized information on "valuable" affiliation partners, which may dynamically change over time according to these partners' behavior. In this way, individuals "learn" with which specific partners they should affiliate.

Sensing

The individuals' sensing capabilities in this model are identical to those used in the introductory paper on the EMO-model (Evers et al., 2014). Individuals in our model may perceive the location, certain behaviors and signals of other group members, but only *locally* within certain distances and within a specific view angle. The exact distances depend on the salience of the perceivable information. Individuals are able to perceive (or know) the dominance strength of other group members and perception of a group member elicits ego's internal valuation of this group member, i.e. its FEAR and LIKE attitude that are assigned to this specific individual.

Interactions

Interactions are implemented identically as described in the introductory paper on the EMO-model (Evers et al., 2014). Social interactions in our model can be categorized as affiliative, submissive and aggressive behaviors. Affiliation comprises grooming, affiliative signaling and approaching; submission comprises leaving, submissive signaling and avoiding; and aggression comprises attacking and aggressive signaling.

Potential interaction partners are the 10 nearest recognizable individuals (within MAX_DIST and ego's current view angle). The potential behavioral probabilities towards these 10 (or less) individuals depend on ego's emotional attitudes (FEAR and LIKE) assigned to those individuals and ego's general emotional state (arousal, anxiety, satisfaction). One behavior towards one specific interaction partner is chosen randomly according to those probabilities.

Some social interactions can only be performed towards group members within a certain distance. Individuals within INTERACT_DIST (1m) can be groomed, left or attacked. Individuals within PERS_DIST (5m) can receive (affiliative, submissive or aggressive) signals. Individuals within MAX_DIST (50m) can be approached and individuals within PERS_DIST (5m) can be avoided.

Stochasticity

In our model, many processes are not implemented deterministically, but include some degree of stochasticity, to produce variability in those processes. Those processes include action selection, the determination of the winner of an escalated fight, the random walk procedure and the timing regime.

Observation

For the analysis of our model, we only used data that were recorded during the last 252 000 time steps of each simulation run, i.e. the last YEAR.

The individuals' levels of arousal, anxiety and satisfaction, the dyadic proximity scores and the levels of dyadic LIKE attitudes were sampled every 3.5 DAYS and then averaged (per individual or dyad, respectively) over one YEAR for each simulation run. The number or duration of dyadic behaviors was recorded per dyad per behavior over each recording interval of 3.5 DAYS and then divided by the duration of the recording interval to obtain average hourly behavioral rates.

To assess the average dyadic proximity score, i.e. the average rate of being located in each other's proximity, we scored for each individual which other group members were found within close proximity (1m) at the time of sampling using the *one-zero* sampling technique. Thus per dyad, possible scores were 1 (in proximity) or 0 (not in proximity) per sample. Note, that proximity is by definition a symmetric measure, while LIKE attitudes and social interactions are always directed from an actor to a receiver and are thus not symmetric by definition. Per individual this translates into possible scores between 0 (no other group member was in proximity) and 19 (all other group members were in proximity).

Details

Initialization

The initial settings are summarized in Table S4.1 and are identical to the introductory paper on the EMO-model (Evers et al., 2014), with the exception of fixed LIKE attitudes in the control model. At the initialization of each simulation run, the x-coordinates and the y-coordinates of the 20 individuals were drawn randomly from a predefined circular sphere with an arbitrary diameter of 50 m. The individual's initial heading was set to a random orientation between 1° and 360° and the initial view angle was set at 120° for each individual. Each individual's level of arousal was set to the default arousal level (0.09) and the level of anxiety and satisfaction was set to 0.0. In the dynamic attitude model, LIKE attitudes were initialized at 0.0. In the control model, the fixed attitude model, LIKE attitudes were fixed and calculated as a function of (absolute) rank-distance: $LIKE_{ij} = \max(0, 0.243 - \text{abs}(myDOM_j - myDOM_i) * 0.36)$. The initial schedule time for each individual was drawn randomly from a normal distribution with a mean of 1 minute and a standard deviation of 0.05 minutes.

Submodels

The implementation of all processes in our model, except for the fixed LIKE attitudes in the control model, is identical to the introductory paper on the EMO-model (Evers et al., 2014). This section broadly describes the main processes implemented in the EMO-model. It covers the implementation of the emotional state (arousal, anxiety and satisfaction), the partner-specific emotional attitudes (LIKE and FEAR), the process of action selection, perception and signalling processes, scanning, movement, grouping, grooming and resting, and attack, counter-attack and escalated fight. For a detailed description, the substantiation, parameterization and validation of our model we refer the reader to our earlier paper (Evers et al., 2014).

Arousal In our model, an individual's arousal level, i.e. its responsiveness or tendency to be active, increases in response to receiving, executing or observing aggression or when in proximity (*PERS_DIST*) of a dominant individual. On the other hand, arousal may decrease over time and in response to receiving submissive or affiliative behavior and executing affiliative behavior. The extent of arousal change depends on the emotional salience of the stimulus (see Table S3.5 in Chapter 3). Arousal level was scaled between 0 (inactive) and 1 (highly stimulated), with 0.09 being the baseline level (*DEF_AR_LIMIT*). Higher arousal was implemented to result in an increased probability of performing active behaviors (any behavior except resting) and in an increased probability to employ social vigilance, i.e. scanning behavior.

Anxiety In our model, anxiety level, i.e. an individual's general *fearfulness* in response to negative stimuli within the current social environment, was scaled between 0 (not anxious) and 1 (highly anxious). Anxiety increases over time and in response to aggression, i.e. *Receiving* or *Giving an attack*, *Receiving an aggressive signal*, *Losing an (escalated) fight* or *Observing an escalated fight nearby*, and decreases in response to successful aggression, submission and affiliation, i.e. *Winning an (escalated) fight*, *Receiving a submissive or affiliative signal* and *Receiving* or *Giving grooming*. The extent of anxiety change depends on the emotional salience of the stimulus (see Table S3.5 in Chapter 3). High anxiety levels generally result in increased probabilities of affiliation and submission and decreased probabilities of aggression.

Satisfaction In our model, satisfaction level, i.e. an individual's general *contentedness* in response to positive stimuli within the current social environment, was scaled between 0 (not satisfied) and 1 (highly satisfied). Satisfaction increases in response to affiliation, i.e. *Receiving* or *Giving grooming*, and decreases over time. The extent of satisfaction change depends on the emotional salience of the stimulus (see Table S3.5 in Chapter 3). High satisfaction results in decreased probabilities of affiliation.

FEAR attitudes In our model, individuals assign a partner-specific FEAR attitude to each group member. FEAR attitudes resemble the difference in dominance strength between an individual (i) and another group member (j) and are calculated as $FEAR_{ij} = myDOM_j - myDOM_i$, i.e. ranging from -0.95 to +0.95. Thus, FEAR attitudes are directional and not symmetric. FEAR attitudes are fixed over the course of our simulation and are, thus, not affected by social interactions. Yet, they do affect the individual's valuation of its potential aggression risk related to the respective group member. High FEAR attitudes result in decreased probabilities of aggression (i.e. attack, aggressive signal) and increased probabilities of submission (i.e. leaving, submissive signal, avoidance) towards the respective group member.

LIKE attitudes $LIKE_{ij}$ describes an individual's (i) affiliative valuation of a specific group member (j). LIKE attitudes may have values ranging from 0.0 (neutrally valued affiliation partner) to +1.0 (highly valued affiliation partner). In the current paper, we compare two types of the EMO-model, in which LIKE attitudes are either dynamically updated in response to received grooming (*dynamic attitude model*) or fixed over the course of a simulation run (*fixed attitude model*). In both, the dynamic and fixed attitude model, a high LIKE attitude affects ego's judgement of the affiliative *value* of the respective group member and results in increased probabilities of affiliation (i.e. grooming, affiliative signaling and approaching) towards this specific group member.

In the control model (fixed attitude model) LIKE attitudes are reversely related to the (absolute) rank-distance of two individuals and calculated as $LIKE_{ij} = \max(0, L_0 - L_S * \text{abs}(myDOM_j - myDOM_i))$. Here, L_0 and L_S are fixed conversion parameters set to $L_0 = 0.243$ and $L_S = 0.36$, to result in a distribution of LIKE attitudes similar to the one emerging in the dynamic attitude model. In the fixed attitude model, by definition LIKE attitudes are symmetric within a dyad.

In contrast, in the dynamic attitude model, LIKE attitudes are not symmetric per se, as they are dynamically updated upon receiving grooming. The exact increase of $LIKE_{ij}$ depends on individual i's current increase in satisfaction in response to grooming received exclusively from individual j, described by the partner-specific variable $PARTNER_SAT_{ij}$, which increases

and decreases with the same rate as the general satisfaction level (GR_SAT_INC). Partner-specific LIKE attitudes are then used to integrate earlier affiliation received from a partner, i.e. the changing level of $PARTNER_SAT_{ij}$ over time as follows:

$$LIKE_{ij}(t_n) = \max \left\{ \frac{LHW * LIKE_{ij}(t_{n-1}) + (t_n - t_{n-1}) * PARTNER_SAT_{ij}(t_n)}{LHW + (t_n - t_{n-1})}, PARTNER_SAT_{ij}(t_n) \right\} \quad (4.1)$$

Here, t_n is the current time, t_{n-1} is the time of the last update and $(t_n - t_{n-1})$ is the time since the last update (in MINUTES). $LIKE_{ij}(t_n)$ is the updated value of the LIKE attitude assigned from individual i to j and $LIKE_{ij}(t_{n-1})$ is the former level of LIKE to be updated. LHW (LIKE-HISTORY WEIGHT) is a fixed parameter (arbitrarily set to 1 DAY), which causes (emotional responses to) earlier affiliation history to weigh stronger than (emotional responses to) affiliation received recently (within the last few MINUTES). While current affiliation received from a partner may quickly increase LIKE and/or maintain a high LIKE, the lack of current affiliation will result in a slowly decreasing LIKE attitude.

Action selection In our model, activated individuals may select one of various possible actions. These actions may be directed to other individuals or may involve resting or random movement within the group.

The probability to execute a specific behavior towards another group member depends on a) the distance of the individual to ego, b) ego's emotional state (arousal, anxiety and satisfaction), c) ego's FEAR and LIKE attitudes assigned to the potential interaction partners and d) the parameter setting of LIKE-PARTNER SELECTIVITY (LPS), i.e. the degree to which high LIKE attitudes are important for the selection of affiliation partners. The emotional state facilitates behavior that is appropriate to the individual's position and situation within the social group in general, while emotional attitudes facilitate behavior that is appropriate towards specific group members.

First, the 10 (or less) potential interaction partners are determined. Then the possible behaviors towards each of these individuals are determined dependent on their distance to ego. Finally, the probabilities for those possible behaviors towards each potential interaction partner are calculated. According to these probabilities, one of the possible behavior-partner combinations is randomly selected and executed. The details on the calculation of the probabilities for affiliation, aggression, submission and avoidance are described elsewhere (Evers et al., 2014) and are summarized hereafter.

Ego's probability to direct affiliation towards individual j increases with increased $LIKE_{ij}$ (given that $LPS > 0$) and with increased intrinsic affiliation motivation of ego, i.e. when satisfaction is low or anxiety is high. At $LPS = 0$, the level of $LIKE_{ij}$ has no effect on the affiliation probability. With higher LPS ego becomes more selective and affiliates with high-LIKE partners relatively more often than with low-LIKE partners. Ego's probability to direct aggression towards individual j decreases with increased $FEAR_{ij}$. Moreover, increased anxiety results in the aggression probability to be more conservative or risk avoiding. Ego's probability to direct submissive behaviors towards individual j increases with increased $FEAR_{ij}$ and with increased anxiety.

Perception and signaling Individuals in our model can individually recognize other group members within a maximum perceivable distance of 50 m (MAX_DIST) and within the currently employed view angle. The view angle is by default 120° (VIEW_ANGLE) or else 360° (MAX_ANGLE)

when ego is scanning. Model entities can judge whether at least three other group members are present within 20 m (NEAR_DIST) and within the currently employed view angle. Furthermore, individuals in our model are capable to judge whether their distance to the furthest group member exceeds 100 m (FAR_DIST). The two latter criteria are used by ego to decide whether grouping behavior should be executed. Individuals can also perceive signals, which were directed at them from others within 5 m (PERS_DIST).

Scanning When employing scanning behavior, an individual is turning its head right and left, thus expanding its view angle to 360° (MAX_ANGLE) instead of the default view angle of 120° (VIEW_ANGLE). The probability to perform scanning behavior increases with ego's current arousal level (Evers et al., 2014).

Movement Concerning movement behavior, individuals in our model may either move towards or away from other group members (approaching, grouping, fleeing, leaving and avoiding) or they may execute random movement within the group. Movement behavior in our model takes time and is implemented as movement bouts. During such a movement bout, movement is executed *step by step*. After starting a movement bout, ego is activated each 3 SECONDS to execute the movement it was to perform during this time interval and to decide whether movement is to be continued (see also Figure 3.1 in Chapter 3).

After ending a movement bout ego always performs a proximity update. Ego checks whether any individuals towards which it directs a (high) FEAR attitude (i.e. higher-ranking group members) are now (or still) nearer than 5 m (PERS_DIST), as this has consequences for the level that ego's arousal will approach over time (myAROUSAL_LIMIT). Additionally, other individuals who direct (high) FEAR attitudes towards ego are updated on ego's new spatial location, which may in turn affect the level their arousal will approach over time.

Grouping Before selecting a social behavior, model entities always check whether grouping should be executed. Grouping will be selected if less than three (MIN_OTHERS) group members are located within 20 m (GROUP_DIST) and 360° (MAX_ANGLE) or whenever any group member is further away from ego than 100 m (FAR_DIST). When grouping is to be performed, ego simply approaches any randomly selected group member.

Grooming and resting In our model, grooming and resting behavior are implemented as a duration behaviors, which are executed in bouts. When starting a grooming or resting bout, ego's next activation is scheduled several minutes later to choose its new behavior. Ego may be disturbed and activated earlier in response to receiving an attack or a signal, or after observing an escalated fight nearby.

Attack, counter-attack and escalated fight Upon receiving an attack the respective model individual is immediately activated to respond with either fleeing or a counter-attack. When a counter-attack was selected in response to an attack, we call this an escalated fight. The winner and loser of such a fight is determined randomly according to the individuals' win chance. When no counter-attack is selected in response to an attack, the attacked individual is defined as the loser and the attacker as the winner of this aggressive interaction. After an attack or an escalated fight, the loser flees from the winner, while the winner is scheduled

anew shortly after. Whenever an escalated fight takes place, individuals nearby get activated and their arousal level gets increased. Moreover, these individuals are activated shortly after to enable an appropriate reaction in response to the event.

Simulation experiments

In this paper we present the results of two different types of our model. First, we describe the *dynamic attitude model* (emotional bookkeeping model), in which individuals dynamically update their LIKE attitudes according to earlier received affiliation by specific group members and subsequently use these LIKE attitudes to choose affiliation partners. Second, we describe the *fixed attitude model*, in which LIKE attitudes are also used to choose affiliation partners, but where LIKE attitudes are only dependent on rank-distance and thus fixed. In the fixed attitude model, there is no feedback from affiliative behavior onto LIKE attitudes. Therefore, the fixed attitude model serves as a control model to assess the importance of this dynamic feedback from behavior to emotional attitudes for the emergence of certain group patterns.

In the dynamic and the fixed attitude model, we varied the parameter LIKE-PARTNER SELECTIVITY (LPS), which describes the degree to which individuals prefer to selectively affiliate with group members towards whom they assign a high LIKE attitude. LPS was set to 0.0, 0.5, 0.9, 0.95 or 0.99. LPS = 0.0 resembles a special null model setting. Here, individuals have no preference to select specific affiliative partners concerning LIKE attitudes whatsoever. In other words, individuals do not use LIKE attitudes during affiliative partner selection. Therefore, the null model setting of the dynamic and the fixed model are identical. The null model setting serves as a control setting to assess the effect of the presence of any affiliative partner preference based on emotional bookkeeping.

For each setting of LPS, 10 independent simulations were run for the dynamic and the fixed attitude model, resulting in a total of 100 independent simulation runs.

Statistical analysis

We first explain how specific summarized measures were calculated from the recorded data, e.g. how data on dyad level were transformed to obtain measures on individual or (sub-)group level. We continue with the statistics that were used to compare the properties of different subgroups or individual categories. Finally, we explain how we calculated specific group properties, i.e. Shannon index, group-level reciprocity, partner-specificity and predictability. All statistical analyses were performed in R 2.15.2 (R Core Team, 2012).

Individual proximity scores, strength of LIKE attitudes and behavioral rates were calculated as the sum of all dyadic proximity scores, LIKE attitudes or behavioral rates that an individual directed to others. Group means of behavioral rates were calculated as the mean of all individual behavioral rates. To calculate the mean proximity score, strength of LIKE attitude and behavioral rates per rank category, we divided the 20 group members into 10 lower-ranking (subordinates) and 10 higher-ranking (dominants) individuals and averaged the respective individual proximity scores, strength of LIKE attitudes and behavioral rates per subgroup. To calculate the average proximity scores, strength of LIKE attitudes and behavioral rates per rank-distance category, we divided all dyads into two similar-sized groups. Dyads for which the absolute difference in dominance strength was less than 0.35 were defined as similar-ranking dyads (N=99 for symmetric measures and N=198 for directed measures). Dyads for which the difference in dominance strength was more than or equal to 0.35 were defined as

distant-ranking dyads (N=91 for symmetric measures and N=182 for directed measures). We then averaged the respective dyadic proximity scores, strength of LIKE attitudes and behavioral rates per subgroup.

To assess how evenly individuals distributed their proximity, LIKE attitudes and social behaviors among all potential partners, we calculated the Shannon index (H). This diversity measure has frequently been used in earlier primate research (e.g. Castles et al., 1996; Nakamichi and Shizawa, 2003). H of individual i was calculated as:

$$H_i = - \sum_j p_{ij} \log p_{ij}, \quad (4.2)$$

where i is the actor, j are all potential receivers and p_{ij} is the relative proportion of grooming given by the actor i to the j th receiver. We calculated H using the dyadic grooming rates averaged over one YEAR. To compensate for group size, an evenness index was applied to the Shannon index following Buzas and Gibson (1969) as:

$$H_i^* = \frac{e^{H_i}}{N - 1}, \quad (4.3)$$

where N is the group size. H^* describes whether grooming is directed equally often to all possible partners ($H^* = 1$) or only restricted to one partner (H^* approaches 0). H^* was calculated per individual and then averaged over the group.

To assess the reciprocity of behaviors and LIKE attitudes at the group level we calculated the Kendall's tau row-wise matrix correlation between the dyadic interaction matrix (or the LIKE matrix) and its transposed matrix (Hemelrijk, 1990; de Vries, 1993) using the R software package DyaDA (Leiva et al., 2010).

To assess the variation in proximity scores, strength of LIKE attitudes and behavioral rates within dyads of same rank-distance, we calculated the standard deviation (SD) over those dyads. To calculate the SD we used the dyadic proximity scores, strength of LIKE attitudes and behavioral rates averaged over one year. We calculated the SD over all dyads of the same rank-distance, i.e. difference in dominance strength, between actor and receiver. We excluded the dyads of rank-distance -0.95 and 0.95, as they were the only dyads with this rank-distance, which did not allow for calculation of SD. The SD per rank-distance were then averaged over the group.

To investigate how well either absolute rank-distance or LIKE attitudes corresponded to the behavioral patterns (including also the proximity scores), we calculated the row-wise Pearson correlation coefficients (de Vries, 1993) between behavioral patterns and either rank-distances or LIKE attitudes, respectively. To do this we used the dyadic proximity scores, LIKE attitudes and behavioral rates averaged over one year. We calculated the correlation coefficients per simulation run and then averaged them over all runs using a Fisher-z-transformation.

RESULTS

We present the results of two different types of our model. We describe the dynamic attitude model (emotional bookkeeping model), in which individuals dynamically update their LIKE attitudes according to earlier received affiliation from specific group members and subsequently

use these LIKE attitudes to choose affiliation partners. Then we compare the dynamic attitude model to the fixed attitude model, in which LIKE attitudes are also used to choose affiliation partners, but where LIKE attitudes are fixed and strictly dependent on rank-distance.

In both, the dynamic and the fixed attitude model, we varied the LPS parameter, i.e. LIKE-PARTNER SELECTIVITY, which describes the degree to which individuals prefer to selectively affiliate with group members towards which they direct a high LIKE attitude. LPS=0 describes the null model setting. In this setting, LIKE attitudes have no effect on affiliative partner selection. Therefore, the null model setting of the dynamic and the fixed model yield the same behavioral patterns.

Dynamic attitude model

In this section we only present the results concerning reciprocity, affiliative partner selectivity and the differentiation between rank-distance categories (similar-ranking and distant-ranking dyads). Results concerning the differences between rank categories (subordinates and dominants), as well as a detailed description of the causal interrelations between the social interactions of the model entities on one hand, and the entities' arousal, emotional state and LIKE attitudes on the other hand, were already described in an earlier paper (Evers et al. 2014).

In the dynamic attitude model LIKE attitudes incorporate information on earlier received affiliation from group members. Here, individuals restrict their affiliative behaviors to group members towards which they direct a high LIKE attitude. The degree to which they prefer to affiliate with such individuals depends on the exact setting of LPS, with higher LPS resulting in higher selectivity.

Enhanced preference for similar rank at increased LIKE-partner selectivity

We first examined how the behavioral patterns differed between similar-ranked and distant-ranked dyads in the dynamic attitude model. We describe these differences for the null model setting (LPS=0) and assess the effect of increased LPS. The findings are shown in Figure 4.1, unless indicated otherwise. Additionally, we calculated the Shannon index (H') for the behavioral patterns (Figure S4.1).

Individuals directed grooming and affiliative signals more often to similar-ranking than to distant-ranking group members independently of the setting of LPS. At increased LPS, rates of grooming and affiliative signals generally increased between similar-ranked dyads, while they decreased between distant-ranked dyads. Thus, the preference to affiliate with similar-ranking partners, which was already present at the null model setting (LPS=0), was reinforced at increased LPS.

The preference to affiliate with similar-ranking group members in turn resulted in higher LIKE attitudes between similar-ranking dyads than between distant-ranked dyads. At increased LPS, values of LIKE attitudes were generally decreased, but they decreased more between distant-ranked dyads than between similar-ranked dyads. This differentiation of LIKE attitudes between similar-ranking and distant-ranking dyads at increased LPS in turn also reinforced the differences in affiliation rates, approach rates and proximity between dyads of different rank-distance categories. At LPS=0, similar-ranking dyads had slightly higher proximity scores than distant-ranking dyads. Proximity scores were generally decreased at increased LPS, but they decreased more between distant-ranked dyads than between similar-ranked dyads.

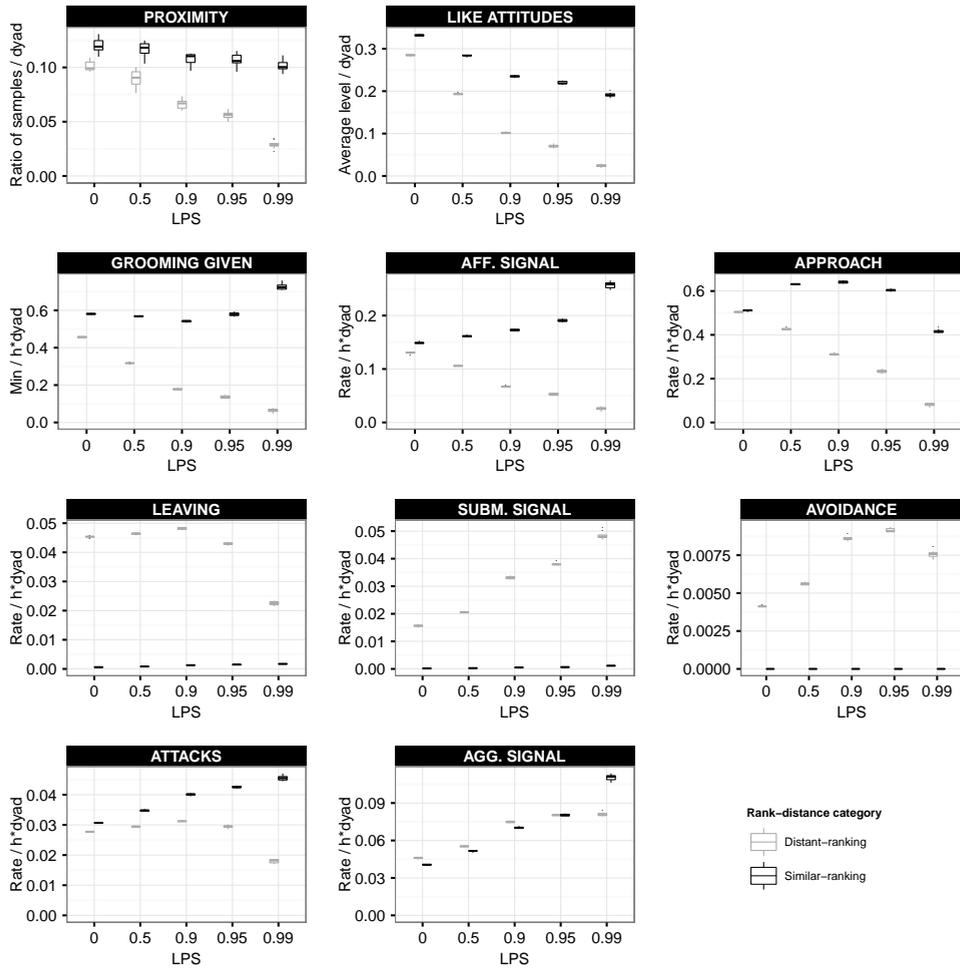


Figure 4.1: Behavioral rates per rank-distance category in the dynamic attitude model. This figure shows the averaged behavioral rates for distant-ranked (grey box-plots) and similar-ranked (black box-plots) dyads at different settings of selectivity (LPS) in the dynamic attitude model. Note that the setting LPS=0 refers to the null model setting. Proximity is measured as the ratio of samples in which the members of a dyad were observed in proximity. The level of LIKE attitudes was measured as the average level of all dyadic LIKE attitudes directed to (distant- or similar-ranking) group members. Grooming given is measured in MINUTES per HOUR per dyad. Signals, approach, leaving, avoid and attacks are measured in occurrences per hour per dyad. The box-plots show the results of 10 simulation runs, averaged over 1 YEAR.

At increased LPS, the Shannon index of the LIKE attitudes, the proximity scores and affiliative behavioral frequencies were decreased (see black box-plots in Figure S4.1). Hence, at increased LPS, individuals restricted their affiliative behaviors, their proximity and high LIKE attitudes to fewer group members than at lower LPS. This decrease in number of selected interaction partners explains the slight decrease in proximity scores and LIKE attitudes at high LPS. Averaged over the whole group of similar-ranking dyads these values decrease, while they still

increase for those few dyads that mutually prefer each other most (see also Figures 4.2 and S4.2).

At LPS=0, approach rates were very similar for distant-ranking and similar-ranking dyads. At increased LPS, approach rates were always lower between distant-ranked dyads than between similar-ranked dyads and, similarly to proximity, affiliation and LIKE attitudes, approach rates of distant-ranking dyads decreased. On the other hand, approach rates of similar-ranking dyads first increased at increased LPS (LPS<0.9), as individuals focussed more on individuals with high LIKE attitudes, which were usually similar-ranking group members. At even higher LPS (LPS>0.9) approach rates of similar-ranking individuals decreased again, as individuals became even more selective and focussed on a few affiliative partners (see above).

Attacks were always more frequent between similar-ranking dyads than between distant-ranked dyads, independently of LPS. At increased LPS, attack rates increased between similar-ranked dyads. As individuals at increased LPS are more often in proximity of similar- than distant-ranking group members, probabilities for attacks are also increased. First, probabilities for aggression directed up the hierarchy are higher when opponents are of similar rank compared to opponents of distant rank. Second, probabilities for counter-aggression are higher when opponents are of similar rank compared to opponents of distant rank (see also Figures 4.2 and S4.2).

Rates of attacks generally decreased between distant-ranked dyads at increased LPS. In our model, attacking another individual is by definition only possible when this individual was in close proximity. As proximity scores between distant-ranked dyads decreased at increased LPS, there are simply less opportunities to direct aggression to distant-ranked individuals.

On the other hand, rates of aggressive signaling, which required only near (5 m) and no close (1 m) proximity, were very similar between distant- and similar-ranked dyads. Only at highest LPS (LPS=0.99), similar-ranked dyads used aggressive signals more often than distant-ranked dyads. This may be a result of the fact that at this setting, the relative difference in proximity scores was highest between similar-ranking and distant-ranking dyads and now affected behaviors within not only close, but also near proximity.

At increased LPS, the Shannon index of aggressive behavioral frequencies was only slightly decreased (see black box-plots in Figure S4.1). Hence, at increased LPS, individuals restricted their aggressive behaviors to slightly fewer group members than at lower LPS, due to their restricted encounters with group members.

Submissive behaviors (leaving, submissive signal, avoidance) were almost exclusively employed (by subordinates) in distant-ranked dyads, independent of the setting of LPS. At increased LPS, rates of leaving, i.e. moving away from someone in close proximity, were generally decreased, simply because individuals spent less time in close proximity of distant-ranking individuals.

At high LPS, rates of submissive signals were generally increased. This can be explained as follows. Submissive signals are by definition almost exclusively employed by subordinates, and at low LPS, subordinates may direct either affiliative or submissive signals towards distant-ranking dominants within a certain distance. At increased LPS, affiliative signals are more and more restricted to *LIKEd* individuals, which are usually similar-ranking. Thus, as the chance of directing affiliative signals towards distant-ranking individuals decreased at increased LPS, the relative chance to direct submissive signals towards these *LIKEd* individuals increased. Similarly, at low LPS, subordinates may either approach or avoid distant-ranked individuals.

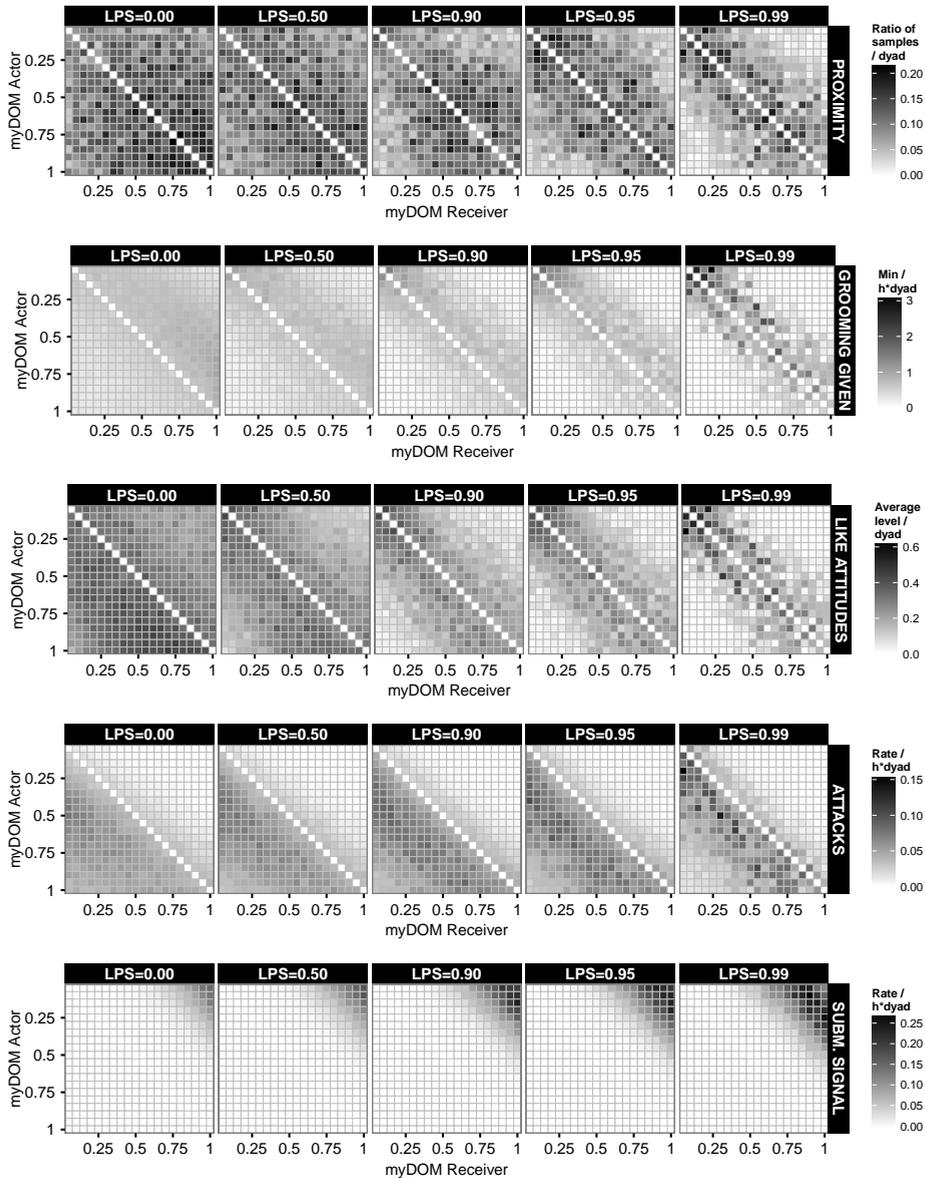


Figure 4.2: Interaction matrices of behaviors in the dynamic attitude model. This figure shows the dyadic behavioral rates of a group at different settings of selectivity (LPS) in the dynamic attitude model. Behaviors are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking (myDOM=0.05) to high-ranking (myDOM=1.0) individuals. Proximity is measured as the ratio of samples in which a dyad was observed in proximity. Grooming given is measured in MINUTES per HOUR. LIKE attitudes are measured as the average level of an individual's LIKE attitude directed to another group member. Attacks and submissive signals are measured in occurrences per HOUR. The plot shows the behavioral rates of one example run averaged over one YEAR. Dark shades represent high rates or values. Values at the diagonal are by definition not applicable. Additional patterns are presented in Figure S4.2.

As the chance of approaching distant-ranked group members decreased at higher LPS (see above), the relative chance to avoid such individuals generally increased.

At increased LPS, the Shannon index of submissive behaviors showed a minor increase (see black box-plots in Figure S4.1). Hence, at increased LPS, individuals directed submissive behaviors to slightly more group members than at lower LPS (see also Figures 4.2 and S4.2).

To summarize, the preference for similar-ranking individuals that was already present in the null model setting (LPS=0) was reinforced at increased LPS due to the mutual positive feedback between affiliative behavior and the LIKE attitudes. Higher LIKE attitudes towards similar-ranking individuals resulted in higher preferences to approach and affiliate with these individuals, which in turn resulted in the maintenance of high LIKE attitudes towards similar-, but not distant-ranking individuals. In this way, higher LPS resulted in a stronger differentiation between similar- and distant-ranking dyads, with similar-ranking dyads engaging in more affiliation and aggression than distant-ranking dyads. The more LPS is increased, the more individuals restrict their affiliation, proximity and aggression towards a few preferred partners (Figure S2). The stronger differentiation between similar and distant-ranking dyads at increased LPS is also apparent from the average dyadic values of the behavioral frequencies, proximity scores and LIKE attitudes (Figures 4.2 and S4.2).

Enhanced reciprocity at increased LIKE-partner selectivity

To examine the effect of LPS on the group-level reciprocity of the behaviors employed, we calculated the Kendall's tau row-wise matrix correlation between the dyadic matrix and its transposed. Note, that proximity is by definition a reciprocal measure. Note further, that row-wise tau values could not be calculated for submissive behaviors (leave, submissive signal and avoidance), as these matrices were sparse. At increased LPS, the row-wise tau values of LIKE attitudes and affiliative behaviors increased (see black box-plots in Figure 4.3), indicating enhanced group-level reciprocity. Similarly, at increased LPS the row-wise tau values of aggressive behaviors increased from negative values towards values around zero (see black box-plots in Figure 4.3), indicating decreased group-level imbalance.

The increased reciprocity of affiliation at increased LPS can be explained as follows. In the null model setting (LPS=0), individuals do not use LIKE attitudes to select affiliation partners. As grooming was directed up the hierarchy, LIKE attitudes were directed down the hierarchy, but had no feedback on affiliative behaviors. At increased LPS (LPS>0), individuals affiliated more selectively with individuals towards which they directed high LIKE attitudes. More frequent affiliation with these individuals reinforced the differentiation between preferred and non-preferred partners. Moreover, this feedback between affiliation and LIKE attitudes resulted in LIKE attitudes becoming more symmetric. At increased LPS (LPS>0), individuals also approached more selectively those individuals towards which they directed high LIKE attitudes. Therefore, proximity was increasingly determined by affiliation and LIKE attitudes and individuals were more often in proximity of similar-ranking individuals. This also allowed aggressive behaviors to become less imbalanced, as similar-ranked individuals also had more similar win chances than distant-ranked individuals.

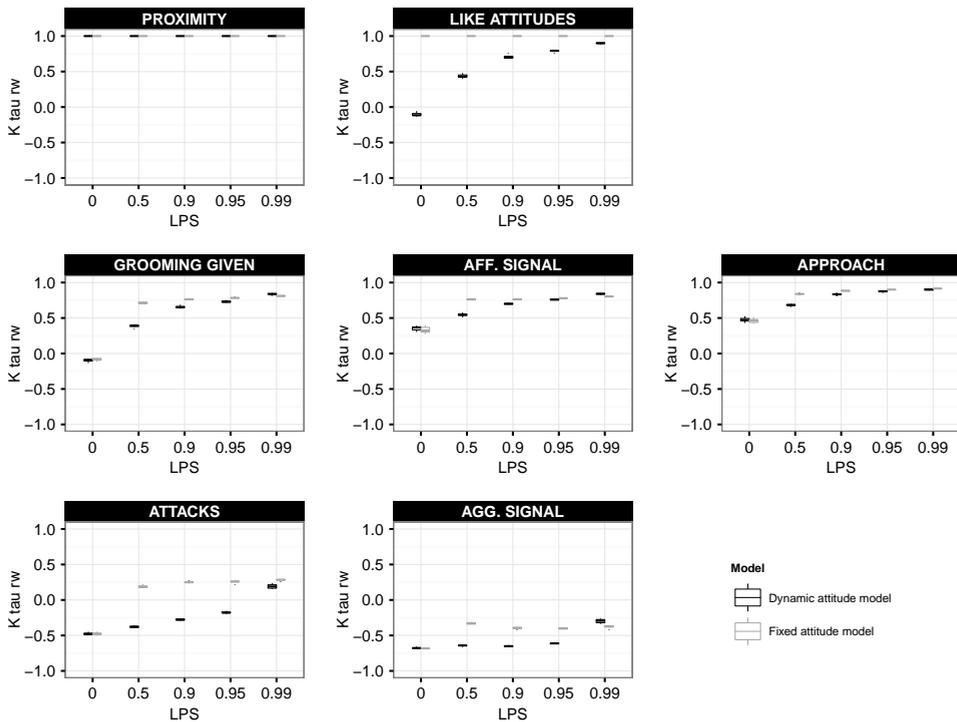


Figure 4.3: Reciprocity of behaviors. This figure shows the group-level reciprocity of behaviors at different settings of selectivity (LPS) in the dynamic (black box-plots) and the fixed (grey box-plots) attitude model. Group-level reciprocity is measured as Kendall row-wise tau. Positive row-wise tau values indicate that behaviors are reciprocated. Negative row-wise tau values indicate that behaviors are imbalanced. Row-wise tau values were calculated based on behaviors averaged over one YEAR. The box-plots show the row-wise tau values of 10 simulation runs.

Dynamic vs. fixed attitude model

Above we have shown that when LPS was increased in the dynamic attitude model, reciprocity and the preference for similar-ranking individuals were reinforced. Here, we compare these results to the behavioral patterns that emerged in the fixed attitude model at increased LPS. In the fixed attitude model, affiliative partner preference is fixed and simply inversely related to rank-distance, with lower rank-distances corresponding to higher LIKE attitudes (cf. Figure 4.4 middle row). Thus, in the fixed attitude model, higher LPS results in higher selectivity for similar-ranking individuals. Remember, that when LPS is 0 in the fixed attitude model, the model has exactly the same settings as LPS=0 in the dynamic attitude model; this is the null model setting, where individuals do not use their LIKE attitudes.

General rank differences, i.e. the differences in emotional states, behavioral rates and proximity of subordinates and dominants, and how these changed at increased LPS were very similar for the dynamic and the fixed attitude model (compare Figure 3.4 in Chapter 3 and Figure S4.3 in the current Chapter). These general patterns and their causation within the dynamic attitude model were described in detail in Chapter 3.

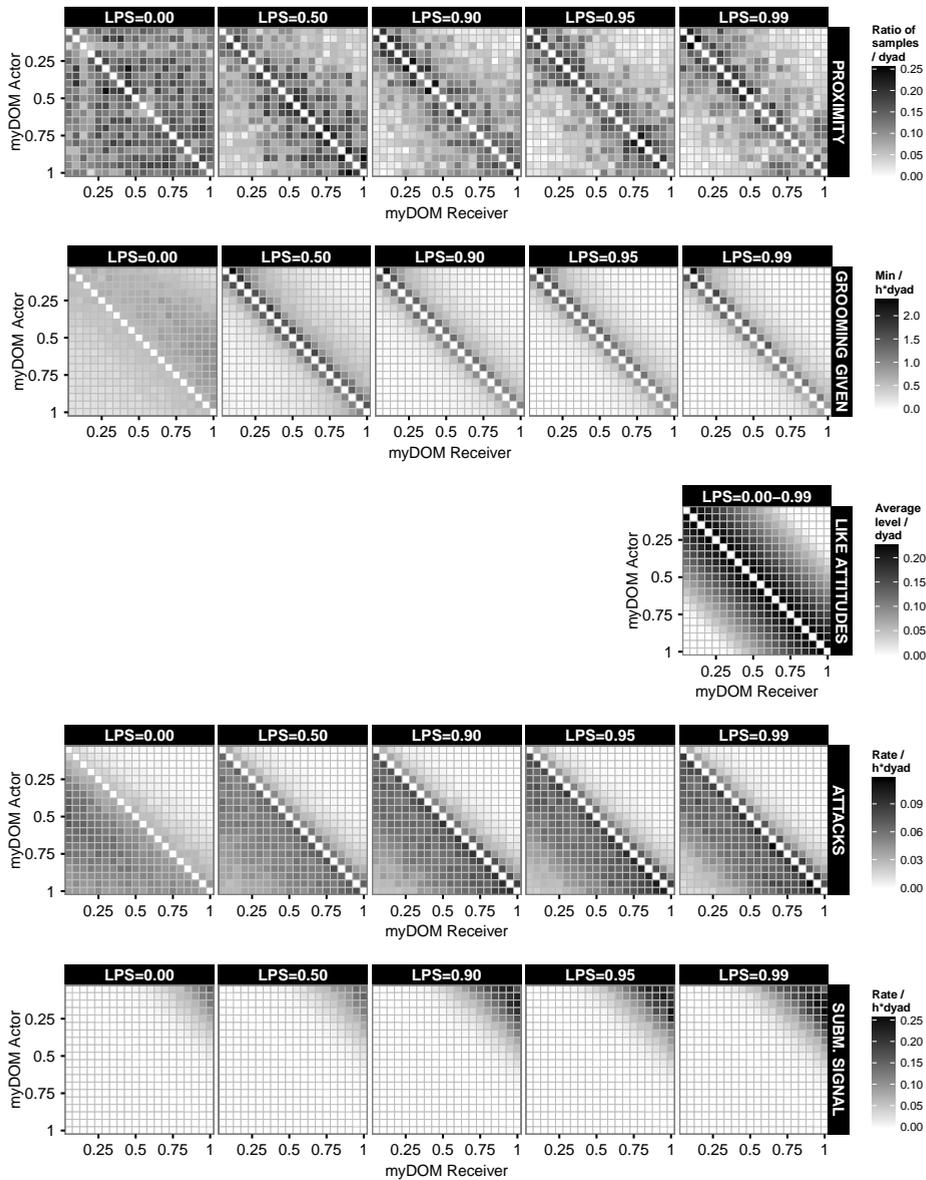


Figure 4.4: Interaction matrices of behaviors in the fixed attitude model. This figure shows the dyadic behavioral rates of a group at different settings of selectivity (LPS) in the fixed attitude model. For more details on the specific behaviors and how they were measured see caption of Figure 4.2. The plot shows the behavioral rates of one example run averaged over one YEAR. Dark shades represent high rates or values. Values at the diagonal are by definition not applicable. Additional patterns are presented in Figure S4.5.

In both models, the dynamic and the fixed attitude model, slight differences in behavioral rates towards similar-ranking and distant-ranking group members were already present in the null model (LPS=0), and got generally reinforced at increased LPS (compare Figure 4.1 and Figure S4.4). Of course, in the fixed attitudes model, LIKE attitudes do not change at increased LPS as they are by definition the same for all LPS.

In both models, at increased LPS the Shannon index decreased for agonistic and especially affiliative behaviors, and slightly increased for submissive behaviors (Figure S4.1), i.e. individuals restricted affiliative and aggressive behaviors to fewer group members and directed submission to slightly more group members. Also, at increased LPS affiliative behaviors were more reciprocated and aggressive behaviors were less imbalanced in both models (Figure 4.3). Note, however, that in the fixed attitude model a low Shannon index and high reciprocity were already apparent at intermediate LPS (LPS \geq 0.5) in the fixed attitude model, whereas this only emerged at high LPS (LPS=0.99) in the dynamic attitude model (see further below).

A clear difference between the dynamic and fixed attitude model was found in the dyadic distribution of some behavioral patterns. In the fixed attitude model, affiliative behaviors (grooming, affiliative signaling and approach) were more focussed on a few very similar-ranking partners, usually ranking just above or below ego (Figure 4.4 and S4.5), while partners were more diverse in the dynamic attitude model (Figure 4.2 and S4.2). Moreover, a strong preference for similar-ranking affiliation partners was already apparent at intermediate LPS (LPS \geq 0.5) in the fixed attitude model (Figure 4.4 and S4.5), whereas this only emerged at high LPS (LPS=0.99) in the dynamic attitude model (Figure 4.2 and S4.2). This was due to the fact that LIKE attitudes in the dynamic attitude model changed dynamically over time and needed to be maintained regularly, which is difficult at low LPS. In contrast, in the fixed attitude model, LIKE attitudes were fixed and did not need to be maintained. Here, individuals always prefer the same group members most, namely those that are most LIKEd, which are by definition most similar in rank. Hence, with LIKE attitudes being fixed, their effect on affiliative partner choice was stronger and already apparent at lower LPS compared to the dynamic attitude model, which was also reflected in the Shannon index (Figure S4.1) and reciprocity (Figure 4.3).

Moreover, the dynamic and fixed attitude model differed in the partner-specificity of some behavioral patterns. In the fixed attitude model, affiliative partner choice is purely based on rank-distance (via fixed LIKE attitudes that are based on rank distance) and as a result behavioral rates within the dyads of the same rank-distance showed low variation. In contrast, in the dynamic attitude model affiliative partner choice is dependent on the specific identity of actors of earlier received affiliation. As a result, affiliative relationships were highly individualized and behavioral rates within dyads of the same rank-distance showed high variation. To quantify this, we calculated the standard deviation (SD) over the behavioral rates for all dyads of a certain rank-distance and then averaged the SD over all rank-distances.

At LPS=0, SD was similar for both models (except of course for the differently defined LIKE attitudes), as here individuals in both models had no preference for specific affiliative partners (Figure 4.5). At increased LPS, the SD of LIKE attitudes, affiliative behaviors (especially grooming) and attacks increased in the dynamic attitude model, while they increased not at all or to a lesser degree in the fixed attitude model (Figure 4.5). Thus, in the dynamic attitude model, dyads of the same rank-distance showed more variation in their LIKE attitudes, the resulting rates of affiliation and in the rates of attack than in the fixed attitude model. This pattern is also apparent from the matrix plots (compare Figure 4.2 with 4.4 and Figure S4.2 with S4.5). For instance, when comparing the matrix of grooming given at LPS=0.99 in both models (Figure 4.2 and Figure 4.4), dyads with rank-distance of 1, i.e. dyads just above or below the

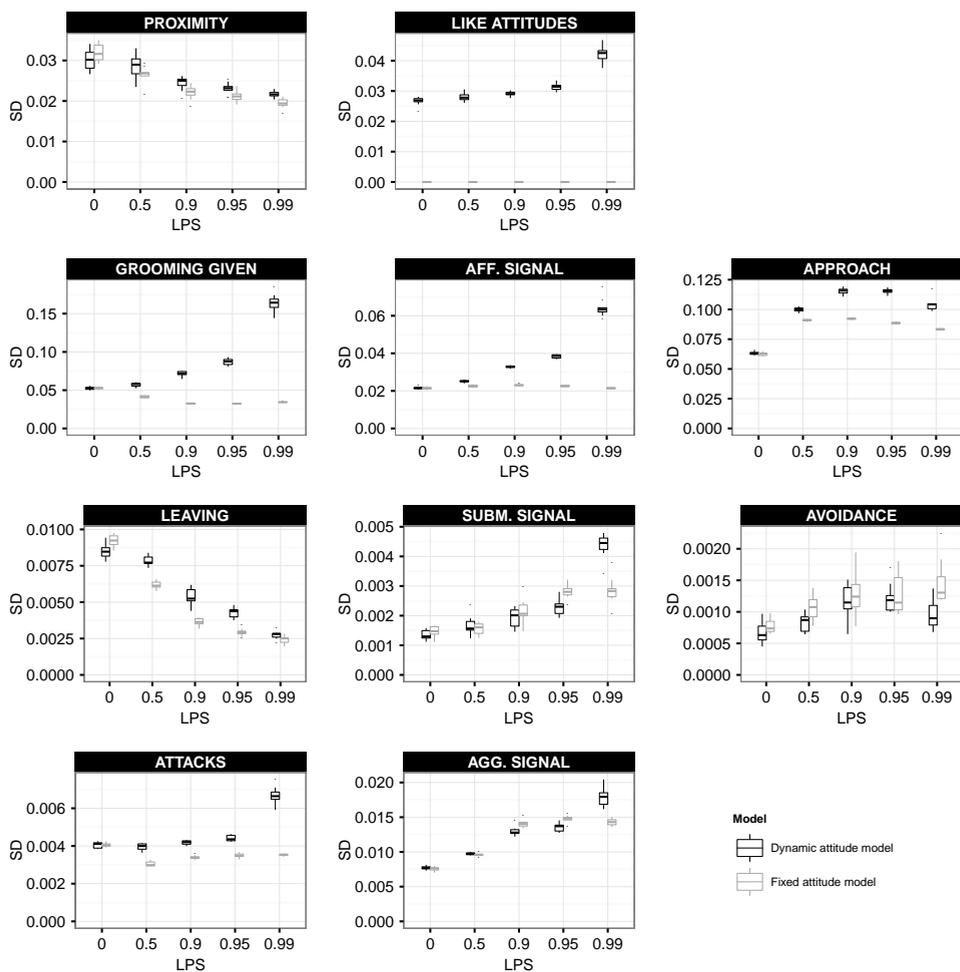


Figure 4.5: Partner-specificity of behaviors. This figure shows the standard deviation (SD) over the behavioral rates of dyads with the same rank-distance in the dynamic attitude model (black boxplots) and the fixed attitude model (grey boxplots). SD was calculated over all dyads of the same rank-distance based on the behavioral matrices averaged over one YEAR, and then averaged over all rank-distances. The box-plots show the results of 10 simulation runs. Note that LIKE attitudes in the fixed-attitude model are strictly based on rank-distance and therefore SD across dyads of same rank-distance is by definition zero.

diagonal, varied less in their grooming rate in the fixed than in the dynamic attitude model. This shows that affiliation, attacks and LIKE attitudes in the dynamic attitude model were not purely influenced by rank-distance, but were also dependent on the individual-specific history of received affiliation, especially at high LPS.

At increased LPS, the SD of proximity scores and leaving rates decreased and that of agonistic signals and avoidance increased similarly for both models (Figure 4.5). This suggests that the distribution of these behaviors was in both models mostly dependent on rank-distance.

Moreover, it is interesting to note that affiliative patterns of our model are not purely a result of spatial group patterns.

Predictability within the dynamic attitude model

Above we showed that high selectivity for affiliative partners (LPS) is necessary for the emergence of enhanced reciprocity and preference of similar-ranking affiliation partners within the group. Moreover, at high LPS only dynamic and not fixed LIKE attitudes allow for individual-specific relationships, in which behavioral rates vary across dyads of the same rank-distance. This raises the question how well the affiliative relationships in the dynamic attitude model are predicted by either rank-distance or LIKE attitudes and how this predictability depends on LPS. To investigate this, we calculated the row-wise correlation coefficients between the behavioral patterns and, respectively, LIKE attitudes or rank-distances. The results are shown in Figure 4.6, except when stated otherwise.

First, note that the correlation between the dynamic LIKE attitudes and absolute rank-distance first increased at increased LPS ($LPS < 0.9$), but decreased again at even higher LPS ($LPS > 0.9$) (see second panel of first row in Figure 4.6). This means that LIKE attitudes corresponded well to rank-distance at intermediate LPS, but less at low or high LPS. At low LPS, LIKE attitudes were mainly directed down the hierarchy (Figure 4.6). Therefore, LIKE attitudes were less well correlated to the symmetric rank-distance. On the other hand, at high LPS, LIKE attitudes were more based on individual-specific affiliative histories and therefore less derivable from rank-distance.

Proximity, grooming and affiliative signals were slightly better predicted by absolute rank-distance than by LIKE attitudes at lower LPS ($LPS \leq 0.5$), however at high LPS ($LPS \geq 0.95$) this was the other way around. Approach was generally best predicted by LIKE attitudes, especially at high LPS ($LPS = 0.95$).

Aggressive behaviors were best predicted by LIKE attitudes, especially at high or low LPS. This can be explained as follows. At low LPS, both LIKE attitudes and aggression are directed down the hierarchy, while absolute rank-distance is symmetric. At high LPS, LIKE attitudes and attacks become more reciprocated and symmetric, but also more individual-specific. Only submissive behaviors were always better predicted by rank-distance independently of LPS. This was due to the fact that submissive behaviors were not affected by LIKE attitudes or resulting proximity, as they were mostly directed towards group members distant in rank, which were also often distant in space.

To summarize, LIKE attitudes were best predictors of proximity, affiliative and aggressive behaviors, given that affiliative partner preference was high enough ($LPS > 0.9$). At lower LPS, rank-distance corresponded better to grooming, lip-smacking and proximity and would, therefore, be a better (and cognitively simpler) cue to use when selecting affiliation partners.

DISCUSSION

Emotional bookkeeping versus fixed attitude model

Using the *EMO-model* (Evers et al., 2014), we explored two different processes that may result in reciprocation of affiliative behaviors. The *dynamic attitude model* includes a form of emotional bookkeeping. Here, individuals incorporate emotional experiences of earlier affiliation with

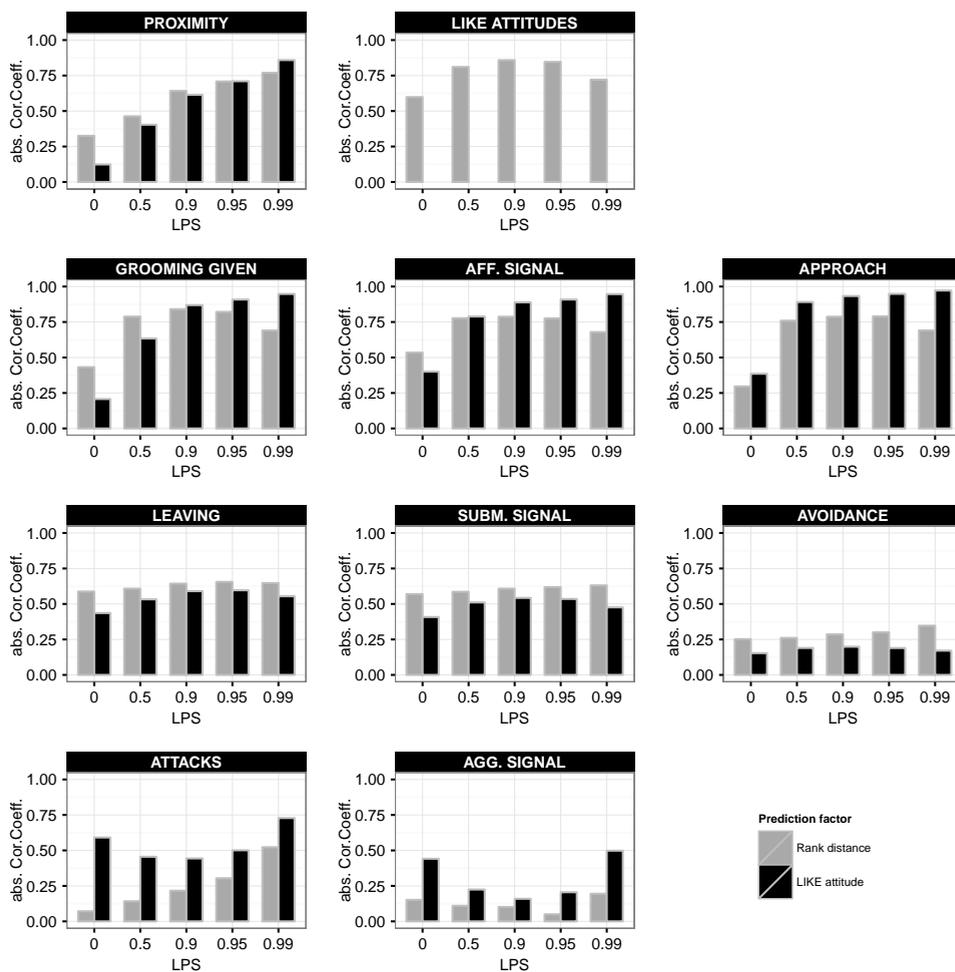


Figure 4.6: Correlation between behaviors and LIKE or rank distance in the dynamic attitude model. This figure shows the absolute row-wise Pearson correlation coefficients between the behavioral patterns and two predictive factors: Rank distance (grey) and LIKE attitudes (black). We used matrices of the behaviors and LIKE attitudes averaged over one YEAR. The correlation coefficient was calculated for each of 10 simulation runs and then averaged using a Fisher-z transformation.

others into partner-specific LIKE attitudes, which can change dynamically. We compared this *dynamic attitude model* to the *fixed attitude model*. In this cognitively simpler model, both, LIKE and FEAR attitudes are fixed and merely dependent on rank distance.

In the dynamic attitude model individuals could develop LIKE attitudes towards individuals that directed affiliative behavior to them. Since these dynamic LIKE attitudes represent a way to model emotional bookkeeping, we expected that reciprocity in LIKE attitude and affiliative behavior would emerge. Indeed, LIKE-attitudes developed, yet only at very high LIKE partner selectivity (LPS = 0.99) did this result in enhanced partner-specific reciprocity of both, LIKE

attitudes and grooming. Maintenance of these partner-specific reciprocal affiliative relations occurred via the following feedback loop: grooming increases the LIKE attitude towards the groomer, in turn this high LIKE attitude results in grooming of this *LIKEd* partner, but only when LIKE partner selectivity (LPS) is high enough. This shows that emotional bookkeeping can mediate partner-specific reciprocal patterns in LIKE-attitudes and grooming.

In the dynamic LIKE attitude model, individuals also showed an enhanced rate to affiliate with similar-ranking individuals at both intermediate and high partner selectivity, whereas the rates to affiliate with distant-ranked individuals decreased at higher partner selectivity. In addition, the LIKE attitudes changed from being directed down the dominance hierarchy in the null model (i.e. without partner selectivity) to more symmetric appreciation at higher LIKE partner selectivity. Rank distance was a factor predicting LIKE attitudes across a broad range of LPS and only with very strong partner selectivity did affiliation become partner-specific. To explore whether the emotional bookkeeping is necessary for partner-specific reciprocity to arise, or whether rank similarity alone may already be sufficient we constructed the fixed attitude model, a model that does not include emotional bookkeeping.

In the fixed attitude model, the LIKE attitude towards an individual depends merely on the rank difference with that individual; similar-ranked dyads were given a higher LIKE value than distant-ranked ones. So, here, by definition the LIKE attitudes are symmetrical and inversely related to rank distance. This model generated many patterns that were similar to the dynamic attitude model. This concerned general patterns of rates and direction of aggression, submission and affiliation. The average levels of arousal and emotional states, anxiety and satisfaction were quite similar as well. Similarly to the dynamic attitude model, affiliative patterns were more reciprocal at higher settings of LPS, thus when (fixed) LIKE-attitudes had a stronger effect on partner selection. However, the two models differ in two aspects. First, in the fixed attitude model the emerging grooming patterns showed high rates only for adjacently ranked individuals, whereas in the dynamic LIKE attitude model preferred partners consisted of individuals within a broader range of rank distances, which is what we see in real primate groups (Xia et al., 2013; Silk et al., 2006b). Second, in the fixed attitude model there is no partner-specific variation in affiliation within subgroups of dyads having a similar rank-distance, whereas reciprocal partner-specific LIKE attitudes and corresponding grooming exchanges are clearly present in the dynamic LIKE attitude model.

This comparison of the two models generates new predictions: when individual recognition and emotional bookkeeping are present, reciprocal partner-specific affiliation may emerge and partner-specific emotional attitudes are better predictors of affiliative relationships than similarity characteristics of dyads, such as in this case rank distance. More speculatively, a system in which relationships are developed and maintained on the basis of emotional bookkeeping is expected to be less vulnerable to the evolution of cheaters than a system where affiliative partner choice is determined by a (fixed) similarity characteristic. In this light, the emotional bookkeeping model serves as a promising candidate model for the development and maintenance of affiliative relations in many primate species.

Determinants of the behavioral patterns in the dynamic attitude model

Although partner-specific affiliation was an important feature in the dynamic LIKE attitude model, both rank distance and LIKE attitude were associated with patterns in behavior. We determined which of the two better predicted these patterns. LIKE attitudes were the best predictors of proximity, affiliative and aggressive behaviors, given that affiliative partner selectivity

was high enough ($LPS \geq 0.95$). At lower LPS, rank-distance corresponded better to grooming, lip-smacking and proximity and would, therefore, be a better (and cognitively simpler) cue to use when selecting affiliation partners. Submissive behaviors were better predicted by rank distance, independently of partner selectivity. Submission is directed mainly towards distant-ranking group members, towards which LIKE attitudes are generally low and not differentiated. Thus, the dynamic LIKE attitude model does not exclude dyadic similarity effects, but adds additional variation resulting in partner-specific relationships.

That LIKE attitude was a better predictor of attacks than rank distance is interesting and not straight forward. At low partner selectivity, dominants were groomed often by subordinates. This resulted in LIKE attitudes directed down the hierarchy, which coincides with the pattern of aggression. On the other hand, at high partner selectivity, reciprocal LIKE attitudes developed mainly between similar-ranking individuals. Here, LIKE attitudes coincided with the bidirectional pattern of aggression, which was a result of smaller rank distances and was additionally mediated by frequent proximity of similar-ranking individuals. Empirical data show similar patterns of high rates of both grooming and aggression among individuals with close relationships, such as kin (grooming: e.g. Silk et al., 2010a, 2006b; aggression: Bernstein and Ehardt, 1986).

Another ABM, the GrooFiWorld model, also generates reciprocal patterns in grooming (Puga-Gonzalez et al., 2009). Besides the obvious precondition of grouping allowing repeated interactions, the GrooFiWorld model shows that none of the three cognitive capacities (individual recognition, memorizing earlier or recent affiliative interactions and partner selectivity) considered necessary for reciprocity are actually required. The entities in this model do not recognize or remember each other (they only perceive each others dominance rank). "Choosing" whom to groom occurs randomly from the animals that happen to be nearby. Thus, this model shows that it is possible that group living entities which lack the three mentioned cognitive capacities can indeed show a correlation between giving and receiving of grooming at a group level. However, whether reciprocity in the GrooFiWorld model is simply based on dyadic similarity or whether it is partner-specific is not presented. Given the implementation of the model, it is likely that proximity determines reciprocity; indeed, grooming reciprocation at a group level disappears, when the spatial structure was taken out of the model (Puga-Gonzalez et al., 2009: Tables 4 and 5).

The spatial proximity pattern in the GrooFiWorld model is caused by the aggressive interactions and therefore reflecting the rank distances (Evers et al., 2011; Hemelrijk, 2000; Puga-Gonzalez et al., 2009). In contrast, in the EMO-model the proximity pattern is caused by agonistic interactions (involving fleeing upon being attacked, leaving or avoiding a potential aggressor) regulating repulsive movements among the model entities *as well as* by the approach behavior steered by the LIKE attitudes, regulating attractive movements. Both rank distance and LIKE attitude were about equally predictive of proximity.

In a very recent modified version of the GrooFiWorld model, *FriendsWorld* (Puga-Gonzalez, 2014), group members with whom individuals engage most in grooming (top quartile) have been defined as "friends" and model individuals preferably approach such "friends". However, preference for grooming or grooming partner choice is not affected by these "friendships". Similarly to the EMO-model, preferred proximity to "friends" in *FriendsWorld* shapes the spatial structure of the group and in this way reinforces reciprocity and interchange of certain behaviors, as compared to a model without preferred proximity to "friends". Whether this model yields partner-specific grooming reciprocity or whether reciprocity is deducible from dominance relations is not presented.

In another recent ABM study (Campenni and Schino, 2014), obligate cooperators always direct their cooperative behavior towards those (available) group members from which most cooperation was received over the past. As a result, individuals develop differentiated reciprocal relationships. Compared to the EMO-model, this model differs in many underlying assumptions. First, previous events are remembered equally well, no matter how long ago or recently they took place, while in the EMO-model some sort of memory decay was implemented. Second, always the best cooperators are chosen as interaction partners, which would be equivalent to a partner selectivity (LPS) of 1.0 in the EMO-model. Third, individuals in this model only engage in a single behavior, namely cooperation; they only chose whom to direct it to. In contrast, individuals in the EMO-model choose from a broad repertoire of potential behaviors (e.g. affiliation or agonism) towards the potential interaction partners. Fourth, in contrast to the EMO-model, no affordance for additional social or spatial structure, e.g. dominance hierarchy or proximity to affiliates, was included in the model of Campenni and Schino (2014) and the model was not spatially explicit.

When the number of available interaction partners was constrained to a very high or very low degree, the degree of reciprocation slightly decreased in the model of Campenni and Schino (2014). Differentiation of relationships decreased with constrained partner choice. Yet, this constrained partner choice is not comparable to the socio-spatial group structure that arises in the EMO-model, which not only constrains, but also naturally structures and is reinforced by the availability of specific interaction partners. In other words, socio-spatial group structure results in repeated interaction between the same individuals. As seen in the FriendsWorld model (Puga-Gonzalez, 2014), this type of constraint is expected to result in reinforced reciprocation. Similarly, in the EMO-model, increased partner selectivity (LPS) constrains the probability of affiliative behaviors towards available interaction partners and results in increased reciprocity and more differentiated, i.e. partner-specific reciprocal relationships.

The model of Campenni and Schino (2014) also varied the number of previous interactions that individuals can remember. Increased memory resulted in stronger reciprocity and differentiation. The role of memory, i.e. the timeframe of emotional bookkeeping, can also be varied in the EMO-model and is likely to have effects on the degree of reciprocity and the degree of partner-specificity as well. This will be presented elsewhere (Chapter 5).

For future research, it would be also interesting to include evolutionary processes in the EMO-model. This has been done in the model by Campenni and Schino (2014). Here, individuals employed defective or cooperative strategies, where cooperation implied a fitness cost for the actor and a benefit for the receiver. When the benefits of receiving cooperation were high enough, cooperation was evolutionarily stable. In the EMO-model, the evolutionary success of individuals that differ for instance in partner selectivity or the timeframe of emotional bookkeeping may then be investigated.

Cognitive processes underlying reciprocity

Reciprocity of affiliative behavior has been found in primates. In particular grooming is often exchanged for grooming. That reciprocity is found is no longer surprising and the current discussion focuses on the cognitive processes that determine this reciprocity, ranging from simple to complex (see Introduction). In real primates, it is difficult to disentangle which cognitive process underlies reciprocity. When simpler factors, such as rank distance or proximity, can explain (a certain degree of) reciprocity, these are preferred over more complex ones.

In contrast to earlier models (Campenni and Schino, 2014; Puga-Gonzalez, 2014), the current study explicitly implemented different cognitive processes into model entities. Both, the fixed and dynamic attitude model generate reciprocity in affiliation. However, they differ when high partner selectivity determines partner choice. The fixed attitude model results in a small number of dyads with reciprocal affiliation, all similar in characteristics and strength of the affiliating dyad. In contrast, the emotional bookkeeping model generates a broad range of dyads, where affiliation is not purely based on rank-distance and where reciprocity is thus partner-specific. In primates, partner-specific affiliative relationships, i.e. social bonds or friendships, are found that cannot be explained solely on the basis of similarity in rank, kinship or age (Leinfelder et al., 2001; Silk et al., 2006b; Silk, 2002b). Moreover, primates recognize their group members (vocalisations: Cheney and Seyfarth, 1999, 1980; pictures: Schell et al., 2011; cross-modal recognition: Adachi and Hampton, 2011). This suggests that the partner-specific affiliative behavior resulting from emotional bookkeeping may occur, possibly in combination with some dyadic similarity characteristic, but clear empirical evidence is lacking.

Several suggestions have been made how the process of emotional bookkeeping may be addressed empirically (Jaeggi et al., 2013; Tiddi et al., 2011). Although it is difficult to study “LIKE attitudes” in primates directly, one can study the development of newly started affiliative relationships by scoring the time course of affiliative behaviors, from which the corresponding temporal pattern of LIKE attitudes of both A and B can be inferred. Two studies, both addressing the mechanisms of reciprocity in primates (Jaeggi et al., 2013; Tiddi et al., 2011), make similar suggestions. In addition, new empirical evidence suggests how updating of “LIKE attitudes” may take place: grooming with favoured partners may strengthen the bond by increasing oxytocin levels, while grooming with non-favored partners does not have such an effect (chimpanzees: Crockford et al., 2013; see also Dunbar, 2010). Therefore, primates may start and maintain relationships based on affiliative interactions, consistent with the emotional bookkeeping hypothesis.

Besides studying the time course of affiliative behavior in specific dyads in a group, another suggestion for future research concerns the role of partner choice. In our dynamic LIKE attitude model the LPS parameter controls the degree of selectivity to choose a *LIKEd* partner. In line with Tiddi et al. (2011), our modelling study also suggests to investigate the combined role of partner choice and temporal pattern of affiliative events in the emergence of reciprocity. More particularly, since in our model only very high values of LPS result in partner-specific reciprocal relationships, the question arises whether this strong selectivity of grooming partners also occurs in primate groups, or whether some form of LIKE updating is used by primates, differing from the one implemented in our model.

Partner selectivity can be promoted through spatial proximity. In turn, proximity can be promoted through partner selectivity, as highly *LIKEd* partners are approached more often than less *LIKEd* ones. Preferential engagement with partners, either based on fixed characteristics, such as rank-distance or kinship, or based on dynamic LIKE attitudes, can generate group patterns of social behavior. This suggests that individual recognition may be an important organizing principle of social behavior that does not necessarily require spatial differentiation, although the social interaction patterns in the group may be enhanced by spatial differentiation. Indeed, in experimental set-ups of providing benefits to others (i.e., pro-social behavior) that control for spatial distance, individuals behave differently to individuals with whom they have different relationships: they differentiate between close social partners and other individuals and on the basis of relative dominance position (Cronin, 2012; Massen et al., 2010b). Close associates and lower-ranking individuals are more often benefited than random group members or higher-ranking individuals (Cronin, 2012). This suggests that primates may possess partner-specific attitudes and may use them in their behavioral decisions.

In sum, there are clear indications that primates may use emotional bookkeeping to establish and maintain relationships. They have individual recognition, exert partner choice and have partner-specific attitudes. This does not preclude effects of rank-distance or other dyadic similarity characteristics, but may be used next to them. However, convincing empirical evidence of emotional bookkeeping is still lacking.

Conclusion

In sum, reciprocity of grooming may depend on simple rules, as modeled in the fixed attitude model, where FEAR and LIKE attitudes are both fixed and purely dependent on rank distance, and where individual recognition does not play a role. However, this model fails to generate partner-specific reciprocal affiliative dyads, and therefore cannot explain such patterns found in primates (e.g. Leinfelder et al., 2001). In the dynamic attitude model partner-specific reciprocity patterns emerge due to emotional bookkeeping. Here, two emotional dimensions regulate and are regulated by social behavior, allowing for self-reinforcing feedback loops between behavior selection and partner preferences. Embedding behavioral decision making into a framework of emotional processes promises to provide a better understanding of the links between different levels of organization (e.g. Giske et al., 2013). Thus, using an ABM to model relatively complex cognitive processes can inform us on the group-level consequences of these capacities relative to simpler processes. Our EMO-model suggests that emotional bookkeeping in combination with a high degree of partner selectivity (“choosiness”) may result in partner-specific affiliative relationships, suggesting that more complex processes like calculated reciprocity are not necessary for the emergence of differentiated social bonds.

Acknowledgments

We want to thank the anonymous reviewers for some useful suggestions for improvement of the manuscript.

SUPPLEMENTARY MATERIAL

State Variable Name	Description	(Initial) Value	Possible Range or Values	Fixed / Dynamic
General state variables				
<i>myTIME</i>	Waiting time until next scheduled activation	1 ± 0.05 min (mean \pm SD)	May range between 0.0 (attack received) and 7.5 ± 0.375 min (rest/groom) (depending on the social context)	Dynamic
<i>myDOM</i>	Dominance strength	Between $1/N$ and 1.0	Scaled between $1/N$ (lowest-ranking) and 1.0 (highest-ranking)	Fixed
<i>mySCAN_PROB</i>	Probability of employing scanning	Depends on arousal and current behavior	May range between 0.0 and 1.0 (depending on arousal and current behavior)	Dynamic
<i>myVIEW_ANGLE</i>	Width of currently employed view angle	120°	May be either 120° (not scanning) or 360° (scanning)	Dynamic
Emotional state variables				
<i>myAROUSAL</i>	Arousal state	0.09	May range between 0.0 (inactive) and 1.0 (aroused)	Dynamic
<i>mySATISFACTION</i>	Affiliation-related emotional state	0	May range between 0.0 (unsatisfied) and 1.0 (satisfied)	Dynamic
<i>myANXIETY</i>	Agonism-related emotional state	0	May range between 0 (not anxious) and 1 (anxious)	Dynamic
<i>myAROUSAL_LIMIT</i>	Arousal level that is approached over time	0.09	May be 0.03 (grooming received), 0.04 (grooming given), 0.09 (default), 0.12 (dominant perceived), 1.0 (aggression)	Dynamic
<i>myANXIETY_LIMIT</i>	Anxiety level that is approached over time	0	May be 0.0 (not anxious) or 1.0 (anxious)	Dynamic
<i>mySATISFACTION_LIMIT</i>	Satisfaction level that is approached over time	0	May be 0.0 (not satisfied) or 1.0 (satisfied)	Dynamic
Emotional attitude variables				
<i>FEAR_{ij}</i>	Agonism-related emotional attitude from individual <i>i</i> to <i>j</i>	$myDOM_j - myDOM_i$	$myDOM_j - myDOM_i$	Fixed
<i>LIKE_{ij}</i> (dynamic attitude model)	Affiliation-related emotional attitude from individual <i>i</i> to <i>j</i>	0	May range between 0 (neutral) and 1 (preferred affiliation partner)	Dynamic
<i>LIKE_{ij}</i> (fixed attitude model)	Affiliation-related emotional attitude from individual <i>i</i> to <i>j</i>	$0.243 - abs(FEAR_{ij}) * 0.36$	$0.243 - abs(FEAR_{ij}) * 0.36$	Fixed

Table S4.1: Individual-specific state variables of the model entities.

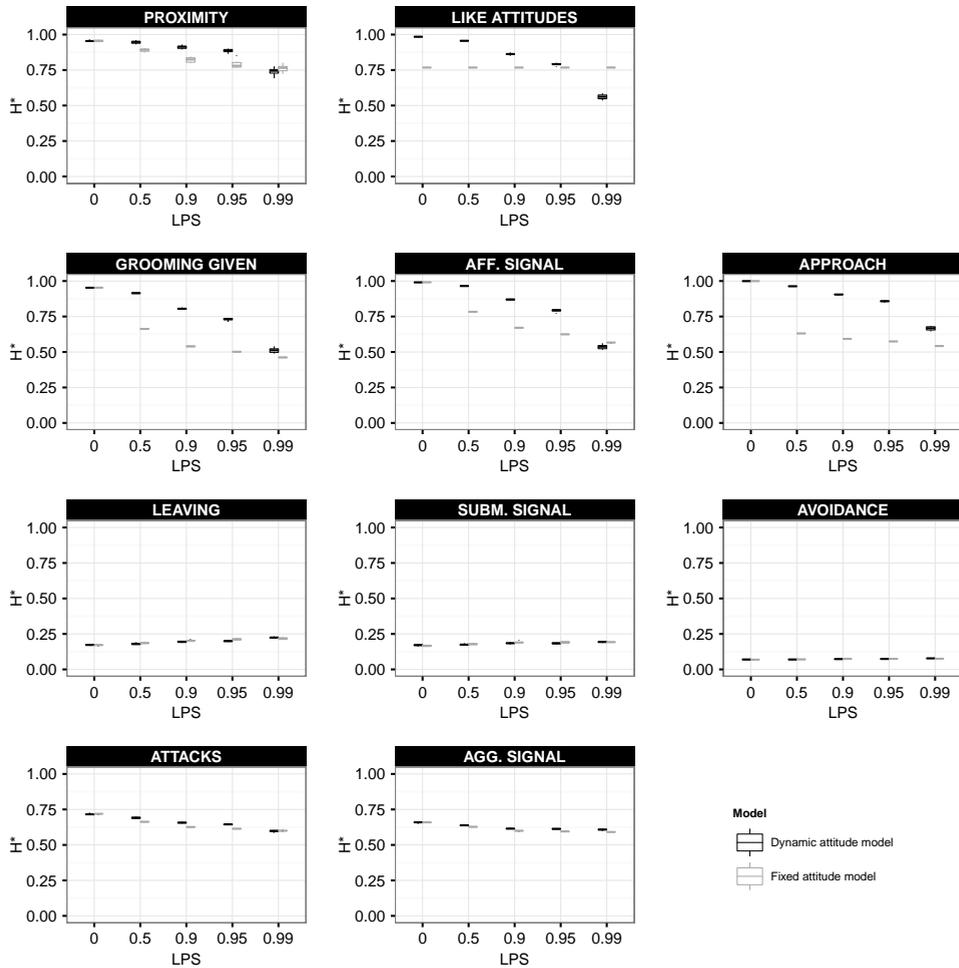


Figure S4.1: Shannon indices for the behaviors. This figure shows Shannon indices (H^*) of the behaviors at different settings of selectivity (LPS) in the dynamic (black box-plots) and the fixed (grey box-plots) attitude model. A Shannon index of 1 indicates that the behavior is distributed equally among all potential receivers, while a lower H^* indicates that the behavior is directed more selectively at certain individuals. $H^* = 0$ would indicate a behavior that is only directed at one group member. Shannon indices were calculated based on the interaction matrices averaged over one YEAR. The box-plots show the group means of 10 simulation runs.

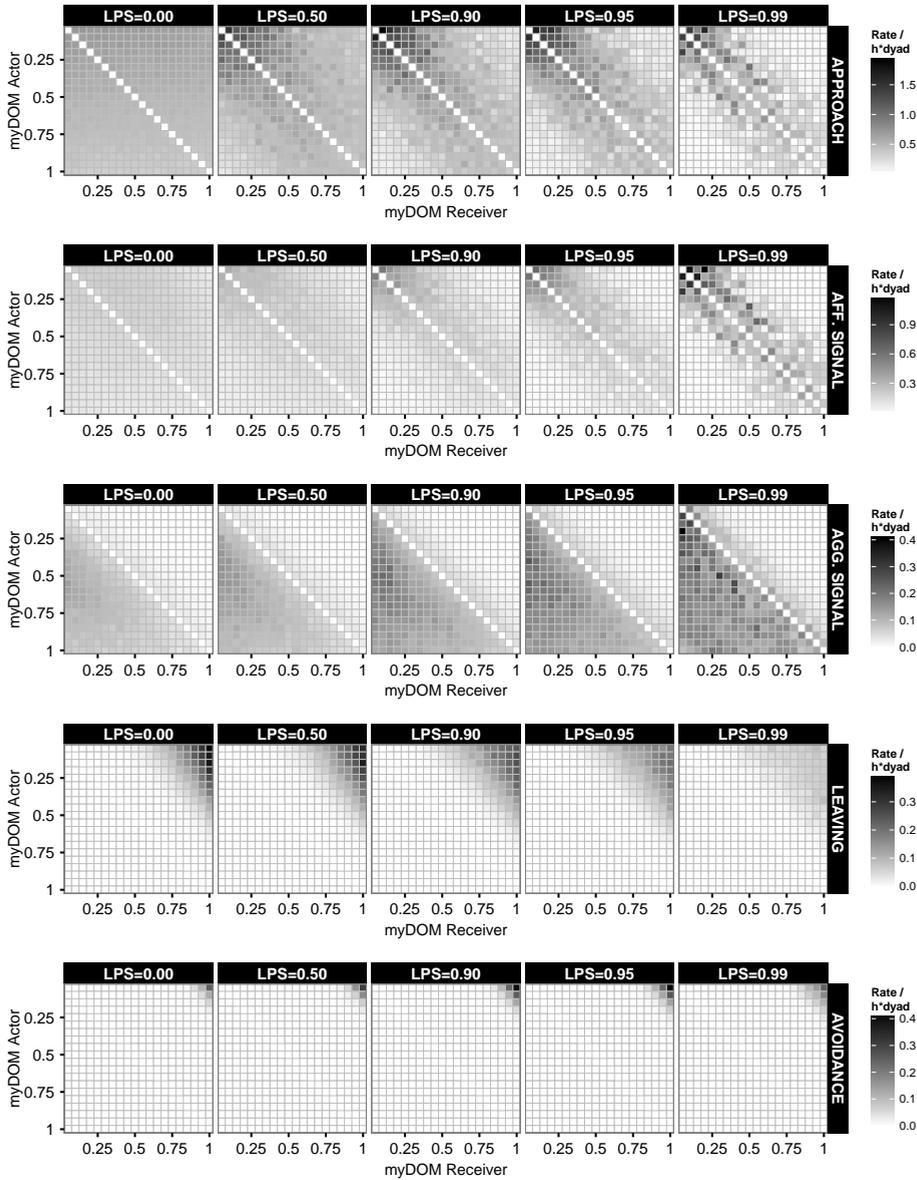


Figure S4.2: Interaction matrices of additional behaviors in the dynamic attitude model. This figure shows the dyadic behavioral rates of a group at different settings of selectivity (LPS) in the dynamic attitude model. Behaviors are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking ($\text{myDOM}=0.05$) to high-ranking ($\text{myDOM}=1.0$) individuals. All behaviors are measured in occurrences per HOUR. The plot shows the behavioral rates of one example run averaged over one YEAR. Dark shades represent high rates. Values at the diagonal are by definition not applicable. The distribution of proximity scores, LIKE attitudes, grooming given, attacks and submissive signals are presented in Figure 4.2.

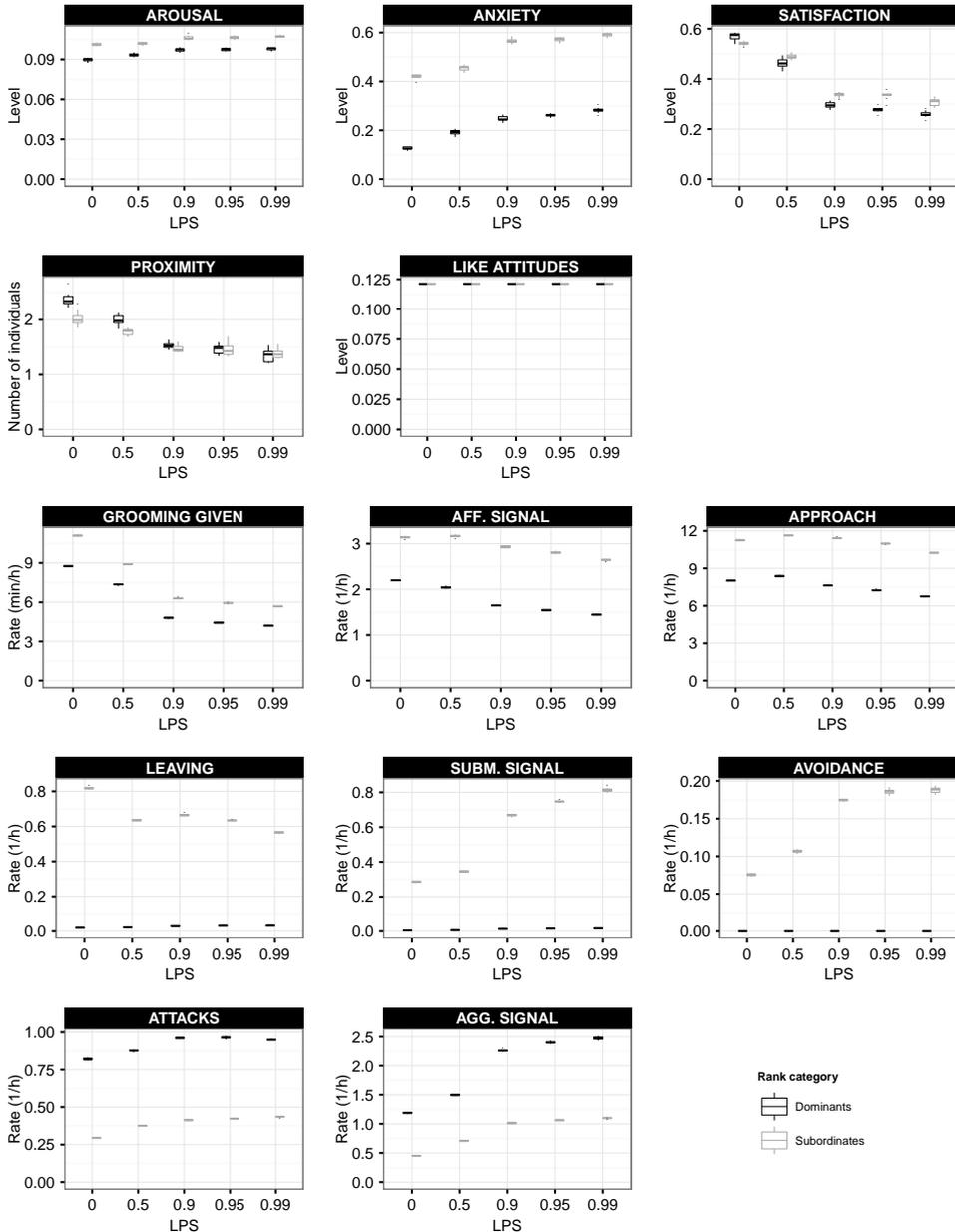


Figure S4.3: Emotional levels and behavioral rates per rank category in the fixed attitude model. This figure shows the averaged levels of the emotional state and the rates of behavior per individual for dominants (black box-plots) and subordinates (grey box-plots) at different settings of selectivity (LPS) in the fixed attitude model. For more details on the measures see caption of Figure 4.1 in the current Chapter and Figure 3.4 in Chapter 3. The box-plots show the results of 10 simulation runs, averaged over 1 YEAR.

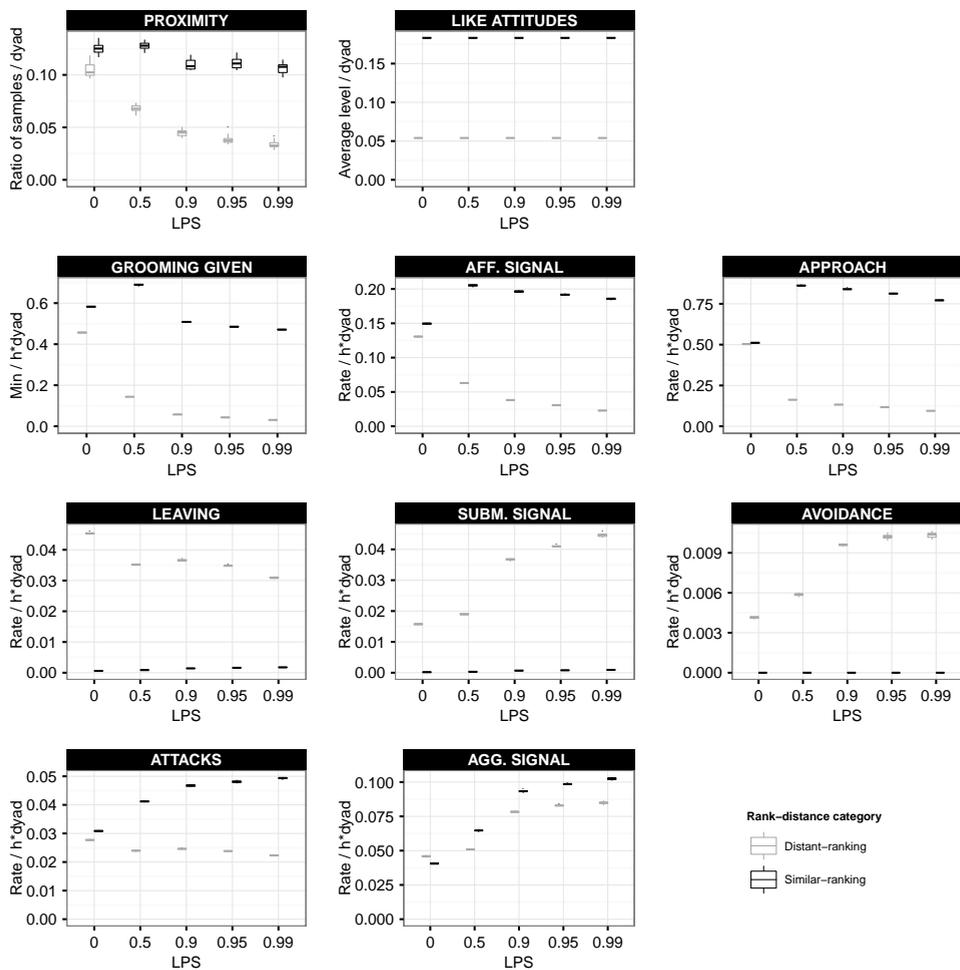


Figure S4.4: Behavioral rates per rank-distance category in the fixed attitude model. This figure shows the averaged behavioral rates for distant-ranked (grey box-plots) and similar-ranked (black box-plots) dyads at different settings of selectivity (LPS) in the fixed attitude model. For more details on the specific behaviors and how they were measured see caption of Figure 4.1. The box-plots show the results of 10 simulation runs, averaged over 1 YEAR.

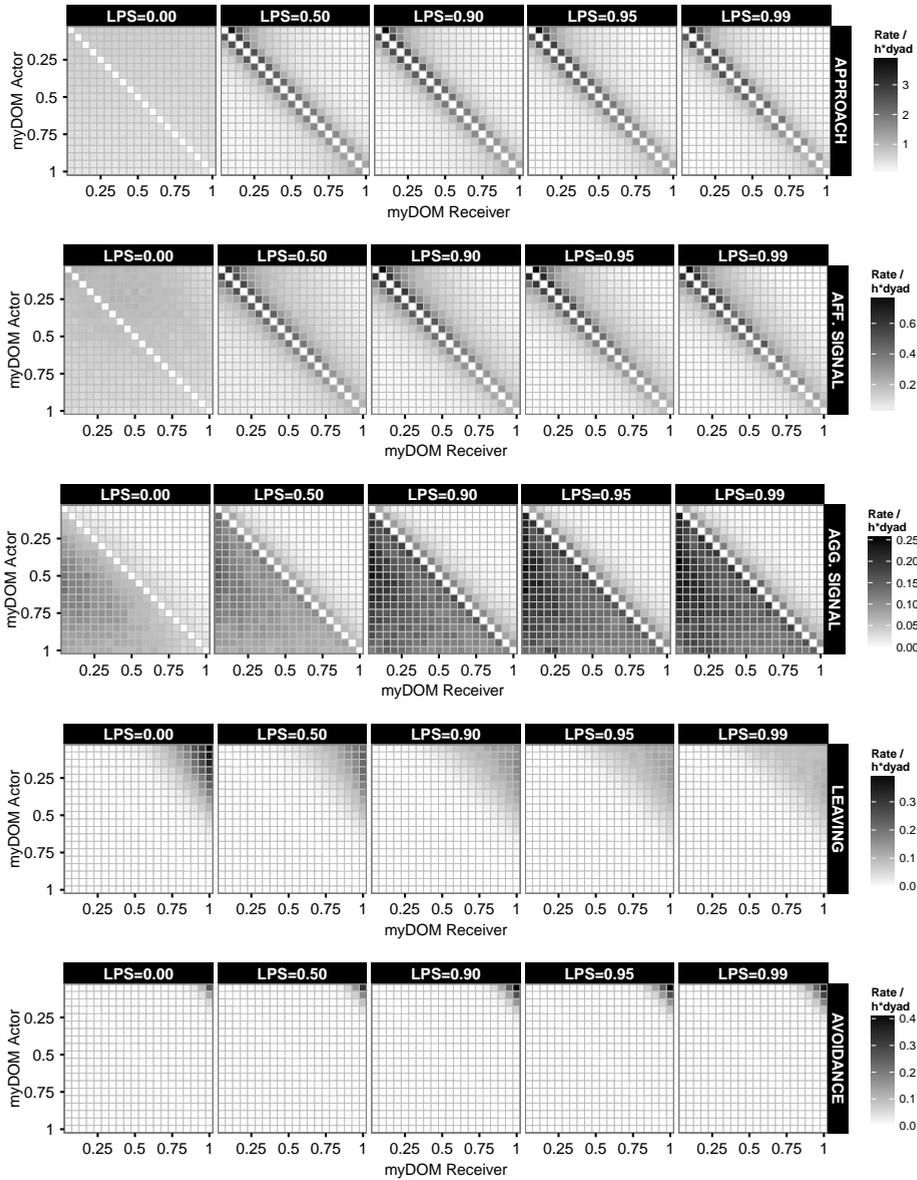


Figure S4.5: Interaction matrices of additional behaviors in the fixed attitude model. This figure shows the dyadic behavioral rates of a group at different settings of selectivity (LPS) in the fixed attitude model. Behaviors are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking ($myDOM=0.05$) to high-ranking ($myDOM=1.0$) individuals. All behaviors are measured in occurrences per HOUR. The plot shows the behavioral rates of one example run averaged over one YEAR. Dark shades represent high rates. Values at the diagonal are by definition not applicable. The distribution of proximity scores, LIKE attitudes, grooming given, attacks and submissive signals are presented in Figure 4.4.

5

Intermediate, not long-term or short-term emotional bookkeeping is necessary for the maintenance of long-term reciprocal grooming partner preferences in an ABM of primates

ABSTRACT

Whether and how primates are able to maintain long-term affiliative relationships is still under debate. Emotional bookkeeping, the partner-specific accumulation of emotional responses to earlier interactions, is a candidate mechanism that does not require high cognitive abilities. Emotional bookkeeping is difficult to study in real animals, due to the complexity of primate social life. Therefore, we developed an agent-based model, the EMO-model, that implements arousal and two emotional dimensions, anxiety-**FEAR** and satisfaction-**LIKE**, that regulate social behavior. To implement emotional bookkeeping, model individuals assign dynamic **LIKE** attitudes towards their group members, integrating partner-specific emotional responses to earlier received grooming episodes. Two key parameters in the model were varied to explore their effects on long-term affiliative relationships; 1) the timeframe over which earlier affiliation is accumulated into the **LIKE** attitudes; and 2) the affiliative partner selectivity. Emotional bookkeeping over short and long timeframes gave rise to low variation in **LIKE** attitudes and grooming partner preferences were only maintained over one or two months. Only emotional bookkeeping over intermediate timeframes resulted in enough variation in **LIKE** attitudes, which, in combination with high partner selectivity, enables individuals to differentiate between regular and incidental grooming partners. These specific settings resulted in a strong feedback between differentiated **LIKE** attitudes and the distribution of grooming, giving rise to strongly reciprocated partner preferences that could be maintained for longer periods, occasionally up to one or two years. Moreover, at these settings the individual's internal, emotional memory of earlier affiliative episodes (**LIKE** attitudes) corresponded best to the external, measurable behavior (grooming partner preferences). In sum, our model suggests that intermediate **LIKE** dynamics and high partner selectivity seem most plausible for primates relying on emotional bookkeeping to maintain their social bonds.

INTRODUCTION

Group-living animals can have varied social relationships with their group members. In primates, this variation has been extensively investigated and different types of relationships are distinguished, for example dominance relationships, kinship and affiliative relationships (social bonds). Relationships among kin usually show high rates of proximity and mutually high

grooming frequencies, and are therefore considered of higher quality than non-kin relationships with scarce grooming (e.g. Silk et al., 2006b,a). However, non-kin relationships can vary in their quality based on high or low rates of proximity and grooming (Silk, 2002b; Massen et al., 2010a; Massen and Sterck, 2013). The quality of social relationships may not only be affected by, but may also affect patterns of social behavior (Hinde, 1976). Moreover, social relationships provide a substrate for evolution, as strong bonds with kin and non-kin partners may provide fitness benefits (baboons: Silk et al., 2003, 2009, 2010b; feral horses: Cameron et al., 2009; bottlenose dolphins: Frère et al., 2010 and rhesus macaques: Kulik et al., 2012; Massen et al., 2012). Therefore, the nature and number of relationships are important features of group living animals.

Social relationships are defined as (consistent) patterns in social interactions between two individuals and are the elements underlying the social (group) structure (Hinde, 1976). Whether such relationships only exist in the mind of the observing researcher (Barrett and Henzi, 2002; Barrett et al., 2007) or are also represented in the mind of the interacting animals themselves (Schino and Aureli, 2009) is debated. Some interaction patterns, which may be abstracted by the observing researcher as relationships or social structure, may arise without the participants' knowledge of such relationships or social structure. For instance, interaction patterns may simply arise as a consequence of non-random proximity patterns (de Waal and Luttrell, 1988) that emerge from the movements of the individuals relative to each other. Model studies have shown that spatial centrality of dominants, a socio-spatial group pattern often reported in primates (Evers et al., 2011), may simply arise as a result of differential fleeing, avoidance, velocity or social vigilance (Hemelrijk, 2000; Bryson et al., 2007; Evers et al., 2011, 2012), even when the model individuals have no preference for any particular spatial location or any particular group member whatsoever. Such spatial structuring determines who encounters whom and may thus also determine the interaction structure, e.g. resulting in more frequent interactions between similar-ranking individuals compared to distant-ranking (Hemelrijk, 2000; Evers et al., 2011, 2012). Besides spatial proximity, also short-term benefits may affect the behavior of individuals and their choice of interaction partners (Barrett and Henzi, 2002; Barrett et al., 2007). This may also result in consistent interaction patterns, which are not necessarily perceived by the involved individuals themselves. For instance, immediate returns to be gained from grooming, such as a positive emotional state, hygiene or access to infants, may be sufficient to explain grooming reciprocity in baboons (Barrett et al., 1999; Barrett and Henzi, 2002). In light of the parsimony principle (Occam's razor), such simple explanations of social interaction patterns would be favored over cognitively more demanding ones.

However, research suggests that primates are able to recognize their social relationships with others (Cheney and Seyfarth, 1990b) and even relationships among others (e.g. kinship: Cheney and Seyfarth, 1986, 1990b; Dasser, 1988; dominance: Cheney and Seyfarth, 1982; Bergman et al., 2003; Massen et al., 2011; pair bonds: Kummer et al., 1974) and has led to the common view that primate social relationships are not only distinguished by researchers, but are also of primates discern.

Different candidate mechanisms have been proposed to explain how individuals may internally represent their relationships with others. A cognitively relatively simple mechanism is emotional bookkeeping (Aureli and Schaffner, 2002; Aureli and Schino, 2004; Schino and Aureli, 2009): the emotional impact of previous interactions with a specific partner is integrated in an emotional valuation of the relationship with this particular partner, i.e. an emotional attitude, and may affect subsequent behavior towards this partner. The internal representation of such an emotional attitude relies on individual recognition (Aureli and Schaffner, 2002), but does not require a specific memory of who did what and when (*episodic-like memory*: Crystal, 2009).

Perceiving another group member may simply elicit the current emotional attitude associated with that animal. A cognitively more complex process is calculated bookkeeping (required for *calculated reciprocity*, de Waal and Luttrell, 1988; Brosnan and de Waal, 2002): individuals keep track of the previous interactions employing mental scorekeeping of given and received behaviors.

Emotional bookkeeping may explain some behavioral patterns in primates and other species. For instance, a study on macaques reported that coalition formation in the mating season could be predicted by affiliation patterns several weeks earlier, even after controlling for affiliation in the mating season itself (Berghänel et al., 2011). Moreover, many empirical studies have reported evidence of highly individualized affiliative relationships in animals, where strong social bonds with a few (kin and/or non-kin) partners were often more reciprocal than weak social bonds and could be maintained over long periods of time, up to several years (baboons: Silk et al., 2006a, 2010a, 2012; macaques: Massen and Sterck, 2013; chimpanzees: Langergraber et al., 2009; Lehmann and Boesch, 2009; Mitani, 2009; Koski et al., 2012; African elephants: Archie et al., 2006; Moss et al., 2011 and bottlenose dolphins: Connor et al., 2000, 2001; Wiszniewski et al., 2010, 2012). However, these studies cannot completely rule out that the emerging interaction patterns (taken as indicative of the social relationships) result from simple association rules. In short, which cognitive processes are necessary (and sufficient) for variation in relationship quality and long-term social bonds is difficult to investigate in real animals. Agent-based models form a theoretical tool complementary to empirical research to investigate this. (Evers et al., 2014).

Agent-based models (ABMs) are a well-established tool to systematically study and understand structuring mechanisms in a complex system of interacting entities (Hogeweg and Hesper, 1979; Bryson et al., 2007). The implemented rules and internal (emotional/cognitive) processes of the model entities determine their selection of behaviors (concerning interactions, partner choice and movement), but depend on and in turn affect the (local) social environment, thereby resulting in specific social and spatial structures on the group-level. Agent-based modeling is an ideal tool to compare the effect of different behavioral rules and internal processes, since these are explicitly formulated and their consequences are measurable in a way that is not possible for real group-living individuals. One specific advantage of ABMs, especially in the context of studying social interactions of animals in relation to their perceptual, emotional, cognitive and communicative abilities, is the requirement to be explicit, which forces the modeler to focus on these abilities from the point of view of the animal (de Vries and Biesmeijer, 1998).

In a previous paper (Evers et al., 2014), we presented an ABM, dubbed the *EMO-model*, in which we implemented emotional bookkeeping and its underlying mechanisms. In this model, social interactions elicit a positive or negative emotional response (satisfaction/anxiety) in the individuals, which may affect an individual's subsequent behavior on the short term. Moreover, individuals in the model assign positive or negative attitudes to their group members, which affect partner-specific behavioral tendencies concerning affiliation (LIKE attitude) and agonism (FEAR attitude) over a longer term (see Figure 3.2 in Chapter 3). In the EMO-model the FEAR attitude is fixed and linked to the difference in (fixed) dominance rank (cf. Evers et al., 2011, 2012 and the model in the appendix of Bryson et al., 2007). In contrast, LIKE attitudes are dynamically changing upon (the lack of) affiliation received from group members. The partner-specific LIKE attitude quickly integrates the positive emotional responses to received affiliation from the respective partner and slowly decreases over time. Thus, strong LIKE attitudes may develop fast, but are only maintained towards regular groomers. In this way, dynamic partner-specific LIKE attitudes represent a form of emotional bookkeeping (cf. Aureli and Schaffner, 2002; Aureli and Schino, 2004; Schino and Aureli, 2009).

Previous investigation of the EMO-model concerned how the emergent interaction patterns in the group depend on LIKE-PARTNER SELECTIVITY (LPS), i.e. the degree to which individuals prefer to affiliate with partners that are assigned high LIKE attitudes (Chapter 4). When LIKE attitudes did not affect partner choice (LPS=0), developing affiliative relationships were purely based on proximity and dominance relations. At intermediate partner selectivity (LPS= 0.5 or LPS=0.9), rank difference was a good predictor of affiliative relationships, i.e. the correlation between rank difference and LIKE attitudes was enhanced. Only high partner selectivity (LPS=0.95) resulted in the emergence of individualized affiliative relationships that depended on the partner-specific affiliation history (LIKE attitudes). A control-model with fixed LIKE attitudes (based on rank-distance), did not yield such individualized affiliative relationships, even when partner selectivity was high. This shows that, in our EMO-model, dynamical emotional bookkeeping and high partner selectivity are necessary and sufficient for the emergence of individualized affiliative relationships (Chapter 4). In the EMO-model, high partner selectivity allows for a strong coupling of received grooming, developing LIKE attitudes and subsequent grooming partner selection, yielding self-reinforcing affiliative relationships.

The conditions under which emotional bookkeeping can lead to long-term stability of social bonds are still unclear (Aureli and Schaffner, 2002; Schino and Aureli, 2009; Schino et al., 2009). Whether social bonds are maintained or exist only temporarily may depend on a) how often individuals encounter each other; b) the impact of affiliative behavior on the perceived quality of the relationship (i.e. the LIKE attitude towards the partner); c) whether the perceived relationship quality (LIKE attitude) may saturate (i.e. additional affiliation does not result in a higher LIKE attitude); and d) how quickly LIKE attitudes (*emotional memory*) decay over time (Stevens and Hauser, 2004). In the current paper we specifically explore the latter factor, i.e. the temporal dynamics of emotional bookkeeping, and its effect on long-term affiliative relationships.

Thus, we investigated in the EMO-model which temporal conditions of emotional bookkeeping are sufficient (and necessary) to yield long-term stability of individualized affiliative relationships. To do this, we systematically varied the decay of LIKE attitudes, i.e. the timeframe over which emotional responses to earlier received affiliation could be remembered. Additionally, we varied the degree of partner selectivity (LPS), i.e. the degree to which (short-term or long-term) emotional bookkeeping affects the individuals' partner choice and behavior. We investigated which specific settings of *emotional memory decay* and *partner selectivity* would yield long-term social bonds. Particularly, we were interested in the number, duration, stability and reciprocity of (strong) social bonds, and in how well the internal representation of affiliative relationships (LIKE attitude) corresponded to its expression in external measurable affiliative behavior.

METHODS

Simulations were run using NetLogo 5.0.2 (Wilenski, 2007). The program code of all models will become available via the website of the first author¹. Below, we describe our models according to the updated ODD protocol (Grimm et al., 2010), which is a standardized method of describing agent-based models. This ensures the model description to be more complete and better comparable to other models, allowing also reproducibility of the model. The ODD protocol contains an *Overview*, *Design concepts*, and *Details*. The detailed ODD protocol information on the EMO-model can be found elsewhere (Evers et al., 2014). Additionally, this methods section includes parts on the *Simulation experiments* and the *Statistical analysis*, which are not part of the ODD protocol.

¹<https://sites.google.com/site/elleneversutrecht/models>

Overview

Purpose

The purpose of this model is to explore certain capacities of socio-emotional information integration (emotional bookkeeping) that may be used in macaques to develop and maintain social relationships, and their effect on the emergent properties of affiliative relationships. First, we studied the timeframe over which earlier affiliation (in contrast to current affiliation) is incorporated into LIKE attitudes. In other words, the appreciation of affiliation partners may be based either on a short-term or long-term summary of earlier grooming experiences, and this is expected to affect the structure and stability of affiliative relationships. Second, we varied the affiliative partner selectivity, i.e. the degree to which individuals prefer affiliation partners towards whom they assign a high LIKE attitude, to study its effect on the stability and duration affiliative relationships.

Entities, state variables and scales

We simulated the movements and interactions of 20 primate-like model individuals. These individuals are characterized by a number of state variables (see Table S3.1 in Chapter 3 and see below). These state variables are identical to the ones used in the introductory paper on the EMO-model (Chapter 3).

Individuals are characterized by their dominance strength (`myDOM`), which does not change over time or after interactions (Bryson et al., 2007; Evers et al., 2011, 2012, 2014). Individuals differ in their schedule time (`myTIME`), their (current) scanning probability (`myPscan`) and in the current width of their view angle (`myVIEW_ANGLE`), which all change dynamically over the course of the simulation.

Our model entities are further described by their emotional state, consisting of arousal, anxiety and satisfaction (`myAROUSAL`, `myANXIETY` and `mySATISFACTION`), i.e. an individual's state of alertness and an aversive and a pleasant dimension of the emotional state. Arousal, anxiety and satisfaction may change dynamically over time depending on the social context ego (i.e. a model entity) had experienced. Depending on the social context, arousal, anxiety and satisfaction approach a respective limit value over time (`myAROUSAL_LIMIT`, `myANXIETY_LIMIT`, `mySATISFACTION_LIMIT`). Model individuals are also characterized by partner-specific emotional attitudes (LIKE and FEAR), which they assign to each group member. In our model, agonism-related FEAR attitudes are fixed, while affiliation-related LIKE attitudes are dynamically changing over time depending on partner-specific affiliation history.

General model parameters are identical to those used in the introductory paper on the EMO-model (Chapter 3) and are summarized in Table S5.1. The modeled environment is a continuous two-dimensional grid (300 × 300 grid units) with a torus shape to exclude disturbing border effects. The length of one grid unit resembles 1 “meter”. We did not explicitly implement ecological features of the environment; in the model an individual's environment is purely social.

One time step in the simulation resembles 1 MINUTE. One HOUR consists of 60 MINUTES and we defined 12 HOURS as one DAY, 7 DAYS as 1 WEEK and 50 WEEKS as 1 YEAR. To define one MONTH we divided one YEAR (350 DAYS) into 12 equal periods of ca. 29 DAYS. Simulations were run for 504 000 time steps, i.e. 2 YEARS, plus a prior stabilization period.

In contrast to earlier papers (Chapter 3-4), we here varied two parameters across the simulation experiments, namely the LIKE-HISTORY WEIGHT (LHW) and the LIKE-PARTNER SELECTIVITY (LPS). LHW describes the timeframe over which earlier affiliation (in contrast to current affiliation) is incorporated into the LIKE attitudes and was set to 0, 180, 720, 5 400 or 21 600 MINUTES, respectively. LPS defines the degree to which individuals selectively prefer valuable individuals as grooming partners and was set to 0.00, 0.50, 0.90, 0.95 or 0.99, respectively (see Table S5.1). LHW directly affects the speed of the LIKE dynamics, as higher LHW result in a slower decrease and stabilization of LIKE attitudes and other related patterns (see Submodel LIKE attitudes). Therefore, settings of high LHW required longer stabilization periods prior to the data-recording period of 2 YEARS, than low LHW (see Table S5.1). Thus, the duration of the stabilization period ($TIME_{STAB}$) was dependent on the setting of LHW and defined as follows:

$$TIME_{STAB} = \begin{cases} 100 \text{ HOURS} & \text{if } LHW < 200 \text{ MINUTES} \\ 30 * LHW & \text{else} \end{cases} \quad (5.1)$$

Note, that the minimum duration of the stabilization period was set to 100 HOURS.

Process overview and scheduling

Our model is event-driven. Most social behaviors are modeled as discrete events in time, except for moving, resting and grooming, which are modeled as continuous duration behaviors. Time is modeled on a continuous scale and during a simulation run individuals' activations are regulated by a timing regime. The general process overview and the scheduling are identical to those used in the introductory paper on the EMO-model (see Chapter 3 and Figure 3.1).

Each time, the agent with the lowest schedule time is activated first. Whenever an individual is activated, first all model entities update those state variables that may have increased or decreased over the time interval that has passed since the last activation of an entity (arousal, anxiety, satisfaction, LIKE attitudes). If the activated individual had scheduled a movement action, that action is executed; else, ego checks the grouping criteria and, if necessary, employs grouping. If no grouping and no movement are to be performed, ego may select a social behavior, resting or random movement within the group. Which behavior (and which interaction partner) gets selected depends on ego's own emotional state, as well as on it's emotional attitudes towards the potential interaction partners. Subsequently, the selected behavior may affect emotional attitudes of involved individuals, as it may affect the emotional state of ego, of receivers and observers of the behavior. As a consequence, ego, receivers and observers may be activated sooner or later, depending on the behavior executed.

Thus, after activation, the next activation of ego, but also that of interaction partners or bystanders, is scheduled anew. The exact time until an individual's next activation depends on the behavior performed, received or observed, respectively. As movement, resting and grooming are implemented as duration behaviors, they are performed in bouts. After starting a movement bout ego is activated each 3 SECONDS to execute the last movement "step" and to decide whether the movement bout is to be continued. After starting a grooming or resting bout ego is activated anew after 7.5 ± 0.375 MINUTES (mean \pm SD). Social interactions may involve (and therefore activate) other group members and may also interrupt a grooming or resting bout. Whenever ego receives an attack, it is immediately activated to respond with either fleeing or a counter attack. Whenever ego receives a signal or observes an attack nearby, a fast reaction is required and ego is activated 0.1 ± 0.005 SECONDS (mean \pm SD) later to select an action.

Design Concepts

Basic principles

In our model, receiving affiliation affects the general emotional state (arousal, anxiety and satisfaction) of individuals, as well as their affiliative attitude (LIKE attitude) directed to the actor of affiliation. In turn, an individual's emotional state affects its general short-term probability of executing certain behaviors. In this way, emotional processes regulate spontaneous behaviors as well as appropriate responses to received behaviors. Partner-specific LIKE attitudes summarize earlier received affiliation from specific individuals on a shorter- or longer-term, depending on the setting of LHW (LIKE-HISTORY WEIGHT) in the model. In turn, LIKE attitudes affect the probability of affiliating with these individuals and, in this way, regulate the development and maintenance of affiliative relations. This regulation of behavior via emotional processes and dynamic LIKE attitudes has already been introduced and described in detail elsewhere (Evers et al., 2014). In the current paper, the exploration of different settings of LHW in the model provides insights about the timeframe of emotional bookkeeping and its consequences for the stability and duration of individual-specific affiliative relationships.

Emergence

In agent-based models, individual behavior is imposed by the model rules, while group-level properties are usually not implemented explicitly into the model, but rather emerge from the interactions of the lower-level entities, i.e. the individuals. In our model, behavioral patterns, e.g. affiliation, aggression and proximity, are emergent properties arising from the interactions of the model entities. The structure of the network of LIKE attitudes and group level properties such as reciprocity and partner-specificity are an emergent property arising from the interrelation between emotional attitudes and affiliative behavior.

Adaptation

The model entities change their behavior in response to changes in their general emotional state and their emotional attitudes towards others and individuals (implicitly) seek to increase satisfaction and to decrease anxiety. As appropriate behavior is mediated by emotional processes, this yields a homeostatic regulation system. In this way, we aimed to produce adaptive (in the sense of flexible) behavior and emerging group properties that are representative of observations of the social behavior of real primates.

Learning

Individuals in the dynamic attitude model regularly update their partner-specific LIKE attitudes assigned to other group members, based on earlier grooming received from these individuals. This may be seen as a (basic) form of "learning". Emotional bookkeeping provides individuals with summarized information on "valuable" affiliation partners, which may dynamically change over time according to these partners' behavior. In this way, individuals "learn" with which specific partners they should affiliate.

Sensing

The individuals' sensing capabilities in this model are identical to those used in the introductory paper on the EMO-model (Evers et al., 2014). Individuals in our model may perceive the location, certain behaviors and signals of other group members, but only *locally* within certain distances and within a specific view angle. The exact distances depend on the salience of the perceivable information. Individuals are able to perceive (or know) the dominance strength of other group members and perception of a group member elicits ego's internal valuation of this group member, i.e. its FEAR and LIKE attitude that are assigned to this specific individual.

Interactions

Interactions are implemented identically as described in the introductory paper on the EMO-model (Evers et al., 2014). Social interactions in our model can be categorized as affiliative, submissive and aggressive behaviors. Affiliation comprises grooming, affiliative signaling and approaching; submission comprises leaving, submissive signaling and avoiding; and aggression comprises attacking and aggressive signaling.

Potential interaction partners are the 10 nearest recognizable individuals (within *MAX_DIST* and ego's current view angle). The potential behavioral probabilities towards these 10 (or less) individuals depend on ego's emotional attitudes (FEAR and LIKE) assigned to those individuals and ego's general emotional state (arousal, anxiety, satisfaction). One behavior towards one specific interaction partner is chosen randomly according to those probabilities.

Some social interactions can only be performed towards group members within a certain distance. Individuals within *INTERACT_DIST* (1 m) can be groomed, left or attacked. Individuals within *PERS_DIST* (5 m) can receive (affiliative, submissive or aggressive) signals. Individuals within *MAX_DIST* (50 m) can be approached and individuals within *PERS_DIST* (5 m) can be avoided.

Stochasticity

In our model, many processes are not implemented deterministically, but include some degree of stochasticity, to produce variability in those processes. Those processes include action selection, the determination of the winner of an escalated fight, the random walk procedure and the timing regime.

Observation

For the analysis of our model, we only used data that were recorded during the last 504 000 time steps of each simulation run, i.e. the 2 YEARS after the stabilization phase, to avoid transient spatial and social group effects due to the initial random placement.

Dyadic LIKE attitudes were sampled every 3.5 DAYS and then averaged (per dyad) over the last YEAR for each simulation run. Dyadic grooming rates were recorded (per dyad) over each recording interval of 3.5 DAYS and then divided by the duration of the recording interval to obtain average hourly behavioral rates.

Note that LIKE attitudes and grooming are always directed from an actor to a receiver and are thus not symmetric by definition.

To illustrate the variation in LIKE attitudes over time, we also provide snapshots of the LIKE attitudes at single points in time. For this snapshot, LIKE attitudes were sampled at the time step after the first and the second YEAR of the recording period.

To calculate long-term measures, such as the number of biennial, monthly or preferred partners, the bout duration and the total duration of grooming partner preferences, grooming rates were sampled over the whole recording period, i.e. over 2 YEARS.

Details

Initialization

The initial settings are identical to the introductory paper on the EMO-model (Evers et al., 2014) and are summarized in Table S3.1 in Chapter 3. At the initialization of each simulation run, the x-coordinates and the y-coordinates of the 20 individuals were drawn randomly from a predefined circular sphere with an arbitrary diameter of 50 m. The individual's initial heading was set to a random orientation between 1° and 360° and the initial view angle was set at 120° for each individual. Each individual's level of arousal was set to the default arousal level (0.09) and the level of anxiety and satisfaction was set to 0.0. LIKE attitudes were initialized at 0.0. The initial schedule time for each individual was drawn randomly from a normal distribution with a mean of 1 MINUTE and a standard deviation of 0.05 minutes.

Submodels

The implementation of all processes in our model is identical to the introductory paper on the EMO-model (Evers et al., 2014). This section broadly describes the main processes implemented in the EMO-model. It covers the implementation of the emotional state (arousal, anxiety and satisfaction), the partner-specific emotional attitudes (LIKE and FEAR), the process of action selection, perception and signaling processes, scanning, movement, grouping, grooming and resting, and attack, counter-attack and escalated fight. For a detailed description, the substantiation, parameterization and validation of our model we refer the reader to our earlier paper (Chapter 3).

Arousal In our model, an individual's arousal level, i.e. its responsiveness or tendency to be active, increases in response to receiving, executing or observing aggression or when in proximity of a dominant individual. On the other hand, arousal may decrease over time and in response to receiving submissive or affiliative behavior and executing affiliative behavior. The extent of arousal change depends on the emotional salience of the stimulus (see Table S3.5 in Chapter 3). Arousal level was scaled between 0 (inactive) and 1 (highly stimulated), with 0.09 being the baseline level (*DEF_AR_LIMIT*). Higher arousal was implemented to result in an increased probability of performing active behaviors (any behavior except resting) and in an increased probability to employ social vigilance, i.e. scanning behavior.

Anxiety In our model, anxiety level, i.e. an individual’s general “fearfulness” in response to negative stimuli within the current social environment, was scaled between 0 (not anxious) and 1 (highly anxious). Anxiety increases over time and in response to aggression, i.e. *Receiving* or *Giving an attack*, *Receiving an aggressive signal*, *Losing an (escalated) fight* or *Observing an escalated fight nearby*, and decreases in response to successful aggression, submission and affiliation, i.e. *Winning an (escalated) fight*, *Receiving a submissive or affiliative signal* and *Receiving* or *Giving grooming*. The extent of anxiety change depends on the emotional salience of the stimulus (see Table S3.5 in Chapter 3). High anxiety levels generally result in increased probabilities of affiliation and submission and decreased probabilities of aggression.

Satisfaction In our model, satisfaction level, i.e. an individual’s general “contentedness” in response to positive stimuli within the current social environment, was scaled between 0 (not satisfied) and 1 (highly satisfied). Satisfaction increases in response to affiliation, i.e. *Receiving* or *Giving grooming*, and decreases over time. The extent of satisfaction change depends on the emotional salience of the stimulus (see Table S3.5 in Chapter 3). High satisfaction results in decreased probabilities of affiliation.

FEAR attitudes In our model, individuals assign a partner-specific FEAR attitude to each group member. FEAR attitudes resemble the difference in dominance strength between an individual (i) and another group member (j) and are calculated as $FEAR_{ij} = myDOM_j - myDOM_i$, i.e. ranging from -0.95 to +0.95. Thus, FEAR attitudes are directional and not symmetric. FEAR attitudes are fixed over the course of our simulation and are, thus, not affected by social interactions. Yet, they do affect the individual’s valuation of its potential aggression risk related to the respective group member. High FEAR attitudes result in decreased probabilities of aggression (i.e. attack, aggressive signal) and increased probabilities of submission (i.e. leaving, submissive signal, avoidance) towards the respective group member.

LIKE attitudes $LIKE_{ij}$ describes an individual’s (i) affiliative valuation of a specific group member (j). LIKE attitudes may have values ranging from 0.0 (neutrally valued affiliation partner) to +1.0 (highly valued affiliation partner). LIKE attitudes are not symmetric per se, as they are dynamically updated dependent on earlier affiliation received from specific individuals. A high LIKE attitude affects ego’s judgement of the affiliative “value” of the respective group member and results in increased probabilities of affiliation (i.e. grooming, affiliative signalling and approaching) towards this specific group member.

LIKE attitudes are dynamically updated upon receiving grooming. The exact increase of $LIKE_{ij}$ depends on individual i’s current increase in satisfaction in response to grooming received exclusively from individual j, described by the partner-specific variable $PARTNER_SAT_{ij}$, which increases and decreases with the same rate as the general satisfaction level (GR_SAT_INC). Partner-specific LIKE attitudes are then used to integrate earlier affiliation received from a partner, i.e. the changing level of $PARTNER_SAT_{ij}$ over time as follows:

$$LIKE_{ij}(t_n) = \max \left\{ \frac{LHW * LIKE_{ij}(t_{n-1}) + (t_n - t_{n-1}) * PARTNER_SAT_{ij}(t_n)}{LHW + (t_n - t_{n-1})}, PARTNER_SAT_{ij}(t_n) \right\} \quad (5.2)$$

Here, t_n is the current time, t_{n-1} is the time of the last update and $(t_n - t_{n-1})$ is the time since the last update (in MINUTES). $LIKE_{ij}(t_n)$ is the updated value of the LIKE attitude assigned from

individual i to j and $LIKE_{ij}(t_{n-1})$ is the former level of LIKE to be updated. LHW (LIKE-HISTORY WEIGHT) describes to which degree the updated LIKE attitude depends on earlier (emotional responses to) affiliation history as opposed to recent (emotional responses to) affiliation. The value of LHW differs per setting.

Thus, the updated LIKE attitude ($LIKE_{ij}(t_n)$) combines the current level of satisfaction associated with the partner ($PARTNER_SAT_{ij}(t_n)$) with the recent history of partner-specific satisfaction levels resulting from earlier affiliative episodes that are summarized in the former level of $LIKE_{ij}(t_{n-1})$. However, whenever the current level of $PARTNER_SAT_{ij}(t_n)$ exceeds the updated level of $LIKE_{ij}(t_n)$, $LIKE_{ij}$ is instantaneously increased to the level of $PARTNER_SAT_{ij}$, ensuring that LIKE attitudes are always higher or equal to the current partner-specific satisfaction level.

In the updated LIKE attitude ($LIKE_{ij}(t_n)$), the former level of LIKE ($LIKE_{ij}(t_{n-1})$) and the current level of satisfaction associated with the partner ($PARTNER_SAT_{ij}(t_n)$) are weighted by LHW and $(t_n - t_{n-1})$, respectively. The higher LHW, the less the LIKE attitudes are sensitive to low $PARTNER_SAT$. Note, that LIKE attitudes of all individuals are updated, whenever any individual is activated, which also includes starting or ending grooming bouts or any other change in behavior or state. Thus, the duration of $(t_n - t_{n-1})$ is usually very short, i.e. never longer than a few MINUTES, and certainly of a smaller scale than LHW. This means that the former LIKE is weighted stronger than the current $PARTNER_SAT$ when updating LIKE. In other words, while $PARTNER_SAT$ decreases quickly, earlier affiliation received from a partner is integrated in the LIKE attitude, which is retained and slowly decays over time. Note, that at $LHW=0$ no earlier affiliation is retained and $LIKE_{ij}$ simply equals the value of $PARTNER_SAT_{ij}$.

Whenever $PARTNER_SAT = 0$, i.e. no affiliative behavior was received recently from the respective partner, LHW can be seen as the half-life of LIKE attitudes, which determines the time it takes before LIKE attitudes decrease to half of their initial value. For example at $LHW=180$ MINUTES, it would take 180 MINUTES (3 HOURS) for $LIKE_{ij}$ to decrease from 1.0 to 0.5. Higher LHW result in a longer half-life, i.e. in slower dynamics, of LIKE attitudes (see Figure 5.1). Note, that at $LHW=0$ (i.e. $LIKE_{ij} = PARTNER_SAT_{ij}$), LIKE decreases as fast as satisfaction levels, i.e. it takes 25 minutes for $LIKE=1$ to decrease to $LIKE=0.5$. Note further, that the quick increase of LIKE attitudes during receiving grooming is not dependent on the setting of LHW.

In sum, current affiliation received from a partner may quickly increase LIKE and/or maintain a high level of LIKE, while the lack of current affiliation will result in a slowly decreasing LIKE attitude. How slow LIKE attitudes decrease in the absence of received grooming, depends on the setting of LHW. Thus, LHW determines the regularity and quantity of $PARTNER_SAT$ in response to affiliative interactions that is necessary to maintain a high LIKE attitude on a more long-term basis.

Action selection In our model, activated individuals may select one of various possible actions. These actions may be directed to other individuals or may involve resting or random movement within the group.

The probability to execute a specific behavior towards another group member depends on a) the distance of the individual to ego, b) ego's emotional state (arousal, anxiety and satisfaction), c) ego's FEAR and LIKE attitudes assigned to the potential interaction partners and d) the parameter setting of LIKE-PARTNER SELECTIVITY (LPS), i.e. the degree to which high LIKE attitudes are important for the selection of affiliation partners. The emotional state facilitates behavior that is appropriate to the individual's position and situation within the social group

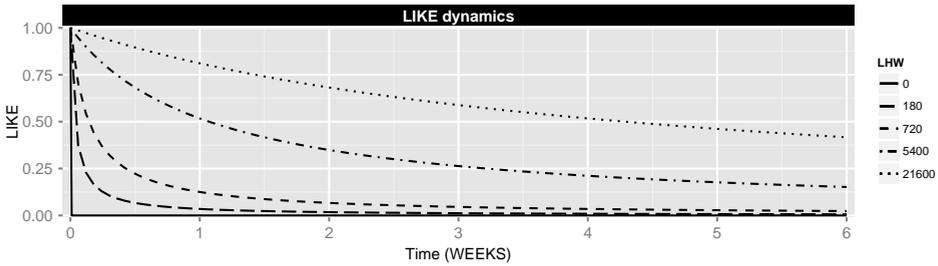


Figure 5.1: LIKE dynamics at different settings of LHW. This figure shows the decrease of the level of LIKE with initial value of LIKE=1.0 for different settings of LHW (solid line: LHW=0, long-dashed line: LHW=180 (half-life = 3 HOURS), dashed line: LHW=720 (half-life = 1 DAY), dot-dashed line: LHW=5400 (half-life = 1 WEEK), dotted line: LHW=21600 (half-life = 1 MONTH)), given that $PARTNER_SAT = 0.0$. Higher LHW results in a slower decrease of LIKE, in a higher half-life of LIKE and, thus, in slower LIKE dynamics. Note, that at LHW=0, LIKE decreases almost immediately from 1.0 to 0.0 (within 50 MINUTES).

in general, while emotional attitudes facilitate behavior that is appropriate towards specific group members.

First, the 10 (or less) potential interaction partners are determined. Then the possible behaviors towards each of these individuals are determined dependent on their distance to ego. Finally, the probabilities for those possible behaviors towards each potential interaction partner are calculated. According to these probabilities, one of the possible behavior-partner combinations is randomly selected and executed. The details on the calculation of the probabilities for affiliation, aggression, submission and avoidance are described elsewhere (Chapter 3) and are shortly summarized hereafter.

Ego's probability to direct affiliation towards individual j increases with increased $LIKE_{ij}$ (given that $LPS > 0$) and with increased intrinsic affiliation motivation of ego, i.e. when satisfaction is low or anxiety is high. At $LPS = 0$, the level of $LIKE_{ij}$ has no effect on the affiliation probability. With higher LPS ego becomes more selective and affiliates with high-LIKE partners relatively more often than with low-LIKE partners. Ego's probability to direct aggression towards individual j decreases with increased $FEAR_{ij}$. Moreover, increased anxiety results in the aggression probability to be more conservative or risk avoiding. Ego's probability to direct submissive behaviors towards individual j increases with increased $FEAR_{ij}$ and with increased anxiety.

Perception and signaling Individuals in our model can individually recognize other group members within a maximum perceivable distance of 50 m (MAX_DIST) and within the currently employed view angle. The view angle is by default 120° ($VIEW_ANGLE$) or else 360° (MAX_ANGLE) when ego is scanning. Model entities can judge whether at least three other group members are present within 20 m ($NEAR_DIST$) and within the currently employed view angle. Furthermore, individuals in our model are capable to judge whether their distance to the furthest group member exceeds 100 m (FAR_DIST). The two latter criteria are used by ego to decide whether grouping behavior should be executed. Individuals can also perceive signals, which were directed at them from others within 5 m ($PERS_DIST$).

Scanning When employing scanning behavior, an individual is turning its head right and left, thus expanding its view angle to 360° (MAX_ANGLE) instead of the default view angle of 120°

(*VIEW_ANGLE*). The probability to perform scanning behavior increases with ego's current arousal level (Evers et al., 2014).

Movement Concerning movement behavior, individuals in our model may either move towards or from other group members (approaching, grouping, fleeing, leaving and avoiding) or they may execute random movement within the group. Movement behavior in our model takes time and is implemented as movement bouts. During such a movement bout, movement is executed step by step. After starting a movement bout, ego is activated each 3 SECONDS to execute the movement it was to perform during this time interval and to decide whether movement is to be continued (see also Figure 3.1 in Chapter 3).

After ending a movement bout ego always performs a proximity update. Ego checks whether any individuals towards which it directs a (high) FEAR attitude (i.e. higher-ranking group members) are now (or still) nearer than 5 m (*PERS_DIST*), as this has consequences for the level that ego's arousal will approach over time (*myAROUSAL_LIMIT*). Additionally, other individuals who direct (high) FEAR attitudes towards ego are updated on ego's new spatial location, which may in turn affect the level their arousal will approach over time.

Grouping Before selecting a social behavior, model entities always check whether grouping should be executed. Grouping will be selected if less than three (*MIN_OTHERS*) group members are located within 20 m (*GROUP_DIST*) and 360° (*MAX_ANGLE*) or whenever any group member is further away from ego than 100 m (*FAR_DIST*). When grouping is to be performed, ego simply approaches any randomly selected group member.

Grooming and resting In our model, grooming and resting behavior are implemented as a duration behaviors, which are executed in bouts. When starting a grooming or resting bout, ego's next activation is scheduled several minutes later to choose its subsequent behavior. Ego may be disturbed and activated earlier in response to receiving an attack or a signal, or after observing an escalated fight nearby.

Attack, counter-attack and escalated fight Upon receiving an attack the respective model individual is immediately activated to respond with either fleeing or a counter-attack. When a counter-attack was selected in response to an attack, we call this an escalated fight. The winner and loser of such a fight is determined randomly according to the individuals' win chance. When no counter-attack is selected in response to an attack, the attacked individual is defined as the loser and the attacker as the winner of this aggressive interaction. After an attack or an escalated fight, the loser flees from the winner, while the winner is scheduled anew shortly after. Whenever an escalated fight takes place, individuals nearby get activated and their arousal level gets increased. Moreover, these individuals are activated shortly after to enable an appropriate reaction in response to the event.

Simulation experiments

In this paper we present the results of different settings of the EMO-model, in which individuals dynamically update their LIKE attitudes according to earlier received affiliation by specific group members and subsequently use these LIKE attitudes to choose affiliation partners.

We examined five different settings of LPS, i.e. LPS was set to either 0.00, 0.50, 0.90, 0.95 or 0.99, respectively. LPS described the degree to which individuals preferred to affiliate with individuals towards which they directed high LIKE attitudes.

We also examined five different settings for LHW, i.e. LHW was set to 0, 180, 720, 5400 or 21600 MINUTES, respectively. LHW described the speed of the LIKE dynamics in our model, where higher LHW would result in a slower decrease of LIKE attitudes over time.

LPS = 0.0 resembles a special null model setting. Here, individuals have no preference to select specific affiliative partners concerning LIKE attitudes whatsoever. In other words, individuals do not use LIKE attitudes during affiliative partner selection. Therefore, the behavioral rates in the null model setting should yield the same patterns for all settings of LHW. The null model setting serves as a control setting to assess the effect of the presence of any affiliative partner preference based on emotional bookkeeping.

For this paper we examined all 25 combinations of the different parameter settings of LPS and LHW. For each combination of LHW and LPS, 10 independent simulations were run, resulting in a total of 250 independent simulation runs.

Statistical analysis

We first explain how specific summarized measures were defined and calculated from the recorded data. We continue with the statistics that were used to compare the properties of different subgroups or individual categories. Finally, we explain how we calculated specific statistics, i.e. the row-wise Pearson correlation coefficients and group-level reciprocity. All statistical analyses were performed in R 2.15.2 (R Core Team, 2012).

Individual values of LIKE attitudes and grooming rates were calculated as the sum of all dyadic LIKE attitudes and grooming rates that an individual directed to others. Group means of grooming rates were calculated as the mean of all individual behavioral rates.

As biennial partners of ego, we defined those individuals that ego directed any grooming to over the total recording period of 2 YEARS. Thus, to calculate the number of biennial partners per individual we used the dyadic grooming rates averaged over 2 YEARS and counted towards how many partners an individual's average grooming rate was higher than zero.

As monthly partners of ego, we defined those individuals, that ego directed any grooming to over a period of one MONTH. Thus, to calculate the number of monthly partners per individual we used the dyadic grooming rates averaged per MONTH and counted towards how many partners an individual's average grooming rate was higher than zero per MONTH. The number of monthly partners was then averaged over all MONTHS, i.e. over the total recording period of 2 YEARS.

We further determined the preferred partners of ego, based on their relative relevance to ego. To do this, we calculated the percentage of grooming an individual gave to each partner per MONTH, based on the total amount of grooming this individual gave to others during this MONTH. Those partners, which received more than 10% of an individual's total amount of grooming, were called preferred partners (cf. "primary partners" in Barrett and Henzi, 2002). In this way, the preference for specific partners over other partners is described, independent of the total amount of grooming given and independent of the absolute values of the LIKE attitudes. By definition, an individual's preferred partners are a subset of its monthly partners.

The number of an individual's preferred partners was then counted per MONTH and averaged over the total recording period of 2 YEARS.

Note, that individuals with many monthly partners may have less preferred partners compared to individuals with only a few monthly partners. When ego distributes its total grooming equally among many partners, each partner may receive a smaller percentage of ego's total grooming, compared to when ego would distribute its total grooming equally among a few partners. In the extreme case of only one monthly partner, this single partner automatically receives 100% of ego's grooming and is thus by definition a preferred partner. On the other hand, if for example 19 monthly partners would receive an equal amount of grooming by ego, each partner would receive around 5% and no individual would be a preferred individual. However, if ego distributes its grooming equally among 9 group members, each of them would receive more than 10% and would be defined as preferred partner.

A bout of grooming partner preference was defined as a period of consecutive months for which a specific individual remained a preferred partner of ego. To calculate the bout duration of grooming partner preferences, we simply determined the average duration (in MONTHS) of all bouts of grooming partner preference of a dyad over the total recording period of two YEARS. To calculate the total duration of grooming partner preference, we determined the sum of all bout durations of grooming partner preference of a dyad over the total recording period of two YEARS.

To assess the reciprocity of grooming partner preferences at the group level we calculated the Kendall's tau row-wise matrix correlation between the matrix of the total durations of grooming partner preferences over two YEARS and its transposed matrix (Hemelrijk, 1990; de Vries, 1993) using the R software package DyaDA (Leiva et al., 2010).

To examine the relation between LIKE attitudes and grooming rates, we calculated the row-wise Pearson correlation coefficients (de Vries, 1993) between the dyadic grooming rates and the dyadic LIKE attitudes, using the grooming rates and LIKE attitudes averaged over one year. We calculated the correlation coefficients per simulation run and then averaged them over all runs per setting using a Fisher-z-transformation.

RESULTS

General patterns of and the relation between LIKE attitudes and grooming

Distribution of LIKE attitudes

First, we were interested in how the pattern of developed LIKE attitudes within the group depended on the different settings in our model, i.e. the half-life of the LIKE attitudes (LHW, the LIKE-HISTORY WEIGHT, explained in Figure 5.1) and the selectivity of individuals when choosing affiliation partners (LPS). In Figure 5.2 the level of the LIKE attitudes, averaged over one YEAR, between all individuals of one example run are plotted. A large difference in the average level of LIKE attitudes is visible for the different settings of LHW, which determined the speed of the LIKE dynamics over time. At higher LHW, i.e. slower LIKE dynamics, the average value of LIKE attitudes that developed towards others was higher (Figure 5.2).

This can be understood as follows. At high LHW the LIKE attitudes decrease very slowly over time. Therefore, high levels of LIKE attitudes are easily (and often even accidentally) maintained. When LHW was given the extreme value of 21 600 (implying a half life of one MONTH),

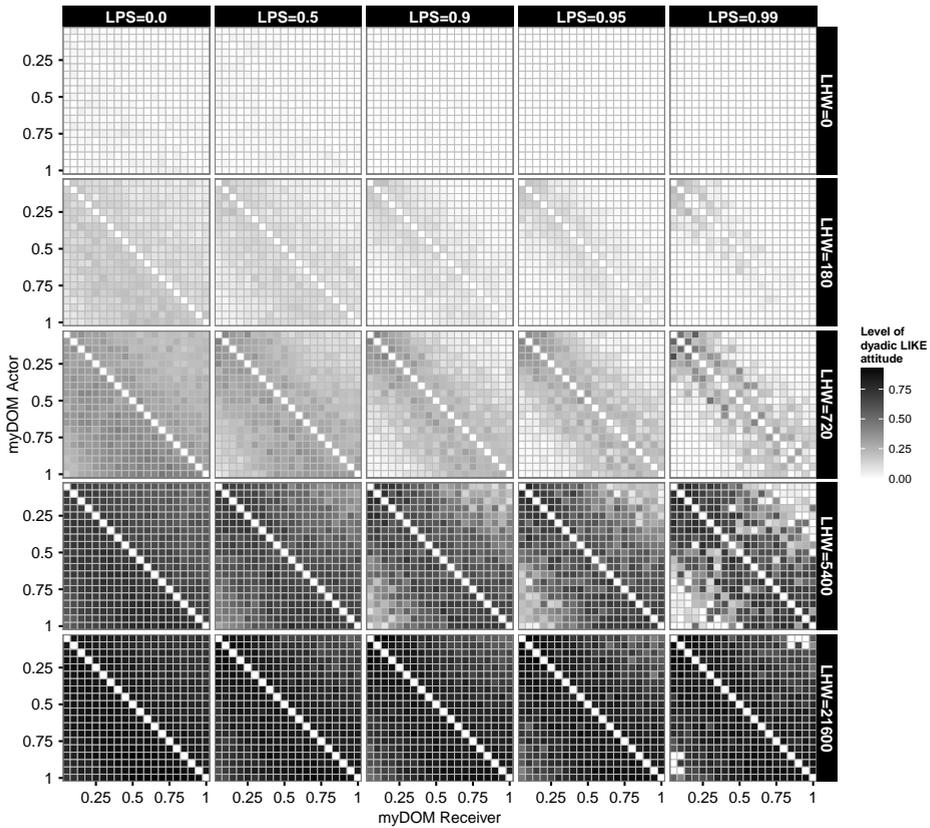


Figure 5.2: Average LIKE attitudes. This figure shows the distribution of LIKE attitudes among the individuals of a group for different settings of partner selectivity (LPS) and LIKE dynamics (LHW). Higher LPS defines a higher preference for affiliation partners with high LIKE attitudes. Higher LHW (LIKE-HISTORY WEIGHT) defines slower LIKE dynamics. LIKE attitudes are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking ($\text{myDOM}=0.05$) to high-ranking ($\text{myDOM}=1.00$). The plot shows the LIKE attitudes of one example run, averaged over one YEAR. Dark shades represent high LIKE attitudes. Values at the diagonal are by definition not applicable.

we found almost no differentiation in average LIKE attitudes among the dyads (Figure 5.2, bottom row matrices). Individuals developed high LIKE attitudes to almost all group members and these attitudes only decreased very slowly in time. As a consequence, all LIKE attitudes were approximately equally high for all dyads. At the other extreme, when $\text{LHW}=0$, the average value of LIKE attitudes was close to zero (Figure 5.2, top row matrices). Here, earlier events (summarized in the LIKE attitude up till that time) were not incorporated when updating the LIKE attitude and only very recent affiliative behavior (which elicited a certain degree of temporary satisfaction, *PARTNER_SAT*) affected affiliative partner choice. Therefore LIKE attitudes hardly developed and could not be maintained on a longer term. This resulted in very low average LIKE attitudes.

Due to the very fast or very slow changing LIKE attitudes at low and high LHW, the setting

of partner selectivity (LPS) had almost no effect on the distribution of LIKE attitudes (see also further below). This was different at intermediate LHW settings (LHW=180, 720 or 5400, implying a half life of 3 HOURS, one DAY and one WEEK, respectively). Here, in the null model setting (LPS=0), where individuals selected affiliation partners irrespective of their LIKE attitudes, LIKE attitudes were relatively equally distributed among all group members (Figure 5.2, first column of rows 2, 3 and 4). So, even when earlier affiliative episodes were incorporated in the LIKE attitudes, due to the absence of affiliative partner selectivity, individuals engaged with others purely on the basis of proximity and the dominance hierarchy. This resulted in slightly higher LIKE attitudes directed down the hierarchy (i.e. the lower triangular half of the matrices), as affiliation was more directed up the hierarchy in this setting (see also Figure 5.3B below). At increased LPS, individuals chose affiliation partners more selectively, based on their LIKE attitudes. As a result, average LIKE attitudes got more symmetric and more differentiated within the group (Figure 5.2, rows 2, 3 and 4). Moreover, LIKE attitudes towards similar-ranked partners were higher than LIKE attitudes towards distant-ranked partners. When $LPS \geq 0.95$, average LIKE attitudes got differentiated also within subsets of similar-ranked dyads, and were not purely based on rank-distance anymore, but (also) on earlier episodes of affiliative behavior (Chapter 4).

Note, that in Figure 5.2 the LIKE attitudes are averaged over one YEAR and this therefore summarizes all LIKE relationships that had developed (and perhaps also vanished again) over the whole period of one YEAR. To also illustrate the dynamics of the LIKE attitudes over time, we compared the averaged LIKE attitudes of Figure 5.2 with snapshots of the LIKE attitudes at a single point in time, i.e. after the first and after the second YEAR of the total recording period of the same simulation run (see supplementary Figure S5.1 and Figure S5.2).

From the LIKE snapshot plots, we noticed that at intermediate LHW settings and in the absence of affiliative partner preference (i.e. null model setting: LPS=0), individuals developed high LIKE attitudes towards only a few individuals simultaneously, strongly suggesting that they regularly switched partners in an almost random fashion over time (compare first column of intermediate panels in Figure S5.1 and Figure S5.2). As a result the averaged LIKE attitudes were almost equally distributed over the whole group (Figure 5.2, first column of intermediate panels). In contrast, when individuals were more selective ($LPS \geq 0.9$) individuals still switched partners, but potential partners were now more restricted to more similar-ranking individuals (compare Figure S5.1, Figure S5.2 and Figure 5.2, last column of intermediate panels).

To summarize, how long LIKE attitudes were maintained over time and also the within-group variation of LIKE attitudes, depended on the specific settings of LHW and LPS. Increased LHW resulted in LIKE attitudes decreasing slower over time. Only at intermediate LHW and high LPS, LIKE attitudes were strongly differentiated within the group (e.g. see last panel in row 3 of Figure 5.2).

Distribution of grooming

Above, we saw how the setting for LHW affected the level of the averaged LIKE attitudes. By definition, higher LHW result in higher LIKE attitudes for all group members, as LIKE attitudes decreased slower over time and got accumulated more easily. LIKE attitudes, i.e. the internal representation of affiliative partner preferences or partner appraisal, are difficult to examine in real animals. Usually, researchers try to derive this internal representation from external and measurable behaviors such as for example the amount of grooming given to others (Barrett and Henzi, 2002; Crockford et al., 2013). Therefore, we were interested in how the distribution

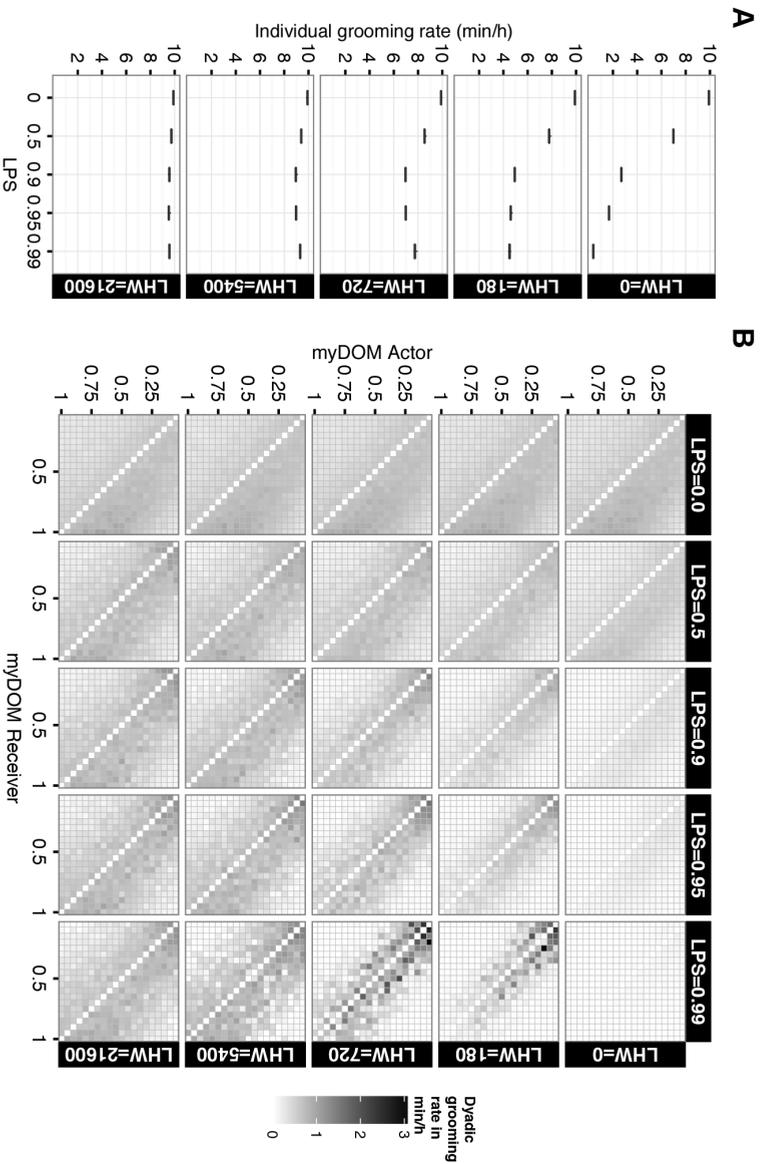


Figure 5.3: Grooming rates. **A:** This figure shows the group mean of the individual grooming rates for different settings of selectivity (LPS) and LIKE dynamics (LHW). The box-plots show individual grooming rates (in minutes per hour) of 10 simulation runs, averaged over one YEAR. **B:** This figure shows the distribution of the dyadic grooming rates within the group for different settings of selectivity (LPS) and LIKE dynamics (LHW). Grooming is directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking (myDOM=0.05) to high-ranking (myDOM=1.00) individuals. The plot shows the grooming rates of one example run (the same run as in Figure 5.2) in minutes per hour, averaged over one YEAR. Dark shades represent high grooming rates. Values at the diagonal are by definition not applicable.

of LIKE attitudes in our model affected the distribution of grooming given to others in our model.

We first examined the average grooming rates per setting. In general, at increased partner selectivity (LPS) grooming rates were decreased and this decrease was stronger at faster LIKE dynamics (lower LHW) (Figure 5.3A). High selectivity (LPS) resulted in more selective grooming towards individuals with high LIKE attitudes, and therefore in less grooming directed to individuals with low LIKE attitudes. As a result, the total grooming rate generally decreased. Note however, that for LHW=720 or 5400 average grooming rate increases again at higher LPS.

To explain the effect of LPS and LHW on grooming rates in more detail, we examined the distribution of dyadic grooming within the group. First, for the null model setting (LPS=0, first column in Figure 5.3B) there is no affiliative partner selectivity, and therefore grooming distributions were similar across all settings of LHW. This can easily be understood: since individuals do not use their LIKE attitudes when choosing grooming partners, the dynamics of the LIKE attitudes do not have any effect on the individuals' behavior. At LPS=0, more grooming was directed up the hierarchy than down the hierarchy, and slightly more grooming was directed towards similar-ranking partners than towards distant-ranking partners (first column in Figure 5.3B).

Next, for the LHW=0 setting (top row in Figure 5.3B), that is, when LIKE attitudes from earlier received affiliation were not retained, individuals maintained high LIKE attitudes towards others only for very short periods. At increased partner selectivity, individuals have a stronger preference for grooming partners with a high LIKE attitude, however, such partners are only rarely available at LHW=0. This resulted in increasingly lower grooming rates throughout the whole group (compare matrices in top row of Figure 5.3B). At increased selectivity (LPS), grooming was still mainly directed up the hierarchy, but was slightly more restricted to similar-ranking partners compared to lower LPS. Note, that due to the very low grooming rates, this pattern is not visible in Figure 5.3B. In the section Grooming partner preferences further below this is illustrated clearer.

Next, at intermediate LIKE dynamics (LHW=180 or 720), LIKE attitudes decreased fast (half life of 3 HOURS or 1 DAY, respectively) between dyads that did not regularly affiliate, which were mainly distant-ranked dyads. Increased selectivity (LPS) resulted in increasingly lower grooming rates among distant-ranked dyads (Figure 5.3B, rows 2 and 3). In turn, this reinforced the within-group differences in LIKE attitudes and grooming rates between similar-ranking and distant-ranking dyads (intermediate panels in Figure 5.2 and Figure 5.3B). While similar-ranking individuals became more regular grooming partners, distant-ranking individuals became more incidental grooming partners. At highest selectivity (LPS=0.99), LIKE attitudes and grooming rates were even differentiated within similar-ranking dyads. For instance, note that the grooming rates in dyads that differ only 0.05 in rank (myDOM), are very different from each other (see the last panel in rows 2 and 3 of Figure 5.3B). A similar differentiated pattern within similar ranking dyads is visible in the corresponding matrices of LIKE attitudes in Figure 5.2. Based on the partner-specific affiliation history individuals differentiated between regular and incidental groomers and this was reinforced by the strong feedback between LIKE attitudes and grooming.

Higher-ranking individuals of (similar-ranked) dyads usually receive more grooming from their lower-ranking partners than vice versa, resulting in higher LIKE attitudes directed from the higher- to the lower-ranking partner rather than vice versa. However, high LPS caused the higher-ranking individuals of similar-ranked dyads to more selectively direct grooming towards their lower-ranking partners with high LIKE attitudes, especially at intermediate LHW, where

LIKE attitudes showed enough within-group variation. This in turn reinforced the LIKE attitudes of lower-ranking partners towards their higher-ranking partners within similar-ranking dyads. In this way, grooming was more reciprocated and less directed up the hierarchy at high LPS compared to low LPS, especially at intermediate LIKE dynamics (LHW) (see intermediate rows in Figure 5.3B).

Finally, at slow LIKE dynamics (LHW=5 400 or 21 600), LIKE attitudes did decrease only very slowly over time and individuals developed high LIKE attitudes towards most other group members, even towards less regular (distant-ranking) groomers (Figure 5.2, lower panels). As a result, high selectivity had only a minor effect on grooming rates, as individuals preferred in fact any group member as a grooming partner. Therefore, at high LHW, the distribution of grooming rates across different LPS settings changed less compared to intermediate LHW (Figure 5.3B, compare rows 2 and 3 with rows 4 and 5). At high LHW, increased LPS resulted in a minor decrease in grooming rates among distant-ranked dyads and grooming was still directed more up the hierarchy (Figure 5.3B, especially row 5).

To summarize, in the absence of affiliation partner selectivity (LPS=0), individuals groomed more up the hierarchy than down the hierarchy and groomed slightly more similar-ranking individuals than distant-ranking ones. High LPS and fast LIKE dynamics (LHW=0) resulted in very little grooming, due to the lack of partners with high LIKE attitudes. At high LPS and intermediate LIKE dynamics, individuals groomed similar-ranking partners more selectively and grooming became more symmetric. With slow LIKE dynamics (LHW=21 600), the grooming distribution at high LPS was very similar to low LPS, as individuals developed high LIKE attitudes to most group members.

Grooming rates and dominance rank

Rank also affected the amount of grooming given to others in our model. In most settings, intermediate-ranking individuals gave more grooming to others than low- or high-ranking individuals (Figure 5.4). As explained earlier (Evers et al., 2014), low-ranking individuals in our model often avoid high-ranking individuals. As a result of this, lower-ranking individuals were limited in their potential grooming partners. On the other hand, dominants in our model are avoided more often than individuals of lower rank, which limited their number of potential grooming partners. Additionally, dominants in our model have a lower motivation to groom others, compared to intermediate and low-ranking individuals, due to their lower levels of anxiety (Evers et al., 2014).

Only when very high selectivity (LPS=0.99) was combined with intermediate LIKE dynamics (LHW=180 or LHW=720), low-ranking individuals groomed others even more than intermediate or high-ranking individuals (intermediate panels of last column in Figure 5.4). In these settings, all individuals focused their grooming activity on a few similar-ranking individuals (Figure 5.3B). Therefore, in these settings lower-ranking individuals were not more restricted in their potential grooming partners than intermediate or high-ranking individuals. Moreover, low-ranking individuals generally have a higher motivation to groom others, compared to higher-ranking individuals, as their levels of anxiety are generally higher compared to higher-ranking individuals (Evers et al., 2014). When focusing on similar-ranking grooming partners the higher grooming motivation of subordinates could be satisfied more easily, as the probability to avoid similar-ranking group members is very low.

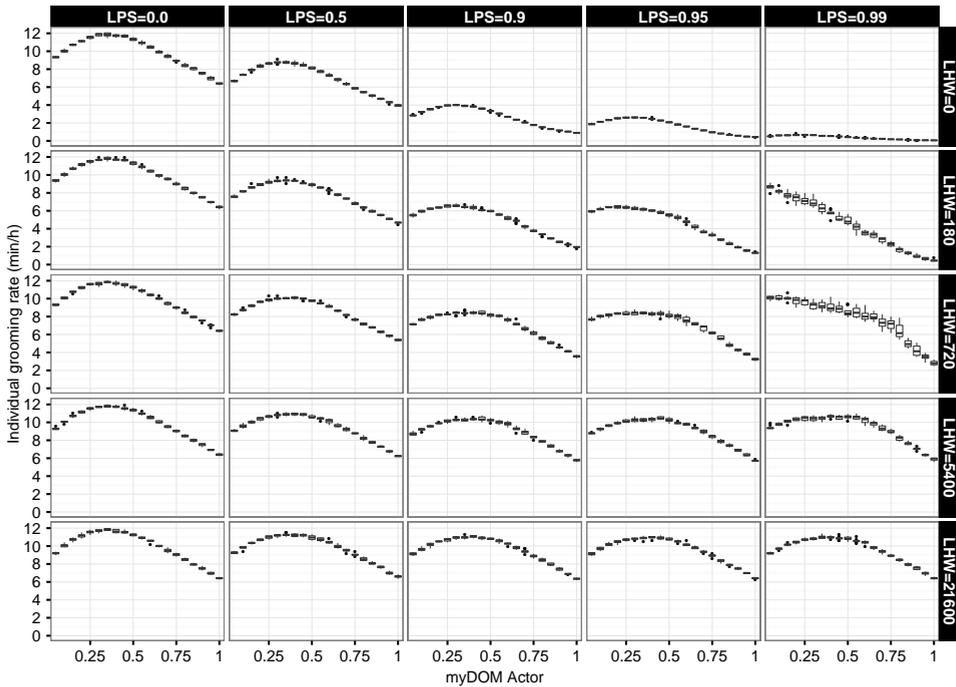


Figure 5.4: Grooming rates and dominance rank. This figure shows the relation between grooming rates and dominance rank for different settings of selectivity (LPS) and LIKE dynamics (LHW). Groomers (x-axis) are ordered by dominance strength, ranging from low-ranking ($myDOM=0.05$) to high-ranking ($myDOM=1.00$) individuals. The box-plots show the individual grooming rates (in minutes per hour) of 10 simulation runs, averaged over one YEAR.

Correspondence of LIKE attitudes and grooming rates

We were interested in how well the LIKE attitudes in our model corresponded to the actual grooming rates of the individuals in our model. LIKE attitudes are an internal, summarized representation of earlier received grooming from other individuals. Depending on the LIKE dynamics (LHW), earlier grooming episodes are taken into account for a short or long amount of time. Depending on the partner selectivity (LPS), this internal representation is more or less important when choosing affiliation partners.

When comparing visually the matrices of the average LIKE attitudes with the average dyadic grooming rates (Figures 5.2 and 5.3B), it is already clear that for several settings LIKE attitudes did not correspond very well to the dyadic grooming rates. To quantitatively examine the relation between LIKE attitudes and grooming rates, we correlated the LIKE attitudes (averaged over one YEAR) with the dyadic grooming rates (averaged over one YEAR).

As described earlier, at the null model setting ($LPS=0$), LHW did not affect the grooming rates, as individuals did not use their LIKE attitudes in this setting. Grooming rates and the decision whom to groom are, in this setting, purely determined by proximity and dominance rank, independently of the LIKE attitudes. Yet, the level of LIKE attitudes did (always) depend on LHW, where higher LHW resulted in higher average LIKE attitudes (see first column in Figure

5.2). While grooming was directed up the hierarchy, LIKE attitudes were directed down the hierarchy, as LIKE attitudes were determined by grooming, but did not feed back on grooming. Therefore, at LPS=0, the correlation between grooming rates and LIKE attitudes was weak and negative (compare the first bars across the panels in Figure 5.5).

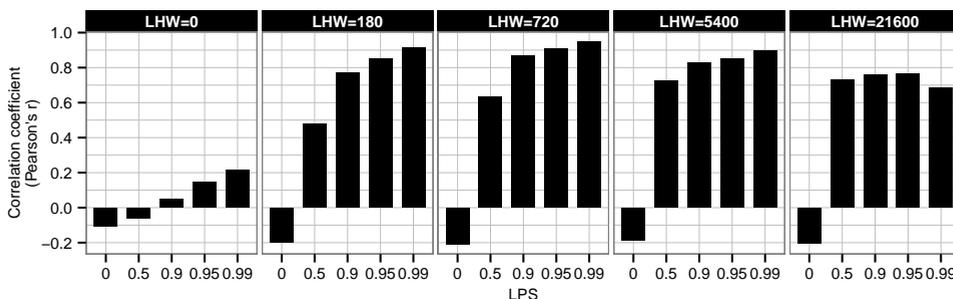


Figure 5.5: Correlation between grooming rates and LIKE attitudes. This figure shows the row-wise correlation coefficient (Pearson's r) between grooming rates and LIKE attitudes for different settings of selectivity (LPS) and LIKE dynamics (LHW). We used matrices of grooming rates and LIKE attitudes averaged over one YEAR. The correlation coefficient was calculated for each of 10 simulation runs and then averaged using a Fisher-z transformation.

Higher partner selectivity (LPS) generally resulted in a higher correlation between LIKE attitudes and grooming rates (Figure 5.5). This came about due to the stronger feedback between LIKE attitudes and grooming partner choices caused by higher selectivity (LPS). At higher LPS, LIKE attitudes were determined by grooming and did also feedback on future decisions on whom to groom. This resulted in higher reciprocity in grooming rates and LIKE attitudes at higher LPS, compared to lower LPS. As grooming rates and LIKE attitudes were more symmetric at higher LPS, they were also more overlapping and corresponding to each other, resulting in higher correlation coefficients between grooming rates and LIKE attitudes.

Furthermore, intermediate LHW settings resulted in higher correlation coefficients between LIKE attitudes and grooming rates, than low or high LHW, especially when LPS was high (compare panels in Figure 5.5). At low LHW (LHW=0), LIKE attitudes decrease too fast to result in a strong feedback from LIKE attitudes to grooming, across all settings of LPS. As no LIKE attitudes could be maintained, LIKE attitudes could also not affect the choice of future grooming partners. Therefore, the correlation between LIKE attitudes and grooming rates was generally very weak at low LHW (Figure 5.5, first panel). At high LHW (LHW=21 600), LIKE attitudes were almost equally high towards all group members and no strongly preferred partners were available. Although increased selectivity (LPS) causes a stronger feedback between LIKE attitudes and grooming rates, the low variation in LIKE attitudes, which was similar for all LPS between 0.5 and 0.99, resulted in similar correlations between LIKE attitudes and grooming rates (Figure 5.5, last panel). Finally, at intermediate LHW, LIKE attitudes corresponded best to grooming rates, given that selectivity was high enough (LPS \geq 0.9). Here, LIKE attitudes decreased slow enough to incorporate earlier affiliative episodes, but fast enough to enable differentiation between regular and incidental partners. The strong feedback between LIKE attitudes and future grooming partners resulted in highly reciprocal LIKE attitudes and grooming rates for similar-ranking dyads. As a result, the correlation between LIKE attitudes

and grooming rates was highest at intermediate LHW (LHW=720) and high LPS (LPS=0.99) (Figure 5.5, middle panel).

To summarize, our model suggests, that (internal) LIKE attitudes only correspond well to (external) grooming rates, when individuals are very selective in their partner choice ($LPS \geq 0.9$) and when LIKE attitudes incorporated earlier affiliative behavior over not short-term, not long-term, but intermediate periods, i.e. when LHW ranges between 180 and 5400. In these settings we obtained correlation coefficients higher than 0.77 and even up to 0.95 (at LHW=720 and LPS=0.99).

Grooming partner preferences

Number of biennial, monthly and preferred grooming partners

Here, we will present the number of *biennial*, *monthly* and *preferred partners* for the different settings in our model. In the next sections, the stability and reciprocity of grooming partner preferences is assessed, and partly explained in terms of the number of *preferred grooming partners*.

Ego's *biennial partners* are those individuals towards which ego directed any grooming over a period of two YEARS. Ego's *monthly partners* are those individuals towards which ego directed any grooming within one MONTH. Ego's *preferred partners* are those individuals that received more than 10% of ego's total amount of grooming within one MONTH. Figure 5.6A shows the group means of the number of partners and Figure 5.6B shows the effect of rank on the number of partners for the different settings in our model. Inspecting Figure 5.6A, we note that for all settings of LHW and LPS, the number of biennial grooming partners was around 19 (black box-plots in Figure 5.6A). Only at very high selectivity (LPS=0.99), extremely high or low-ranking individuals had slightly less biennial partners (black box-plots in the last column of Figure 5.6B). This means that in all settings, most individuals groomed each other group member at least once within the recording period of two YEARS.

In the null model setting (LPS=0) the number of biennial, monthly and preferred partners was independent of the setting of LHW, as individuals did not use their LIKE attitudes to choose grooming partners in this setting. At LPS=0, the mean number of monthly partners was 19 (dark-grey box-plots at LPS=0 in Figure 5.6A). Thus, individuals groomed each other group member at least once per month. As individuals distributed their grooming amongst many group members without any preference for partners with high LIKE attitudes, the number of preferred partners was very low (on average around 1, see light-grey box-plots at LPS=0 in Figure 5.6A).

At stronger partner selectivity (LPS>0), individuals did use their LIKE attitudes to choose affiliative partners and the chance for individuals to affiliate with less *LIKED* individuals decreased. At very high selectivity (LPS=0.95 or 0.99), this generally resulted in a decrease of monthly partners (dark-grey box-plots in Figure 5.6A).

How much the number of monthly partners decreased at higher LPS, depended on the setting of LHW. The number of monthly partners was lower at intermediate LHW compared to high or low LHW (dark-grey box-plots in Figure 5.6A). At very fast LIKE dynamics (LHW=0) and high selectivity (LPS), individuals were not able to develop or maintain LIKE attitudes. As individuals had an equally low preference for all group members, they still groomed many different group

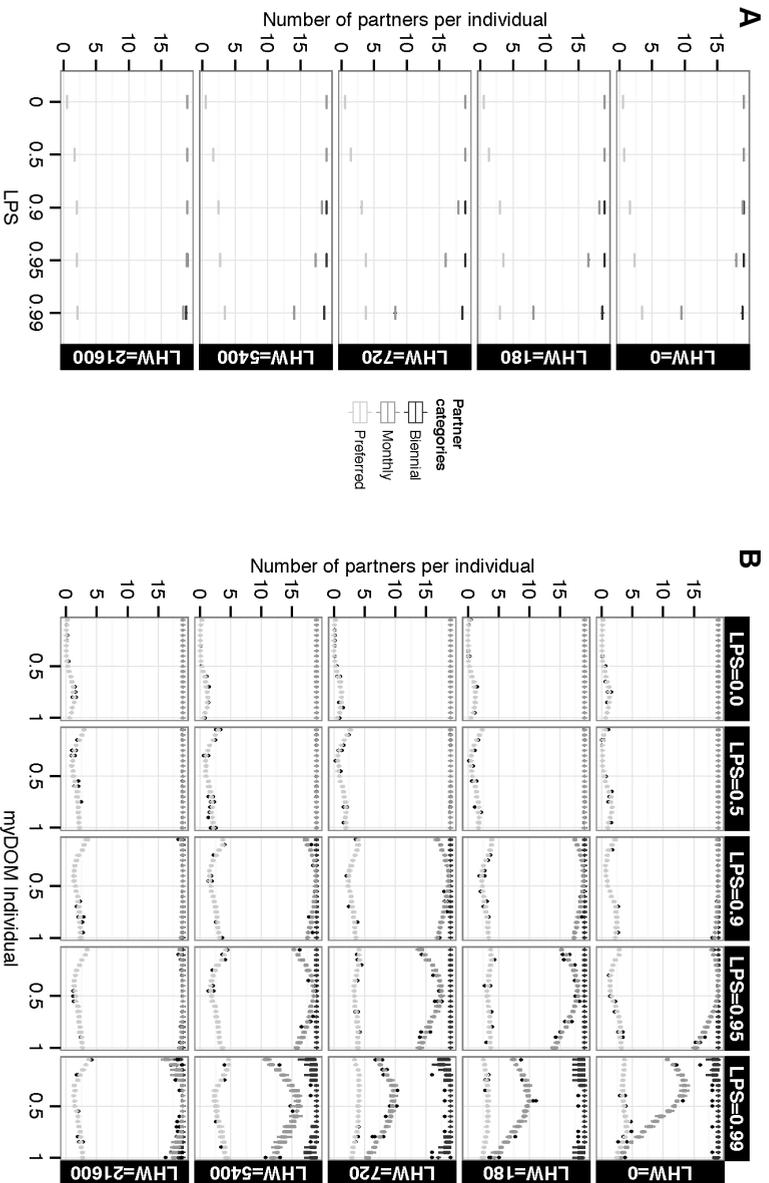


Figure 5.6: Number of biennial, monthly and preferred grooming partners. **A:** This figure shows the number of biennial (black), monthly (dark-grey) and preferred (light-grey) grooming partners for different settings of selectivity (LPS) and LIKE dynamics (LHW). **B:** This figure shows the relation between the number of biennial (black), monthly (dark-grey) and preferred (light-grey) grooming partners and dominance rank for different settings of selectivity (LPS) and LIKE dynamics (LHW). Individuals (x-axis) are ordered by dominance strength, ranging from low-ranking (myDOM=0.05) to high-ranking (myDOM=1.00) individuals. See text for definition and measurement of the biennial, monthly and preferred partners. All box-plots show the number of partners per individual of 10 simulation runs averaged over 2 YEARS.

members. Therefore, the number of monthly partners was still moderately high (around 10) at low LHW and high LPS (dark-grey box-plot at LPS=0.99 in upper panel of Figure 5.6A).

At (very) slow LIKE dynamics ($LHW \geq 5400$) and high selectivity (LPS), individuals had developed high LIKE attitudes to almost all other group members. Therefore the number of monthly partners was still high at high LHW and high LPS (between 14 and 18) (dark-grey box-plots at LPS=0.99 in two lower panels of Figure 5.6A).

At intermediate LIKE dynamics ($LHW=180$ or 720) and high LPS, individuals developed high LIKE attitudes to some group members and low LIKE attitudes to the rest of the group. Thus, individuals had a preference for specific grooming partners and focused most of their grooming on these individuals. Therefore, the number of monthly partners was lowest (around 8) at intermediate LHW and high LPS (dark-grey box-plots at LPS=0.99 in two intermediate panels of Figure 5.6A).

With increasing partner selectivity (LPS), individuals had generally fewer monthly partners. This in turn resulted in a general increase of preferred partners (light-grey box-plots in Figure 5.6A). As explained earlier, when individuals restrict their grooming to fewer individuals (per MONTH), the percentage received by each individual may increase. Thus, more individuals may receive more than 10% of the total grooming and are considered preferred partners.

Looking at the last two columns in Figure 5.6B, an interesting pattern can be seen: intermediate-ranking individuals had usually more monthly partners than low or high-ranking individuals. This resulted from, on the one hand, intermediate-ranking individuals being less often avoided by others than high-ranking individuals and, on the other hand, intermediate-ranking individuals less often avoiding others than low-ranking individuals (Evers et al., 2014), which allowed for more potential grooming partners. Because of this high number of monthly partners, intermediate-ranking individuals had less preferred partners than low or high-ranking individuals (light-grey box-plots in Figure 5.6B). Only when individuals had less than 10 monthly partners (such as at $LHW=720$ and $LPS=0.99$), the number of preferred partners was proportional to the number of monthly partners (compare light-grey and dark-grey box-plots in Figure 5.6B).

To summarize, higher selectivity resulted in a decrease in monthly grooming partners and an increase in preferred grooming partners. The change in number of monthly and preferred grooming partners was strongest for intermediate LIKE dynamics, where the within-group variation of LIKE attitudes was highest.

Stability of grooming partner preferences

Above we have shown that high selectivity (LPS) resulted in the highest number of *preferred grooming partners*. The main interest of this simulation study is the question, whether emotional bookkeeping enables individuals to maintain long-term affiliative partner preferences over time. To answer this question, we present the average duration of consecutive MONTHS for which an individual remained another individual's preferred grooming partner (i.e. received more than 10% of its total amount of grooming given to others), called the *bout duration of grooming partner preferences*. We also investigated the sum of the durations of all bouts of grooming partner preference per dyad, summed over the total recording period of two YEARS, i.e. the *total duration of grooming partner preferences*.

For most settings of LHW and LPS, the average bout duration of grooming partner preferences was between 1.25 and 1.7 MONTHS (Figure 5.7A). Only for intermediate LIKE dynamics

(LHW=720) and high selectivity (LPS=0.99), the average bout duration of grooming partner preferences was longer, namely around 2.25 MONTHS (Figure 5.7A).

In the null-model setting (LPS=0), the average bout duration of grooming partner preferences was independent of the setting of LHW, as individuals did not use LIKE attitudes to choose grooming partners.

At very fast or very slow LIKE dynamics, increased LPS had only a minor effect on the average bout durations of grooming partner preferences (upper and lower panels in Figure 5.7A). The lack of group variation in LIKE attitudes in these settings resulted in only a weak feedback from LIKE attitudes to grooming distribution and caused individuals to choose grooming partners mainly based on proximity and/or rank distance.

At intermediate LIKE dynamics (LHW) and high selectivity (LPS), individuals developed differentiated LIKE attitudes towards others, based on partner-specific affiliative history. From the average bout durations of grooming partner preferences we can conclude that individuals were able to maintain stable grooming partner preferences on average for around 2.25 MONTHS (intermediate panel in Figure 5.7A). However, the bout duration of grooming partner preferences depended strongly on the rank-distance between the partners; similar-ranking dyads were generally able to maintain longer partner preferences than distant-ranked dyads (intermediate panel of last column in Figure 5.7B). At LHW=720 and LPS=0.99, for many similar-ranking dyads the average bout durations of grooming partner preferences lasted up to 4 MONTHS (intermediate panel in last column of Figure 5.7B). Occasionally, bout durations of grooming partner preferences in this setting lasted even longer than 12 MONTHS, with one bout duration in one simulation run lasting even 24 MONTHS.

The total duration of grooming partner preferences was lower than 6 MONTHS for most settings of LPS and LHW (Figure 5.7C). This suggested that individuals in these settings changed preferred grooming partners on a regular basis and had no clear predisposition of preferring certain individuals as grooming partners over repeated bouts.

At intermediate LIKE dynamics and high selectivity the total duration of grooming partner preferences was generally longer, with longest total duration of grooming partner preferences (averaged over the group) longer than 7 MONTHS at LHW=720 and LPS=0.99 (box-plot at LPS=0.99 in intermediate panel of Figure 5.7C). Note, that similarly to the bout duration, also the total duration of grooming partner preferences was strongly dependent on rank-distance between the partners; similar-ranking dyads had generally longer total durations of partner preferences than distant-ranked dyads (data not shown). At LHW=720 and LPS=0.99, for many similar-ranking dyads the total bout durations of grooming partner preferences lasted around 12 MONTHS (data not shown). Occasionally, total bout durations of grooming partner preferences in this setting lasted even longer than 12 MONTHS in this setting, with one total bout duration in one simulation run lasting even 24 MONTHS.

As the bout duration and the total duration of partner preferences were longest for LHW=720 and LPS=0.99, in this setting individuals were able to maintain the most stable partner preferences over time. Comparing the bout durations of grooming partner preferences to the number of preferred partners, we see that this was not a result of any differences in number of preferred partners, as these were similar per LPS setting for different settings of LHW (grey box-plots in Figure 5.6A). Instead, intermediate LIKE dynamics allowed for differentiation between regular and incidental groomers and high LPS allowed for selective maintenance of high LIKE attitudes towards such regular grooming partners.

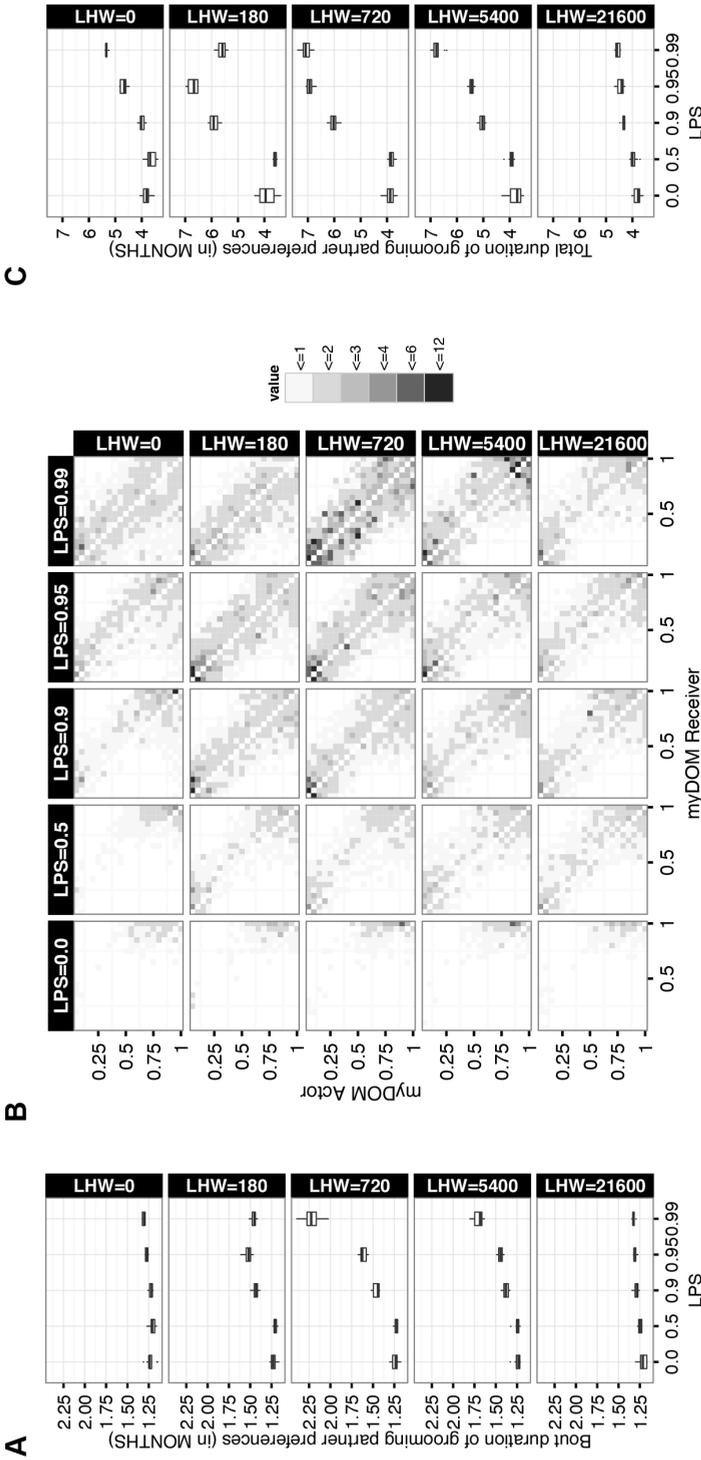


Figure 5.7: Duration of grooming partner preference bouts. **A:** This figure shows the group mean of the average preferred partner bout durations for different settings of selectivity (LPS) and LIKE dynamics (LHW). The box-plots show the duration (in MONTHS) of 10 simulation runs, averaged over two YEARS. **B:** This figure shows the distribution of the average preferred partner bout durations among the dyads of a group for different settings of selectivity (LPS) and LIKE dynamics (LHW). Partner preferences are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking (myDOM=0.05) to high-ranking (myDOM=1.00) individuals. The plot shows the average duration of grooming partner preferences of one example run (the same run as in Figure 5.2) in MONTHS, averaged over two YEARS. Darker shades represent longer preferred partner bout durations. Values at the diagonal are by definition not applicable. **C:** This figure shows the group mean of the total preferred partner durations for different settings of selectivity (LPS) and LIKE dynamics (LHW). The box-plots show the duration (in months) of 10 simulation runs, averaged over two YEARS. See text for definition of bout duration and total duration of grooming partner preferences.

Reciprocity of grooming partner preferences

We also investigated whether grooming partner preference was reciprocated in our model and how the degree of reciprocity was dependent on the different settings in our model. To do this, we compared the total time that A was a preferred partner of B to the total time that B was a preferred partner of A. We calculated the group level reciprocity of the matrix of total preferred partner durations, using Kendall's tau row-wise matrix correlation. A high τ_{rw} indicates a high group-level reciprocity over the total period of 2 YEARS.

At LPS=0, the reciprocity of grooming partner preferences was lowest (around 0.2), independently of LHW, as here individuals did not use their LIKE attitudes to chose grooming partners (Figure 5.8). Thus, at these settings the number of MONTHS in which individual A had individual B as preferred grooming partner was not related to the number of MONTHS that individual B preferred individual A. In these settings, grooming itself was mainly directed up the hierarchy (see Figure 5.3). Therefore, grooming partner preferences were also directed up the hierarchy and were, thus, not reciprocated in these settings.

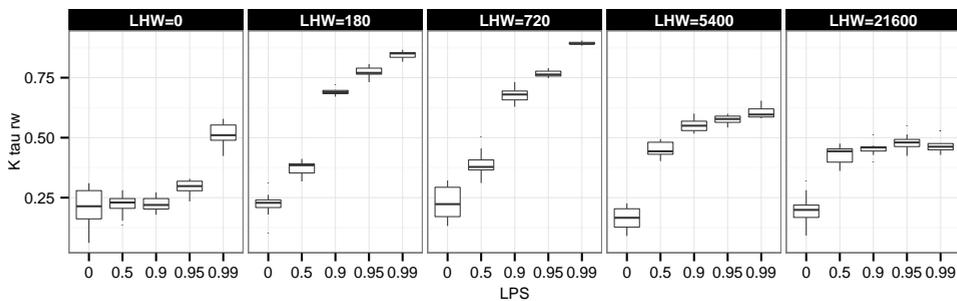


Figure 5.8: Reciprocity of the total durations of grooming partner preferences. This figure shows the group-level reciprocity of the total durations of grooming partner preferences for different settings of selectivity (LPS) and LIKE dynamics (LHW). Group-level reciprocity is measured as Kendall rowwise tau. Higher τ_{rw} values indicate that stronger reciprocity of preferred partner preference. τ_{rw} values were calculated based on the total partner preference durations averaged over 2 YEARS. The box-plots show the τ_{rw} values of 10 simulation runs.

At increased selectivity (LPS), reciprocity of grooming partner preferences was generally increased for all settings of LHW (Figure 5.8). Thus, at higher selectivity grooming partner preferences became more reciprocated. The feedback from LIKE attitudes to grooming partner choices became stronger at high selectivity. As a result, grooming, LIKE attitudes and also grooming partner preferences became more reciprocated. Reciprocity of grooming partner preferences was strongest ($\tau_{rw} > 0.875$) at intermediate LIKE dynamics (LHW=180 or 720) and highest selectivity (see box-plot at LPS=0.99 in intermediate panel of Figure 5.8). At this setting, grooming partner preferences were most stable over time and therefore also most reciprocated.

DISCUSSION

Conditions resulting in long-term bonds in the EMO-model

Long-lasting reciprocal preferences for particular grooming partners emerged in the EMO-model, without requiring a specific (episodic-like) memory of earlier grooming interactions,

given that two conditions were met: first, an intermediate timeframe of emotional bookkeeping of partner-specific earlier grooming episodes, and, second, a high selectivity for grooming partners that are assigned a high LIKE attitude.

Only a high partner selectivity enabled individuals to differentiate between regular and incidental groomers. However, a strong distinction could only be made when LIKE dynamics were intermediate (with a half life decay in LIKE attitudes of about one DAY), not short-term or long-term, which resulted in enough variation in LIKE attitudes between regular and incidental grooming partners. Using this variation as a substrate, high selectivity caused individuals to maintain affiliative relationships with regular groomers and to “neglect” incidental groomers. In turn, differential grooming partner choice reinforced the differentiation of LIKE attitudes. Due to this strong feedback between grooming and LIKE attitudes, both, grooming and LIKE attitudes were most reciprocated in this setting and resulted in the longest, most consistent partner preferences, based on earlier partner-specific affiliation history.

In contrast, at fast LIKE dynamics (low LHW) the emotional response to affiliative events decayed quickly relative to the rate of grooming events. Thus, high LIKE attitudes were maintained only for short periods, which prevented the establishment of a feedback between LIKE attitudes and grooming. Therefore, partner preferences were not reciprocal. At slow LIKE dynamics (high LHW) the emotional response to affiliative events decayed slowly and LIKE attitudes remained high towards many individuals. This resulted in little variation in LIKE attitudes. Consequently, even at high partner preference not much partner specificity in interactions was present. Thus, only intermediate LIKE dynamics resulted in low LIKE attitudes towards incidental, and high LIKE attitudes towards regular groomers. Note, that these results depend on how emotional responses to affiliation was integrated into LIKE attitudes in our model. In a different model study (Campenni and Schino, 2014), individuals are always able to distinguish between better and worse cooperators, even when the difference in cooperation is very small. In their model, increasing the memory of earlier interactions always increased reciprocity and partner-specificity.

In the absence of any partner selectivity (LPS=0), affiliation patterns were mainly based on proximity and, to some extent, the dominance hierarchy. Selected grooming partners were not consistent in time, as partners changed continuously and arbitrarily. Moreover, partner preferences were not symmetric. At low partner selectivity (low LPS), individuals still interacted with many partners, preventing the maintenance of relationships with preferred partners that were assigned high LIKE attitudes. Only when high partner selectivity limited the number of potential interaction partners, the feedback loop between repeated affiliative events and high LIKE attitudes, and thus also mutually high LIKE attitudes, could emerge.

If real primates employ LIKE attitudes to keep track of (the emotional response to) earlier received affiliation, it is expected that this internal representation is also reflected in external, observable behavior. In the EMO-model, this was the case in settings that resulted in partner-specific affiliative relationships. Here, the internal representation of an affiliative relationship (LIKE attitude) corresponded best to the externally measurable behavior (grooming). All in all, these model outcomes suggest that settings of intermediate LIKE dynamics and high selectivity seem most plausible for primates relying on emotional bookkeeping to maintain their social bonds.

Duration of partner preferences

In the EMO-model, at intermediate LIKE dynamics (LHW=720) the half-life of the partner-specific emotional memory was 720 MINUTES (i.e. 1 DAY). At high partner selectivity (LPS=0.99)

preferred grooming partner preferences averaged over all dyads remained stable across 2.25 MONTHS. In this setting, many similar-ranking dyads maintained preferred grooming partner preferences across 4 MONTHS and occasionally even across one or two YEARS.

Interestingly, the conditions that resulted in long total durations of grooming partner preferences were slightly less specific to the parameter settings: LHW between 180 and 5400 and LPS between 0.9 and 0.99 yielded comparable total preferred partner durations. While at LHW=720 and LPS=0.99, this resulted from extended bouts of preferring specific grooming partners, the other settings yielded shorter repeated bouts of maintaining preferred grooming partners. It is yet unclear whether empirical data of primates show a pattern of renewed affiliative bonds due to a predisposition for grooming similar-ranking partners or whether affiliative bonds are continuously maintained over extended periods. Furthermore, the model outcomes indicate that partner similarity, e.g. in dominance rank, may enhance the specificity of emotional bookkeeping. This further suggests that empirical data showing an effect of partner similarity, e.g. concerning dominance rank, do not preclude the involvement of emotional bookkeeping in maintaining partner-specific preferences.

Although the EMO-model yielded partner-specific relationships that lasted for several MONTHS, relationships across one or two YEARS were very rare. Thus, emotional bookkeeping may not be sufficient to generate general long-term partner-specific relationships. Other mechanisms may be required or some specifications of the way emotional bookkeeping was implemented in the model might be modified (see below).

Does the EMO-model apply to empirical situations?

The conditions under which the EMO-model allows maintaining long-term social bonds seem very limiting, since emotional memories of affiliative events should only last for an intermediate period (half-life of one DAY) and a very selective partner preference is required. In the EMO-model it is assumed that the impact of the emotional response to affiliative events on the LIKE update is independent of the current LIKE attitude. Moreover, assumptions were made regarding the ceiling effect of additional affiliative events and regarding the number of partners assigned a high LIKE attitude (see submodel LIKE attitudes in Methods).

In the EMO-model, the impact of an affiliative event on the LIKE attitude is independent from the current value of the LIKE attitude, unless this had reached its predetermined maximum value. However, affiliative events may have a stronger effect when the LIKE attitude is low or high, either promoting relationship quality when it is not yet formed or, in contrast, enhancing existing relationships. New empirical data provide evidence for the latter possibility, since in wild chimpanzees only grooming with regular partners releases oxytocin (Crockford et al., 2013), suggesting a mechanism for emotional bookkeeping that selectively strengthens existing bonds. In addition, particular events may promote the start of a relationship: in chimpanzees food sharing increases oxytocin levels in the recipient and the donor of food, even between non-kin with no established bond (Wittig et al., 2014). Thus, particular processes or events may promote the maintenance or start of a social bond. Similarly, particular aversive events may result in the quick deterioration of a bond, but this effect may again be dependent on the current LIKE attitude. Strong relationships may be more buffered against negative behavior or towards irregular grooming. This requires further empirical research.

Also, in the EMO-model there is no limit to the number of individuals assigned a high LIKE attitude. However, empirical data suggest that primates have social bonds with a limited number

of group members, called grooming cliques (Kudo and Dunbar, 2001). While often individuals interact with many or all group members (network size is a bit lower or similar to group size), the grooming clique is typically much smaller (Kudo and Dunbar, 2001; Table 1). Additional social network analyses in primate species with cohesive groups, e.g. macaques, show that groups often are socially fragmented (Lehmann and Dunbar, 2009). These empirical findings suggest that additional forces, such as partner-specific updates of the social bond and a limit to the number of partners, may cause differentiation in bonding within the group. Thus, the suggested changes in the updating of LIKE attitudes in the EMO-model may enhance the differentiation between partners, promoting the potential for emotional bookkeeping to maintain partner-specific relationships.

Concerning the number of affiliation partners, an interesting side-result from our model is that at high partner selectivity individuals with either very high or very low dominance ranks had fewer preferred partners than intermediate ranking individuals. This was due to the limited number of similar-ranking individuals for those extreme ranking individuals. In empirical data similar patterns have been found, e.g. in horses (van Dierendonck et al., 1995).

Finally, the EMO-model makes assumptions regarding the motivational impact of anxiety and satisfaction on the probability to perform affiliative behavior. High anxiety has a relatively stronger effect than low satisfaction on the motivation to execute affiliative behavior. We chose this relative strength to preclude a direct positive link between satisfaction and the connected LIKE attitude. However, in real animals the relative impact of satisfaction and anxiety may be more equal or even reversed. Primates probably groom not only to reduce anxiety (Dunbar, 2010), since grooming leads to the release of β -endorphins and is rewarding for both the receiving and grooming individual (Keverne et al., 1989; Dunbar, 2010). The relative importance of anxiety and satisfaction remains to be established. Altogether, the implementation of the updates of the dynamic LIKE attitudes in the EMO-model is based on conservative assumptions and empirical data suggest that real primates may employ additional processes that enhance partner differentiation.

Conclusion

In sum, the EMO-model demonstrated that reciprocal preferred social partner preferences and reciprocal affiliation patterns may result from emotional bookkeeping. In fact, only emotional bookkeeping generates partner-specific affiliation patterns, and they were only found in very specific conditions. In the model, only intermediate (not short- or long-term) emotional memory of received affiliation from a particular partner and a strong preference for *LIKEd* partners led to a strong self-reinforcing feedback between high LIKE attitudes and high grooming rates, which generated reciprocal LIKE attitudes and reciprocal grooming that lasted for prolonged periods of time. The EMO-model employs a relatively conservative manner to update LIKE attitudes and has not incorporated self-reinforcing processes where affiliation from preferred partners results in a stronger feedback than that of not preferred partners. However, empirical data suggest that such biased updates may actually be present in primates. Since this will more easily give rise to differentiated relationships with group members, in real primates the conditions that allow emotional bookkeeping to generate prolonged reciprocal affiliative attitudes and behavior may be more common.

SUPPLEMENTARY MATERIAL

Parameter	Description	Value
General model parameters		
<i>N</i>	Number of individuals in the group	20
<i>D</i>	Grid unit	1 m
<i>FIELD_SIZE</i>	Field size	300 x 300 m
<i>MINUTE</i>	Time step	1 min
<i>HOUR</i>	1 hour	60 MINUTES
<i>DAY</i>	1 day	12 HOURS
<i>WEEK</i>	1 week	7 DAYS
<i>MONTH</i>	4 week	350/12 DAYS
<i>YEAR</i>	1 year	50 WEEKS (350 DAYS)
Varied model parameters		
<i>LHW</i>	LIKE-HISTORY WEIGHT, timeframe over which earlier affiliation (LIKE-HISTORY) is incorporated when updating LIKE attitudes	0, 180, 720, 5 400 or 21 600 MINUTES
<i>LPS</i>	LIKE-PARTNER SELECTIVITY, the degree to which valuable individuals are preferred as affiliation partners	0.00, 0.50, 0.90, 0.95, 0.99
<i>TIME_{STAB}</i>	Duration of the stabilization period prior to the data-recording period within a simulation	100, 360, 2 700 or 10 800 HOURS
Sensing parameters		
<i>VIEW_ANGLE</i>	Default view angle	120°
<i>MAX_ANGLE</i>	View angle when scanning	360°
<i>FAR_DIST</i>	Maximum tolerated distance to furthest group member	100 m
<i>MAX_DIST</i>	Maximum distance to individually recognize group members	50 m
<i>NEAR_DIST</i>	Maximum preferred distance to the group	20 m
<i>PERS_DIST</i>	Maximum distance to perceive signals or escalated fights	5 m
<i>INTERACT_DIST</i>	Maximum distance to physically interact with others	1 m
<i>MIN_OTHERS</i>	Minimum preferred number of conspecifics within <i>NEAR_DIST</i>	3
Movement parameters		
<i>SPEED</i>	Movement speed	0.6 m/s
<i>STOP_CHANCE</i>	Probability of ending the current movement bout	0.1

Table S5.1: General model parameters.

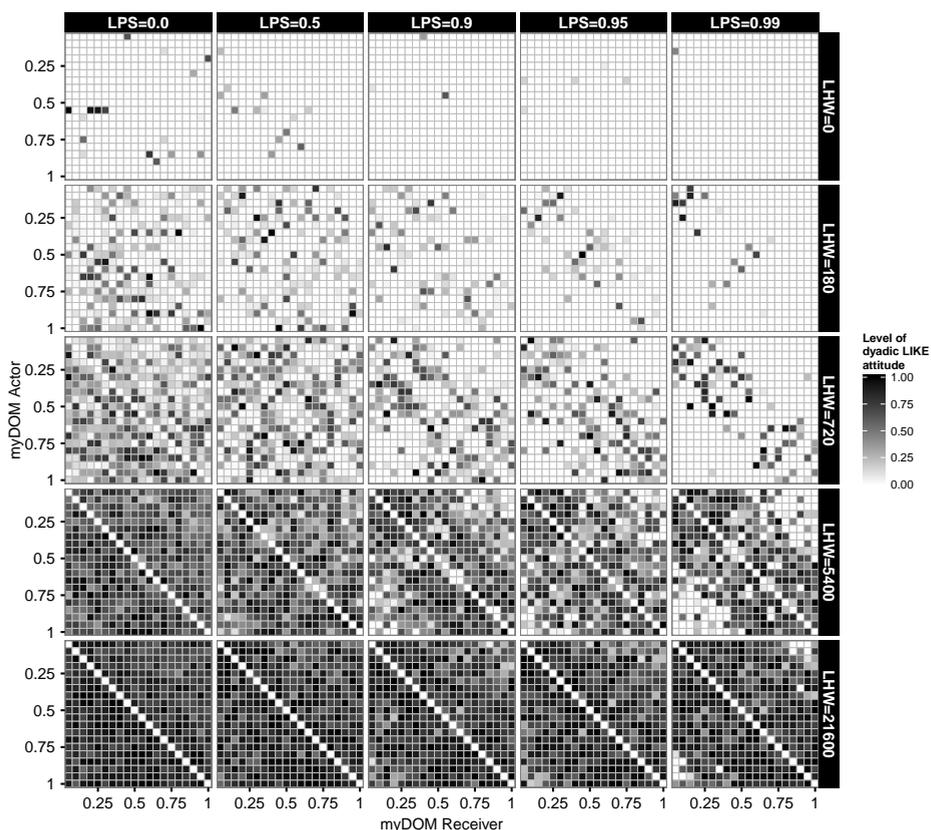


Figure S5.1: Snapshot of LIKE attitudes at TIME = 1 YEAR. This figure shows the distribution of LIKE attitudes among the individuals of a group for different settings of selectivity (LPS) and LIKE dynamics (LHW). LIKE attitudes are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking ($myDOM=0.05$) to high-ranking ($myDOM=1.00$) individuals. The plot shows the LIKE attitudes of one example run (the same run as in Figure 5.2) sampled at one point in time (after one YEAR). Darker shades represent higher LIKE attitudes. Values at the diagonal are by definition not applicable.

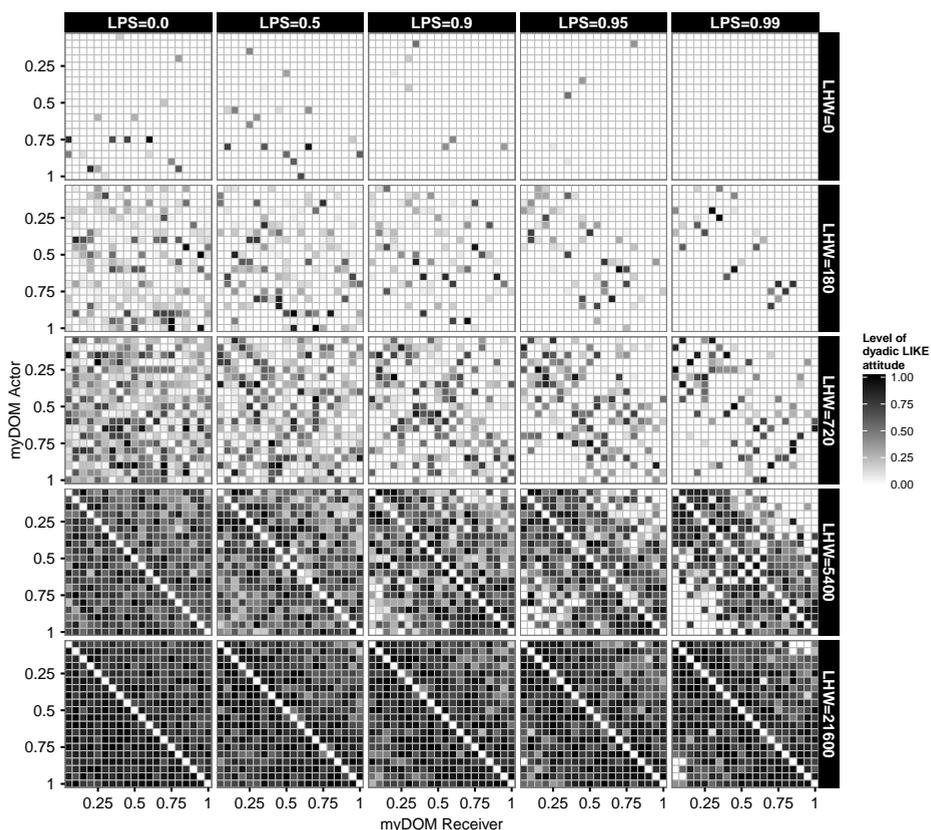


Figure S5.2: This figure shows the distribution of LIKE attitudes among the individuals of a group for different settings of selectivity (LPS) and LIKE dynamics (LHW). LIKE attitudes are directed from actors (y-axis) to receivers (x-axis), both are ordered by dominance strength, ranging from low-ranking ($\text{myDOM}=0.05$) to high-ranking ($\text{myDOM}=1.00$) individuals. The plot shows the LIKE attitudes of one example run (the same run as in Figure 5.2 and Figure S5.1) sampled at one point in time (after two YEARS). Darker shades represent higher LIKE attitudes. Values at the diagonal are by definition not applicable.

Summarizing Discussion

This thesis presents agent-based models (ABMs) inspired by primate behavior that explore the prevention of aggression (Chapter 1-2) and emotional bookkeeping of affiliative relationships (Chapter 3-5). In these models we equipped the model entities with capacities that were more complex than in previous ABMs of primate behavior (e.g. the DomWorld model by Hemelrijk, 1998b, the GrooFiWorld model by Puga-Gonzalez et al., 2009 or the FriendsWorld model by Puga-Gonzalez, 2014), to explore group-level patterns generated by these more complex capacities compared to simple ones. Here, I review and discuss the general importance of our findings. First, I discuss the optimal balance between model simplicity and modeling empirical complexity and provide some striking examples of how more complex models may match and explain empirical data. Second, I review the contribution of the ABMs presented in this thesis. Third, I explore per topic how the presented models differ from previous models of primate behavior and how this contributes to a better modeling and understanding of empirical observations. Last, I recommend further directions for simulation studies and empirical studies of primate behavior. Hopefully, these suggestions will enhance the interchange between models and empirical research. I argue that integrating known complexity of real primate behavior into ABMs and exploring their group-level consequences is essential to find the optimal balance between model parsimony and real life complexity.

All together now - From simple to complex

Modeling studies are always confronted with a trade-off of simplicity against explanatory value (Grimm, 2005). A model too simple is easy to analyze, but it may capture too few mechanisms of the real system, resulting in no additional model predictions. In contrast, a model too complex may include all known processes of the real system, yet it may be too complex for thorough analysis and may limit the model's potential to generate any predictions applicable beyond the specific model system. Following a parsimonious strategy ensures that complexity of a model (and its entities) does not become redundant in terms of explanatory value. However, the optimal limit of model complexity can only be determined by comparing more and less complex model versions (Grimm, 2005).

Specifically concerning ABMs, Grimm proposed that model development should be guided by patterns at multiple levels of the real system (*pattern-oriented modeling*, Grimm, 2005), yielding not only a higher model credibility, but also the opportunity to address and understand several interlocked mechanisms at work in the system (*multi-level modeling*, Hogeweg and Hesper, 1990). Thus, a more complex model that reproduces patterns of the real system at multiple levels better grasps the system's processes than a simpler model, which perfectly reproduces only a single pattern of the system. Similarly, Petit (2011) suggested that modeling studies should be more grounded in empirical research instead of offering oversimplified explanations. Moreover, she considers theoretical models as a prerequisite for empirical research: insights gained from exploring many alternative (even counter-intuitive) hypotheses in simulation studies may provide insights about the importance of distinctive factors, which would

otherwise have remained unnoted, and may in this way guide subsequent empirical research (Petit, 2011). In a number of model studies contrasting simple and more complex hypothesis has shown to be a fruitful endeavor.

In an elegant study on the initiation of collective movement in primates, Sueur et al. (2009) implemented several hypotheses into an ABM and compared the results to empirical data. This revealed that an individual's decision to join an initiated group movement depended on the departure of affiliates (selective mimetism). Alternative hypotheses assumed that departure probability was dependent on a) none of the actions of group members, b) the number, but not the identity of departing individuals, or c) the number of departing relatives. Analyzing multiple group level phenomena, such as departure latencies, associations and the order of individuals at departure, the selective mimetism model explained the empirical observations best.

Huth (1992) developed agent-based models to unravel the underlying movement rules of individual fish within a school. He explored several rules in which individuals adjusted their movement to a) a single neighbor, or b) several neighbors. Concerning one group-level pattern of fish schools, namely nearest neighbor distance, single- and multi-neighbor rules showed similar results. Only comparison of a second group-level pattern, namely the polarization of the group (i.e. the deviation between the swimming direction of each fish and the mean direction of the entire school), showed that a multi-neighbor rule is necessary to generate the patterns observed in real fish schools.

Exploring the rules underlying foraging behavior in bees, de Vries and Biesmeijer (1998) constructed an agent-based model in which they aimed to replicate an experiment conducted with real bees. Here, a colony of bees could forage on two food sources of different profitability, which were switched at intervals. A simple model replicated the empirical data of the first, but not the second day. In this model waggle dancing bees indicated the location of either source to colony members, but only remembered the last visited food source. Two additions to the model were identified necessary to simulate both days of the empirical data: model entities were equipped with more complex memory abilities (memorizing also the time of day a food source was last visited) and reconnaissance flights by inspector bees (to refresh the memory of an earlier visited food source). In a more recent study, Granovskiy et al. (2012) combined a field experiment with a modeling approach to determine the relative importance of the individual memory of inspector bees and the collective memory (via waggle dance communication) on the ability of the colony to adapt to short and long term environmental changes.

These examples underline the necessity to confront model studies with empirical data and show that the comparison of simple and more complex hypothesis within simulation models may reveal new insights.

Agent-based models (ABMs) present an elegant tool to theoretically explore complex group phenomena of social animals, such as primates (Bryson et al., 2007; Hogeweg and Hesper, 1985). Yet, primate social behavior is more sophisticated than represented in many ABMs, especially concerning social information processing and the resulting action selection. In line with Petit (2011) and Grimm (2005), we have developed a series of models in which we equipped model entities with more primate-like behaviors (i.e. behaviors that have been shown to be employed by real primates, but have been neglected in earlier ABMs). Observed patterns of real primate groups are represented in the models at multiple organizational levels, and have been substantiated and validated by empirical data. Comparing several models of alternative (more or less complex) hypotheses, we explored the resulting differences for several group-level phenomena. These comparisons concern ABMs that explore the prevention of aggression (Chapter 1-2) and emotional bookkeeping of affiliative relationships (Chapter 3-5).

Review and contributions to existing theory

The first part of this thesis (Chapter 1-2) focused on the mechanisms underlying the socio-spatial structure in primates, particularly the spatial centrality of dominants observed in a number of macaque species. We elaborated on a well-established model of primate dominance interactions (DomWorld, Hemelrijk, 1998b), in which spatial centrality of dominance simply arises as a consequence of aggressive interactions and the subsequent fleeing of subordinates. However, preventing potentially aggressive encounters is crucial in real primates (Bernstein and Ehardt, 1985; de Waal, 1986; Isbell and Pruettz, 1998; Kutsukake and Clutton-Brock, 2008; Rowell and Olson, 1983; Kaplan and Zucker, 1980). Therefore, we equipped model entities with mechanisms commonly used in a number of primate species to prevent the risk of aggression, such as spatial avoidance (Hall and Fedigan, 1997; Bernstein and Ehardt, 1985; Furuichi, 1983; Isbell and Pruettz, 1998; Jay, 1965; Judge, 2005; Kutsukake and Clutton-Brock, 2008; McBride, 1971; Mori, 1977; Rowell and Olson, 1983; Sommer et al., 2002) and social vigilance (Chance, 1967; Rowell and Olson, 1983; Caine and Marra, 1988; Alberts, 1994; McNelis and Boatright-Horowitz, 1998; Watts, 1998; Blois-Heulin, 1999; Treves, 2000). We investigated the resulting effects on the socio-spatial distribution of individuals within the group and the interaction patterns between the group members.

The second part of this thesis (Chapter 3-5) focused on affiliative relationships and grooming reciprocity in primates. An earlier model study (GrooFiWorld, Puga-Gonzalez et al., 2009) has shown that grooming reciprocity may simply arise from the socio-spatial structuring of the group, which results from dominance interactions rather than from preferential engagement in this model. In contrast to that, primatologists (Schino and Aureli, 2009; Brosnan et al., 2010; Schino and Pellegrini, 2009; Schino and Aureli, 2010a) have proposed that grooming reciprocity in primates may be mediated by emotional bookkeeping (i.e. an emotional-based summary of earlier interactions). Moreover, primates have been shown to engage differentially with others depending on earlier interactions (Silk, 2002b; Brent et al., 2014), and emotional processes are known to regulate behavior (Aureli, 1997; Aureli and van Schaik, 1991; Schino et al., 2007b; Spruijt et al., 1992; Boccia et al., 1989; Shutt et al., 2007; Aureli and Whiten, 2003). Therefore, we developed a model in which entities are capable of emotional bookkeeping, and explored the resulting consequences for the reciprocity, duration and structuring of affiliative relationships.

Here, I will review the findings and insights of the series of model studies presented in this thesis and discuss them in relation to the existing theory.

Preventing aggression - Socio-spatial group structure and individual variation in movement and perception properties

Preventing the potential risk of costly conflicts is crucial, especially in highly aggressive species (Bernstein and Ehardt, 1985; de Waal, 1986; Isbell and Pruettz, 1998; Kutsukake and Clutton-Brock, 2008). Avoiding close proximity towards potential aggressors, i.e. already moving away after perceiving such individuals at a distance, is a simple, but effective behavior that has been reported for a number of primates species (Hall and Fedigan, 1997; Bernstein and Ehardt, 1985; Furuichi, 1983; Isbell and Pruettz, 1998; Jay, 1965; Judge, 2005; Kutsukake and Clutton-Brock, 2008; McBride, 1971; Mori, 1977; Rowell and Olson, 1983; Sommer et al., 2002), and the rank-distance between two individuals is often reflected in the avoidance behavior (Jay, 1965; Chance, 1956). In Chapter 1, we introduced the *avoidance model*, in which aggressor avoidance is determined by two parameters. The parameter *avoidance-dominance*

difference describes the minimum rank-distance between two individuals that elicits avoidance behavior in the subordinate. The parameter *avoidance distance* describes the maximum spatial distance between two individuals that elicits avoidance behavior in the subordinate. Consequently, individuals varied in avoidance behavior and avoidance probability was inversely related to dominance rank. Low avoidance-dominance difference and large avoidance distance characterized high *cautiousness* in the model. We compared the results of different settings of cautiousness in the *avoidance model* to a control model without avoidance, the *fleeing model*.

The fleeing model is an (adapted) reimplementations of the DomWorld model (Hemelrijk, 1998b). Replication of existing models is crucial for understanding and improvement of theoretical models (Bryson et al., 2007; Edmonds, 2003). Moreover, it enabled us to compare characteristics of (our version of) the DomWorld model to other models. The fleeing model confirmed that individual variation in fleeing may result in a central-peripheral group structure (as found in DomWorld, Hemelrijk, 1998b), even with a stable dominance hierarchy (cf. the model in the appendix of Bryson et al., 2007). Exploring the avoidance model, we found that low cautiousness resulted in socio-spatial group patterns similar to the fleeing model, while higher cautiousness resulted in a much more pronounced spatial centrality of dominants and more spread out groups. This socio-spatial structure emerged independently of individual variation in fleeing, i.e. even after excluding individual variation in fleeing tendency from the model (*avoidance with fleeing-control model*). In this way, we identified individual variation in aggressor avoidance as a potentially important structuring factor in primate groups.

In the avoidance model, parameter settings of extremely high cautiousness resulted in an elongated group sorted by dominance rank or even in formation of subgroups consisting of similar-ranking individuals. However, since such group patterns are rarely reported in the context of aggressor avoidance in primates, these extreme parameter settings may not be relevant to real primate groups.

For parameter settings of low cautiousness, the average dyadic distances between individuals in the avoidance model were very similar to the fleeing model. Nonetheless, the two models differed in the frequency and direction of dyadic encounters within the group. In the fleeing model, encounters were almost equally distributed among all possible dyads, whereas in the avoidance model more encounters took place among individuals of similar rank. This shows that social group properties are not deducible from spatial relations alone, especially when individuals engage differentially with group members, not only in close proximity, but also at a distance.

In Chapter 1, we additionally developed a very simple model, the *velocity model*, in which individuals merely differed in movement velocity. In this model, velocity was set inversely related to dominance rank, while individual variation in fleeing or avoidance was excluded. Surprisingly, even this extremely simple model could account for spatial centrality of dominants and, thus, suggests a more general mechanism of differential movement that may potentially underlie this socio-spatial pattern in primates.

Primates do not only spatially avoid potential aggressors perceived by chance, but also employ social vigilance to prevent aggressive encounters. Such pro-active social vigilance is achieved by monitoring the whereabouts of specific potential aggressors that should be avoided and by regularly scanning the social environment to detect further potential aggressors (Chance, 1967; Rowell and Olson, 1983; Caine and Marra, 1988; Alberts, 1994; McNelis and Boatright-Horowitz, 1998; Watts, 1998; Blois-Heulin, 1999; Treves, 2000). Consequently, employing social vigilance is often inversely related to dominance rank (Haude et al., 1976; Deaner et al.,

2005; Alberts, 1994; Pannozzo et al., 2007; McNelis and Boatright-Horowitz, 1998; Keverne et al., 1978; Caine and Marra, 1988) and this individual variation in vigilance has been proposed to structure socio-spatial group properties in primates (Chance, 1967; Chance and Jolly, 1970). To investigate this in Chapter 2, we compared the *avoidance model* (without any social vigilance) to the *monitoring model* and the *scanning model*. In the monitoring model, spatial avoidance of potential aggressors is facilitated by subsequent monitoring of the specific aggressor. In the scanning model, spatial avoidance is preceded by scanning to facilitate the detection of potential aggressors within the group. Both, monitoring and scanning behavior were made inversely related to dominance rank in the models.

In Chapter 2, we found that when subordinates, as compared to dominants, a) more often monitor specific potential aggressors, or b) more often scan the social environment to detect potential aggressors, groups were more spread out and spatial centrality of dominants was more pronounced than in the avoidance model (without social vigilance). In addition, individual variation in scanning tendency alone (in the absence of individual variation in fleeing and avoidance behavior) was sufficient for a central-peripheral group structure to emerge, as was shown in the *scanning control model*. In this way, we identified individual variation in social vigilance as an additional potentially important structuring factor in primate groups.

Individual variation in social vigilance in the monitoring and in the scanning model also affected the frequency and direction of dyadic encounters within the group. In the monitoring model, the subordinates' monitoring of central dominants "distracted" their attention to potential interaction partners (other subordinates at the periphery) and in this way decreased encounter rates. In the scanning model, frequently scanning individuals had a higher chance to perceive other group members, which led to less frequent grouping, more spread out groups and decreased encounter rates. Similar to Chapter 1, this shows that social group properties are not deducible from spatial relations alone, especially when individuals attend to group members differentially.

In Chapter 1 and 2, we have shown that behaviors, which facilitate the prevention of aggression may result in more spread out groups. Empirical (de Waal and Luttrell, 1989; Richter et al., 2009) and theoretical (Hemelrijk, 1999a,b) research suggests that in aggressive primate species, groups are often more spread out as compared to less aggressive species. Our model results suggest aggressor avoidance and social vigilance as possible mechanisms underlying this pattern. However, more empirical research is needed to confirm this hypothesis.

Taken together, the results from Chapter 1 and 2 showed that individual variation in several movement properties (fleeing, spatial avoidance and even sheer velocity) and perception properties (monitoring and scanning) structure the socio-spatial distribution of individuals within a group. Whenever this individual variation in movement or perception properties depends on social characteristics (e.g. dominance rank), group members will be distributed in a non-random fashion across the group, sorted by the specific social characteristic (e.g. dominance rank).

If one would follow a strictly parsimonious approach, rank-related individual variation in velocity (velocity model, Chapter 1) would already be sufficient to explain spatial centrality of dominants in primates. However, equipping model entities with more primate-like abilities, we have identified individual variation in aggressor avoidance and social vigilance as potentially important structuring factors in primate groups. By disentangling the contribution of different factors (known to be employed by primates) within a simulation model, we showed how each factor independently resulted in a specific socio-spatial group structure, a venture that would be impossible in real groups of animals. We conclude that a central-peripheral group

structure may be a robust pattern driven by individual variation in different types of behavior independently and simultaneously.

We propose that movement and perception properties should be taken into account when investigating the socio-spatial group structure in primates. The use of automated observation software and tracking systems may offer an opportunity to collect more accurate data on the movements of individuals with respect to the location of other group members, as well as their visual orientation. Moreover, the comparison of different species or differently composed groups, which vary in the amount of avoidance or social vigilance employed by the individuals may contribute to a further understanding of the structuring role of spatial avoidance and social vigilance in real primates.

Emotional bookkeeping - Reciprocity, maintenance and partner-specificity of affiliative relationships

Primate social life is not only characterized by aggression, but also affiliation. In primates, affiliative relations are developed and maintained through grooming (Silk, 2002b; Massen et al., 2010a; Massen and Sterck, 2013). Primates have been shown to engage differentially with others depending on earlier interactions (Silk, 2002b; Brent et al., 2014) and grooming is often reciprocated (Barrett et al., 1999; Manson et al., 2004; Chancellor and Isbell, 2009; Leinfelder et al., 2001; Schino et al., 2003; Payne et al., 2003). Grooming reciprocity can simply result from the spatial patterning of the group as shown in cognitively simple models (Puga-Gonzalez et al., 2009). However, it is widely accepted that (social) behavior regulates and is regulated by underlying emotional responses. Therefore, it has been proposed that grooming reciprocity and long-term affiliative relationships in primates may be mediated by emotional bookkeeping (i.e. an emotional-based summary of earlier interactions). With the models in the second part of this thesis, we explore how affiliative relationships may differ depending on whether model entities possess more or less cognitive abilities, such as (different degrees of) emotional bookkeeping or a simple preference for similar-ranking group members.

In Chapter 3, we introduced a new model framework, the *EMO-model*, where individual behavior is regulated by short-term emotional responses to the social environment. This model includes not only agonistic, but also affiliative behavior (e.g. grooming). Moreover, model individuals use *emotional bookkeeping* to update long-term partner-specific emotional attitudes that are based on emotional responses to earlier interactions. These emotional attitudes value potential interaction partners and guide partner-specific behavior and movement relative to group members. In this way, the model integrates emotional regulation on several organizational levels (see Figure 3.2 in Chapter 3). The processes implemented in the *EMO-model* have been carefully substantiated, integrating an array of empirical data and several partial hypotheses (on general macaque behavior, emotional regulation of behavior, the two-dimensionality of the emotional system and emotional bookkeeping). We succeeded in producing a representative model that generated many structural properties of real macaque groups on multiple levels. While general behavioral frequencies in the model were tuned to empirical data, group-level patterns (e.g. rank-related differences in behavior and emotional state) arose as a result from the incorporated underlying processes without being explicitly implemented into the model. In Chapter 3, this substantiation and multi-level validation of the *EMO-model* was presented and the causation of the emerging patterns within the model was described.

In Chapter 4-5, the *EMO-model* was then used to further investigate the role of emotional bookkeeping in primate social behavior. Focusing on affiliative behavior, we have systematically explored two main model parameters: a) partner selectivity, i.e. the degree to which

individuals preferred to affiliate with valuable (i.e. *LIKEd*) interaction partners (LPS, LIKE-PARTNER SELECTIVITY), and b) the timeframe over which earlier behavior is summarized in the emotional attitudes (LHW, LIKE-HISTORY WEIGHT). We found that high partner selectivity results in enhanced grooming reciprocity (Chapter 3-5). The main process behind this is the feedback between emotional attitudes and behavior, which reinforces initially small preferences for similar-ranking interaction partners and, this way, weakens the unbalancing effect of high differences in dominance. Interestingly, high grooming reciprocity could also be achieved when valuation of affiliation partners was not based on emotional bookkeeping, but on a fixed characteristic, such as rank-distance (Chapter 4). Thus, preferential engagement with certain individuals (based on fixed characteristics or dynamic interaction history) generally reinforces affiliative reciprocity. However, only the inclusion of dynamic emotional bookkeeping in the model resulted in reciprocal affiliative relationships that were highly partner-specific and not deducible from dyadic rank-distance (Chapter 4). Given that affiliative relationships in primates cannot be solely explained by similarity in rank or other characteristics, our model suggests emotional bookkeeping as a potential underlying mechanism.

In Chapter 5, we varied the timeframe of emotional bookkeeping. Our results show that with emotional bookkeeping over short or long timeframes, individual variation in valuation of potential grooming partners was low. In these settings, earlier grooming episodes were either “forgotten” too fast (short timeframe), or accumulated for almost all group members and not “forgotten” fast enough (long timeframe). Yet, in combination with high partner selectivity, reciprocal partner-preferences did develop. However, these were not maintained continuously over long periods, but individuals switched regularly between several partners. In contrast, emotional bookkeeping over intermediate timeframes resulted in high individual variation in emotional attitudes. In combination with high partner selectivity, this enabled individuals to differentiate between regular and incidental grooming partners. Therefore, this setting allowed for a strong feedback between differentiated emotional attitudes and the distribution of grooming, resulting in the best match between the internal representation of emotional responses to received behavior (emotional attitudes) and actually received behavior (grooming). As a result, this gave rise to strongly reciprocated partner preferences that could be maintained continuously for longer periods, occasionally up to one or two years. We concluded that emotional bookkeeping is a good candidate to underlie partner-specific affiliative reciprocity on the long-term, given that partner-selectivity is high and the timeframe of emotional bookkeeping is not too short and not too long. However, more empirical research is required to illuminate whether primates maintain continuous long-term preferences for affiliation partners or whether they regularly switch preferences between some (similar-ranking) individuals.

We propose that distinguishing between aggressive and affiliative emotions and behaviors will be essential to understand how they contribute each to relationships and group level phenomena. With respect to this, the EMO-model should be explored further. The effect of aggressive and affiliative emotions and behaviors on the development and maintenance of primate relationships should also be further investigated in empirical research. Monitoring behavioral and neurophysiological correlates of the emotional state over longer timeframes and in response to interactions with several group members (e.g. Crockford et al., 2013) may give more insights into the temporal dynamics of relationships. Although ethically more questionable, the manipulation of neurophysiological parameters or group composition (introduction or removal of individuals) and their effects on relationship maintenance and establishment could be explored. Investigating naturally occurring temporal changes of group composition (e.g. fission-fusion, Aureli et al., 2008) may provide further insights on the cognitive capacities necessary and sufficient for primate relationships. Here, prior experiments within the EMO-model may generate testable hypotheses and may guide further empirical work.

Contributions in relation to existing models

The models presented in this thesis elaborated on earlier ABMs of primate behavior. Specifically, the *fleeing model* (Chapter 1) is an (adapted) reimplementations of the DomWorld model of Hemelrijk (1998b), and a number of aspects in the *EMO-model* (Chapter 3-5) resemble the GrooFiWorld model (Puga-Gonzalez et al., 2009) and the FriendsWorld model (Puga-Gonzalez, 2014). With our models, we aimed to implement processes closer to real primate behavior and information processing than thus far done. To evaluate the contribution of modeling more primate-like behavior, we explore the differences in model implementation and the resulting outcomes between simpler and more complex models. While general differences were described above, below we address where these model entities differ in crucial features and whether this has potential consequences for the generated group level patterns. These issues include comparisons of a more technical nature. We compare DomWorld (Hemelrijk, 1998b, 2000; Bryson et al., 2007) to the models of Chapter 1-2 (summarized in Table 6.1), and GrooFiWorld (Puga-Gonzalez et al., 2009) as well as FriendsWorld (Puga-Gonzalez, 2014) to the models of Chapter 3-5 (summarized in Table 6.2).

Dominance

Dominance relationships may be modeled as stable or dynamical relationships. All three models, DomWorld, GrooFiWorld and FriendsWorld, focus especially on the dynamics of the dominance hierarchy and, thus, implemented dynamic dominance ranks, which change upon dominance interactions. Moreover, these models elegantly explain variation in many emergent group patterns by simply varying the impact of dominance interactions on dominance rank (despotic/aggressive vs. egalitarian/relaxed) (Hemelrijk, 1999b; Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014). Since in many primate species the dominance hierarchy can be stable over long periods of time (up to several years, macaques: Bernstein, 1969; Rhine et al., 1989; Ostner et al., 2008; Silk, 1988; gorilla: Robbins et al., 2005; baboons: Samuels et al., 1987; Hausfater et al., 1982; capuchins: Bergstrom and Fedigan, 2010; vervets: Bramblett et al., 1982), we chose to implement a hierarchy that is fixed over the course of a simulation run (≤ 2 years). The *fleeing model* with a fixed hierarchy yielded spatial centrality of dominants very similar to the DomWorld model with a dynamic hierarchy (Table 6.1), as was expected (Bryson et al., 2007) and later confirmed (Puga-Gonzalez et al., 2009). In the same manner, the EMO-model with a fixed hierarchy resulted in grooming reciprocity, similarly to the GrooFiWorld model with a dynamic (or fixed) hierarchy (Puga-Gonzalez et al., 2009). Our results confirm that dynamic dominance relations are not necessary to explain a central-peripheral group structure or grooming reciprocity in primates.

Furthermore, during aggressive interactions, in our models both opponents may decide whether to engage in an (escalated) fight, as a fight only takes place if both opponents agree to it. This is in contrast with DomWorld, GrooFiWorld and FriendsWorld, where the encountered individual always takes part in the fight, if the encountering individual decided to start a fight (Hemelrijk, 1998b; Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014). In real primates however, after receiving signaled or physical aggression individuals may either react submissively (by fleeing or submissive signaling) when the opponent is clearly superior, or react with counter-aggression (resulting in an escalated fight) otherwise (Preuschoft and van Schaik, 2000; de Waal et al., 1976). In our models, the probability to start (or react aggressively in response to) aggression depends on an individual's win chance with respect to the opponent. As suggested by de Vries (2009), we implemented a sigmoid win chance function (Hsu et al., 2005), instead of the relative win chance function used in DomWorld, GrooFiWorld and FriendsWorld. The latter two

Model	DomWorld	Fleeing model (Ch. 1)	Avoidance model (Ch. 1+2)	Monitoring model (Ch. 2)	Scanning model (Ch. 2)	Avoidance with fleeing-control model (Ch. 1)	Velocity model (Ch. 1)	Scanning control model (Ch. 2)
Implemented behavioral rules								
Group size	8 - 20				30			
Default movement	Straight (same direction)							
Grouping behavior	May take two or more time steps (turning randomly 45° until group is perceived and approached)							
Hierarchy	Dynamic				Fixed			
Dominance interaction	Only ego, not the opponent, decides to flee or to start a fight				Both, ego and the opponent, may decide to flee or to start a fight			
Winner turns 45° left or right after chasing loser	Yes				No			
Win chance	Depends on relative dominance difference							0.5 (independent of dominance)
Resulting patterns in the model								
Avoidance at a distance			X	X	X	X		
Monitoring (social vigilance upon avoidance, depending on dominance rank)				X				
Scanning (spontaneous social vigilance, depending on dominance rank)					X			X
Resulting patterns in the model								
Centrality of dominants	Weak - strong (depending on intensity of aggression)	Weak	Weak - strong (depending on cautiousness of avoidance)	Intermediate	Strong	Weak	Weak - strong (depending on max. velocity)	Weak
Group spread	Narrow - wide (depending on intensity of aggression)	Narrow (±36 m)	Narrow - wide (±38-93 m, depending on cautiousness of avoidance)	Intermediate (±75 m)	Wide (±95 m)	Narrow - wide (±31-93 m, depending on cautiousness of avoidance)	Narrow - wide (±18-57 m, depending on max. velocity)	N/A
Subgroups	No	No	Yes, at high cautiousness of avoidance	No	No	N/A	N/A	N/A
More frequent encounters between similar-ranking group members	Weak - strong (depending on intensity of aggression)	Very weak	Weak - strong (depending on cautiousness of avoidance)	Intermediate	Intermediate	N/A	N/A	N/A

Table 6.1: Comparison between DomWorld and the models of Chapter 1-2

adaptations ensured that escalated fights, i.e. counter aggression, between two individuals distant in rank are rare (see Text S1.1 in Chapter 1), which better represents aggression in real primates (Balasubramaniam et al., 2012; Bernstein and Mason, 1963b; Preuschoft and van Schaik, 2000). Concerning the dynamics of the dominance hierarchy, de Vries (2009) also showed that a sigmoid win chance would not yield as unrealistic rank reversals as in the DomWorld model.

Movement

Model results may be sensitive to the implementation of seemingly basic behaviors. Especially when investigating spatial group patterns, the implementation of individual movement should be critically evaluated.

In DomWorld, GrooFiWorld and FriendsWorld, individuals move randomly within the group and only react on the spatial location of others after direct (random) encounters. In contrast to this, individuals in our models may employ goal-directed movement and move away from or towards specific, relevant group members (i.e. potential aggressors or affiliates). This difference is discussed further below (see Socio-spatial information processing).

In our models, when individuals move within the group they employ a random walk and do not turn a random angle (wiggling) after a fight. This is in contrast with DomWorld, GrooFiWorld and FriendsWorld, where individuals by default move straight and, in fact, only change their walking direction after an interaction or when group members are too far away and need to be approached (Hemelrijk, 1998b). Evaluation of the effect of the random turning during movement, yielded that straight movement may result in a higher group spread (Chapter 1). The wiggling, implemented in the DomWorld model to (artificially) prevent too many subsequent interactions is not necessary when individuals follow a random walk procedure. More importantly, straight movement in combination with the wiggling angle may produce centrality of dominance as a model artifact (see Text S1.2 in Chapter 1).

Another aspect that may artificially cause individuals to spend extra time at the periphery is the grouping procedure in DomWorld, GrooFiWorld and FriendsWorld (Hemelrijk, 1998b; Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014). In these models, it may take several trials (and, thus, several time steps) of turning a small random angle, before individuals may perceive other group members again and return to them. Combined with the wiggling of winners (see above) this results in an “advantage” for winning dominants, which may move back to the group faster than losing subordinates. In our models, grouping takes less time, as individuals immediately scan their entire surrounding, to detect and approach group members.

In addition to this grouping procedure, our model groups are forced to not split up into separate groups by implementing a maximum allowed total group spread. This was necessary, since we implemented larger groups consisting of 20 or 30 individuals (instead of 8 (Hemelrijk, 1998b), 10 (Hemelrijk, 2000), 12 (Puga-Gonzalez et al., 2009), 16 (Puga-Gonzalez, 2014) or 20 (model in the appendix of Bryson et al., 2007) individuals), which represents group size in many primate species more accurately (Lehmann et al., 2007; Sueur et al., 2011a). Next to larger group size, behaviors as avoidance or social vigilance additionally increased group spread and without a maximum group spread groups would occasionally split up into separate groups. Real primates may for instance use vocalizations to keep track of the location of more distant group members. Interestingly, a recent study on macaques has shown that individuals indeed ensure group cohesion by using contact calls to monitor spatially distant group members, independently of the number of group members nearby (Sugiura et al., 2014).

Model	GrooFIWorld	FriendsWorld	EMO-model with dynamic attitudes (Ch. 3-5)	Fixed attitude model (Ch. 4)
Implemented behavioral rules				
Group size	12	16	20	
Time	Duration behaviors take no time	Straight (same direction)	Duration behaviors (e.g. moving, grooming) take time	
Default movement			Random walk (walk straight and then either change to random direction (P=0.5) or	
Grouping behavior	May take 2 or more time steps (turning randomly 45° until group is perceived and approached)		Immediately (scan 360° , approach random individual and limited maximum group spread)	
Physical interaction distance (aggression, grooming)		8 m	1 m	
Hierarchy		Dynamic	Fixed (represented by FEAR attitudes)	
Dominance interaction	Only ego, not the opponent, decides to flee or to start fight	Yes	Both, ego and the opponent, may decide to flee or to start fight	
Winner and loser turn 45° left or right after chasing loser			No	
Win chance		Depends on relative dominance difference	Depends on absolute dominance difference (rank distance)	
Action selection and interaction partner selection	According to decision tree; the only potential interaction partner is the nearest individual within interaction distance		According to probabilities; depending on ego's emotional state (arousal, anxiety and satisfaction) and its attitudes (LIKE, FEAR) towards several potential interaction partners (10 nearest within respective distance)	
Avoidance at a distance			X	
Social vigilance (scanning, depending on arousal)			X	
Communicative signaling (aggressive, submissive or affiliative signals)			X	
Arousal			X	
Anxiety		X	X	
Default anxiety change over time		Increase	Decrease	
Satisfaction			X	
LIKE attitudes / "friends"		"Friends"	Dynamic LIKE attitude (depending on emotional responses to earlier received grooming, decreasing over time)	Fixed LIKE-attitude (according to rank distance)
LIKE attitudes / "friends" affect approach probability		X	X	X
LIKE attitudes / "friends" affect grooming probability			X	X
Emotional bookkeeping		Not explicitly implemented	X	
Resulting patterns in the model				
Interaction mainly with similar-ranking group members		Increases with intensity of aggression	Increases with partner selectivity	Increases with partner selectivity
Grooming reciprocity	Decreases with intensity of aggression	Independent of intensity of aggression. Increases with preferred proximity to "friends"	Increases with partner selectivity	Increases with partner selectivity
Partner-specificity (variation among dyads with same rank-distance)		N/A	Increases with partner selectivity and intermediate timeframe of emo. bookkeeping	No
Selective interaction partners		Increases with preferred proximity to "friends"	Increases with partner selectivity	Increases with partner selectivity
Reciprocity of grooming partner preferences		Increases with preferred proximity to "friends"	Increases with partner selectivity and intermediate timeframe of emo. bookkeeping	N/A
Duration of grooming partner preferences		Increases with preferred proximity to "friends"	Increases with partner selectivity and intermediate timeframe of emo. bookkeeping	N/A

Table 6.2: Comparison between GrooFIWorld, FriendsWorld and the models of Chapter 3-5

We conclude that behavioral rules in a model must necessarily simplify the processes at work in real animals. However, researchers should be aware that even seemingly minor implementation details such as the degree of randomness in movement may affect model outcomes and should be thoroughly tested (and replicated) (Bryson et al., 2007; Edmonds, 2003).

Interactions

Primate interactions can have different features: they may be short (e.g. communicative signals), or last considerable time (e.g. grooming). Moreover, they may require physical contact, or be signaled by sounds or facial expression over longer distances.

The *EMO-model* used in the second part of this thesis (Chapter 3-5) resembles several aspects of GrooFiWorld (Puga-Gonzalez et al., 2009) and FriendsWorld (Puga-Gonzalez, 2014). However, in the EMO-model we introduce several new aspects concerning the social interactions between the model individuals. While the GrooFiWorld model implemented grooming as events (with a fixed bout duration), the EMO-model distinguishes between point and duration behaviors, and duration behaviors (e.g. grooming, resting, movement, vigilance) take time. This allowed for temporal behavior patterns and a data-driven validation of the EMO-model concerning average behavioral rates and durations. In real primates, the bout duration of e.g. grooming may be affected by (social) stimuli, for instance interruption by an approaching dominant (Range and Noé, 2005; Sinha, 1998). Such shorter grooming bouts are expected to elicit weaker emotional responses than longer grooming bouts. Implementing the temporal extension of duration behavior in the EMO-model enabled us to account more precisely for the potential effect of group members on behavior duration and the resulting differential emotional responses.

Furthermore, in GrooFiWorld and FriendsWorld individuals may groom or attack individuals that may be at a distance of up to 8 grid units. This is unrealistic for physical acts, but can be achieved by signals. Indeed, primates have been shown to engage in physical interactions mostly when the interaction partner was closer than 1 m and only rarely when the distance was larger (Furuichi, 1983). Therefore, individuals in the EMO-model may only direct such physical interactions towards individuals in close proximity, i.e. at a distance of up to 1 grid unit (resembling 1 m).

In contrast to GrooFiWorld and FriendsWorld, entities in the EMO-model were able to affect the emotional state of group members not only by physical interactions, but also through (less costly) communicative signaling at a distance (by using affiliative, submissive and aggressive signals). Of course, the model entities do not follow conscious, goal-directed strategies of social manipulation, but simply respond appropriately to perceived social stimuli. Distinguishing between physical interactions in close proximity and signaling at a distance allows for a more precise empirical validation of the behavioral frequencies in the model. More interestingly, this allows for specific behavioral sequences, such as appeasement directed from dominants to subordinates to prevent avoidance behavior of the subordinate. Thus, in theory affiliative signals enable affiliative relationships between distant-ranking individuals in our model. Nevertheless, in our model such relationships could not be maintained over long periods of time.

Although, the implementation of interactions in the EMO-model better resembles behavior of real primates and allows for a better translation between model and empirical data, it is not clear whether this also results in more primate-like patterns on a group level.

Socio-spatial information processing

Traditionally, model entities in ABM on animal social behavior use only very localized information. Yet, this local information may result in complex group phenomena that are all the more intriguing. Accordingly, in DomWorld (Hemelrijk, 1998b) and GrooFiWorld (Puga-Gonzalez et al., 2009) model entities only respond to group members in close proximity, except when others are so far away that grouping is necessary. Thus, emergent group phenomena, such as spatial centrality of dominants, arise purely due to aggression, fleeing or grooming upon encountering others. Although intriguing, this does not reflect how real primates *see the world* (Cheney and Seyfarth, 1990a). In macaques (and many other primates), individuals recognize group members and their dominance rank also at greater distances. Spatial avoidance of potential aggressors and social vigilance are common strategies to prevent aggressive encounters. Next to such preference to not interact with certain group members, primates also often show strong preference to approach and engage with specific individuals (kin, mates, affiliative partners), which they may even actively seek out amongst the group members. In other words, real primates do not rely on strictly local information, but also keep track of the movements of other relevant group members (also when not in close proximity) and adjust their own location within the group accordingly (*socio-spatial cognition* cf. Noé and Laporte, 2014; Janson, 1990; Robison, 1981. In part, this was implemented in the FriendsWorld model (Puga-Gonzalez, 2014), where individuals prefer to approach “friends”. We integrated the idea of more primate-like socio-spatial information processing into the models of this thesis to a greater extent, by allowing model entities to spatially avoid potential aggressors already when they are perceived at a distance (Chapter 1-5), use social vigilance (Chapter 2-5) and to selectively approach preferred affiliation partners (Chapters 3-5).

Moreover, in GrooFiWorld and FriendsWorld, entities consider only the nearest individual as potential interaction partner and subsequently follow a hierarchical decision-tree during action selection (Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014). For instance, an individual may perceive an affiliate partner at a distance of 1 meter and a potential aggressor at a distance of 2 meters. Following the decision-tree procedure, the individual would select the affiliative partner as potential interaction partner (nearest individual) and select a behavior (dominance interaction or else grooming), without considering the high risk from the potential aggressor nearby. However, primates typically perceive more than one group member simultaneously and different behaviors may be prioritized for each of the potential interaction partners. For instance, in primates subordinates have shown to leave their grooming partner upon perceiving an approaching dominant (Range and Noé, 2005; Sinha, 1998). Accordingly, the probabilistic selection procedure determining an individual’s behavior in the EMO-model (Chapters 3-5) takes into account several potential interaction partners (up to 10) and all potential behaviors towards these individuals. Following this behavioral probabilities procedure, ego’s decision depends on its emotional state (summarizing ego’s general motivation to groom or to risk aggression) and ego’s attitudes towards the potential interaction partners (summarizing the different partner-specific probabilities of receiving grooming or aggression). This weighing of several behavioral options towards several individuals in our model might, thus, be a better representation of primate decision-making.

Implementing socio-spatial information processing and probabilistic selection of interaction partners and behavior, interaction patterns in our models were not purely deducible from spatial relations (spatial proximity). This is in contrast with causal explanations of interaction patterns derived from the DomWorld or GrooFiWorld model. We conclude that agent-based models of primate behavior should reconsider overly localized information processing, while more empirical research on the effect of specific group members at different distances may

contribute to well-substantiated models of how primates *see the world* and prioritize interactions.

Emotional regulation of behavior

Another contribution of this thesis is the implementation of a new model framework, the EMO-model (Chapter 3-5), in which social behavior is regulated by emotional responses to the social environment. While initial attempts in this direction have been made before (Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014), in the EMO-model a more complete representation of an individual's emotional state was implemented, consisting not only of an aversive component (such as anxiety, as modeled in GrooFiWorld and FriendsWorld, Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014), but also describing a rewarding (satisfaction) and an activating component (arousal), as backed by empirical data (see Chapter 3).

Aversion and reward are also often considered two extremes of the same emotional dimension. However, the differentiation between an aversive and a rewarding dimension of affect or valence has been proposed to better describe a variety of emotional states, also allowing for conflicting emotions that are for instance simultaneously rewarding and aversive (e.g. "guilt", Watson and Tellegen, 1985; Watson et al., 1999; Rolls, 1999; Carver and Scheier, 2001). Moreover, different brain processes seem to be involved in negative and positive reinforcement processes, respectively (Davis, 1992; Tsigos and Chrousos, 2002; Boissy et al., 2007).

In our model, differentiating between an aversive and a rewarding emotional component allowed for a more integrated implementation of the emotional regulation of behavior, while yielding behavioral patterns that match empirical observations. For instance, in the EMO-model anxiety and satisfaction by default decrease over time, but may increase in response to specific behaviors and in turn affect the individual's motivation to execute specific behaviors, aimed to reach a "desirable" emotional state (low anxiety, high satisfaction). In contrast, the GrooFiWorld and the FriendsWorld model lumped these dynamics in one variable (anxiety), which increases or decreases in response to aggression or affiliation. As a result anxiety needs to increase over time to ensure a motivation for grooming in the model (Puga-Gonzalez et al., 2009; Puga-Gonzalez, 2014). However, even in the absence of grooming, (increased) anxiety levels decrease over time towards a baseline level, as has been shown in a number of behavioral primate studies (Kutsukake and Castles, 2001; Majolo et al., 2009; Schino et al., 2007b). Yet, more empirical and experimental data are needed to further illuminate the role of emotions in primate behavior.

Emotional bookkeeping

Emotional regulation processes in the EMO-model were used to implement a possible mechanism of *emotional bookkeeping*. Integrating several emotional responses to specific interaction partners over time into partner-specific emotional attitudes allows model entities to valueate group members, regulating behavior towards others in a partner-specific way. Thus, behavioral probabilities towards group members do not only depend on (fixed) characteristics of interaction partners (dominance rank) and ego's own motivation (summarized in the emotional state), but also on the dynamic interaction-history with specific group members (summarized in the emotional attitude). In this way, the EMO-model presents a suitable (and to our knowledge the first) framework to study the relevance of particular elements of emotional bookkeeping with respect to group-level phenomena, such as grooming reciprocity. Note that to some extent, the FriendsWorld model implemented behavior that may be regulated via emotional bookkeeping,

i.e. a preference for approaching the most regular grooming partners. However, in contrast to the EMO-model, the underlying mechanism of how individuals may distinguish frequent grooming partners from others is not explicitly modeled in FriendsWorld and remains unclear. Another recent ABM study (Campenni and Schino, 2014) showed that reciprocity of cooperation may emerge when individuals are equipped with a memory of their previous interactions and always chose to cooperate with the (available) group member they remember as most cooperative. Campenni and Schino (2014) state that such partner choice based on benefits received may be based on a form of emotional bookkeeping. To investigate this, we developed our EMO-model, where we study which kind of emotional processes, both positive and negative, and what form of emotional bookkeeping, could give rise to reciprocal relationships (Chapter 4) and how long such relationships can be maintained (Chapter 5), in a spatially explicit setting where individuals can engage in both, attractive (such as grooming and approach) and repulsive behaviors (such as aggression, fleeing and avoidance).

The EMO-model allowed us to identify high partner selectivity as a factor that promotes grooming reciprocity and interactions with similar-ranking individuals, offering an alternative explanation contrasting with the purely anxiety-driven patterns found in the GrooFiWorld model (Puga-Gonzalez et al., 2009). Furthermore, only dynamical emotional bookkeeping, not a fixed pre-determined preference for similar group members, led to highly individualized relationships, reflecting dyadic interaction history. The variation found in real primate relationships among rank-, age- or kin-mates (Silk, 2002b) suggests that dynamical emotional bookkeeping is a potential mechanism underlying affiliative relations in primates.

Moreover, we identified the relevance of using emotional bookkeeping over an intermediate timeframe (as opposed to long- or short-term) to obtain the best match between the internal representation of relationships (emotional attitudes) and the external behavioral measures of relationships (grooming). Only in this intermediate setting, emotional attitudes distinguished between occasional and frequent groomers. In turn, reciprocal long-term affiliative relationships could emerge.

The emotional bookkeeping mechanism implemented in the EMO-model does not require complex social cognition in the individuals. Therefore, the EMO-model may be also more generally applicable to other animal species that are capable of individually recognizing individuals, remembering their associated semi-stable characteristics (dominance relationships) as well as the more dynamically changing characteristics (affiliative relationships) (Brent et al., 2014; Seyfarth and Cheney, 2012). This may apply to some bird (Emery et al., 2007; Bond et al., 2003; Boeckle and Bugnyar, 2012; Massen et al., 2014) or fish species (Bshary et al., 2002), several mammal species (e.g. hyenas: Holekamp et al., 2007; horses: Cozzi et al., 2010; Schneider and Krueger, 2012; Cameron et al., 2009; dolphins: Connor, 2007; elephants: McComb et al., 2001) and, without doubt, to many primate species, some of which have been shown to be capable of much more elaborated cognition in the social context than is assumed in this model (Tomasello and Call, 1997). In sum, emotional bookkeeping offers a good candidate hypothesis to explain several affiliative group-level phenomena in primates, such as individualized, reciprocal affiliative relationships. Yet, more empirical and theoretical data are needed to further illuminate the role of emotional bookkeeping in primates.

Future directions

Revealing new insights usually evokes a number of new questions about the system under investigation. Here we present future directions we envision for both, theoretical and empirical research.

Exploring the models in this thesis and potential extensions

In the EMO-model the motivation to engage in affiliative behavior was made dependent on anxiety and satisfaction, where anxiety was given a higher weight. Different weightings of both factors should be assessed systematically in the model, to investigate the consequences for emotional regulation of behavior and resulting group phenomena, such as grooming reciprocity.

In a very recent model study (Dolado et al., 2014), based on the GrooFiWorld model, the motivation to engage in grooming increased depending on the level of anxiety and the degree of relatedness, i.e. a kinship factor. Such a kinship factor corresponds to fixed, unconditional LIKE attitudes in the EMO-model and may also be implemented as such in our model. Interestingly, such unconditional affiliative (kinship) bonds resulted in less grooming reciprocity as compared to the model without kinship bonds (Dolado et al., 2014).

Different implementations of the emotional attitudes, specifically of how they develop and are maintained, can also be investigated in the EMO-model. We have differentiated between an affiliative and an agonistic emotional attitude (LIKE and FEAR), to reflect the rewarding and aversive dimension of the emotional state implemented in the model. Potentially, this also allowed for conflicting attitudes towards individuals. For instance, a high LIKE and FEAR attitude may be associated with a valuable, but very high-ranking group member. Alternatively, LIKE and FEAR may be integrated into a single emotional attitude, such that a positive emotional attitude is only associated with valuable individuals that are either not high-ranking, or very tolerant. Similar to this, researchers have proposed that relationship quality may be a composite of several independent factors (*value, compatibility, security* cf. Fraser et al., 2008).

Moreover, LIKE attitudes in the EMO-model only increase in response to received grooming, while only at very specific parameter settings long-term bonds could be maintained. Alternatively, LIKE attitudes may also incorporate other valuable (e.g. support), or even negative (e.g. aggression) experiences with group members, serving as a common currency that enables comparison of individuals based on different social contexts (Schino and Aureli, 2009). Moreover, the impact of grooming (or the lack of it) on LIKE may depend on the current value of LIKE (Crockford et al., 2013), and even being in proximity to *LIKEd* individuals may already be rewarding, strengthening existing social bonds. This may allow for more relaxed criteria for long-term bonds to arise, even without the need for continuous maintenance. In line with this, several studies have shown that reciprocity is often found at a long-term scale, while not necessarily present on a short-term scale (Schino and Pellegrini, 2009; Schino et al., 2007a, 2009). Thus, also assessing reciprocity at different timescales in the model seems relevant. In addition, a limit to the number of preferred partners might be implemented into the model, as grooming cliques in primates often include only a few of all interaction partners or group members (Kudo and Dunbar, 2001; Lehmann and Dunbar, 2009). This again may result in more relaxed criteria for long-term bonds to be maintained in the model, especially in settings with a long timeframe of emotional bookkeeping, where individuals develop many high, stable LIKE attitudes without the need for regular maintenance (Chapter 5). A recent ABM (Campenni and Schino, 2014) was used to investigate the evolution of cooperation. Individuals could follow defective or cooperative strategies, where cooperation implied a fitness cost to the actor and a benefit for the receiver. Cooperative strategies were evolutionary stable, when benefits of cooperation were high enough compared to costs. It would be interesting to pursue a similar research direction with the EMO-model. The evolutionary success of individuals that differ for instance in partner selectivity or the timeframe of emotional bookkeeping may then be investigated.

In the future it would be also interesting to assess the occurrence of additional behavioral patterns in the EMO-model, such as behavioral contagion, redirection, support in fights, or post-conflict affiliation. We suspect that emotional regulation may play a major role in these behavioral patterns. This could be investigated in the EMO-model and may also yield additional levels of validation or potential improvements of the model. Using a cognitively simpler model (as compared to the EMO-model), Hemelrijk and Puga-Gonzalez (2012) showed that support in fights, and its reciprocation or exchange, may simply emerge as a result of socio-spatial structure and social facilitation (activation of animals due to nearby salient stimuli, i.e. fights), without any need for triadic awareness, record-keeping or rules of thumb. Comparing these results with support patterns in the EMO-model would reveal how the addition of emotional regulation of relationships and attraction to affiliative partners may alter these results. A first step in this direction has been made with the FriendsWorld model, in which individuals preferably approach affiliative partners, while probabilities of grooming are not determined by so-called “friendships” (Puga-Gonzalez, 2014). As compared to the simpler GrooFiWorld (Puga-Gonzalez et al., 2009), the preferred approach of “friends” in FriendsWorld appears to reinforce reciprocation of support and interchange of grooming and support, but does not reinforce reciprocation of grooming.

The models presented in this thesis also offer other opportunities to implement and test hypotheses that have been studied in existing models, such as the effect of a dynamic dominance hierarchy (Hemelrijk, 1996), aggression intensity and different dominance styles (Hemelrijk, 2000, 1998a, 1999b; Puga-Gonzalez et al., 2009), sex differences (Hemelrijk, 1999a; Hemelrijk et al., 2003, 2008), relatedness (Dolado et al., 2014), collective movement (King et al., 2011; Sueur et al., 2009), predation (Lehmann, 2009; Ando, 2005), foraging (Ramos-Fernandez et al., 2006) or effects of food distribution (van der Post and Hogeweg, 2004; van der Post et al., 2009; van der Post and Hogeweg, 2006; Hemelrijk et al., 2003). Comparison of the different model results would give more insights into the additional effects of emotional regulation of behavior and emotional bookkeeping on emerging group phenomena. These may differ, as the socio-spatial structure in the EMO-model is not purely structured by dominance interactions, but also by emerging affiliative relationships (i.e. mutual LIKE attitudes). In addition, a more complete understanding of the importance of emotional bookkeeping as opposed to the socio-spatial structuring of the group may be achieved by removing spatial structure or dominance-related differences from the model (as done in Chapter 1-2 and Puga-Gonzalez et al., 2009). This can be easily investigated in ABMs, while for instance partial correlations fail to completely exclude such effects (Hemelrijk and Puga-Gonzalez, 2012).

Furthermore, our model entities may be equipped with even more elaborate cognitive capacities, such as knowledge of third-party relationships, dynamical bookkeeping of third-party relationships and more elaborate memory of partner-specific interaction history (e.g. *episodic-like memory*), to establish which group phenomena may be ascribed to the use of higher cognition as opposed to simpler behavioral rules. However, this may require more of a cognitive modeling approach. For instance, van der Vaart et al. (2012) developed a cognitive model to investigate food caching (and re-caching) behavior in birds. While this generated interesting new hypotheses about the underlying cognitive architecture of a bird in different experimental settings, interactions and spatial structuring within a group context are not included in this model. A combined approach, i.e. cognitive agents in a spatially explicit, social setting, may be even more challenging, but should be feasible.

Empirical and experimental data needed to test the models in this thesis

The implementation of the models presented in this thesis revealed several gaps in the knowledge of social primate behavior and the underlying regulation mechanisms. More empirical

and experimental data are needed for further substantiation of the models' implementation and validation of the models' predictions. For instance, the spatial positions of animals within a group need to be measured more thoroughly, specifically with respect to other group members, characteristics of the animals, executed and received behaviors and resulting changes in the emotional state. Although the technical facilities are long available (e.g. see local position tracking in cows, Gygas et al., 2010), we still depend on outdated, qualitative or anecdotal descriptions, e.g. concerning the central-peripheral group structure in many primates (Corradino, 1990). Moreover, several aspects of the EMO-model have been implemented, although a clear understanding of how a number of regulation processes work in real animals is still lacking. This concerns for instance the precise dynamics of development and maintenance of affiliative attitudes towards valued group members (LIKE attitudes). Moreover, how real animals decide between several optional behaviors and interaction partners might be investigated more thoroughly. This may be done with multiple-choice experiments, which could be replicated in the EMO-model afterwards. Similarly, experiments concerning the group composition (e.g. introduction or removal of individuals) could be executed in real animal groups and the model in parallel. While controlled experimental manipulation of the group composition may be limited by welfare considerations, replicating the effect of naturally occurring introductions (offspring and immigration) or removals (mortality and emigration) in the model may be a good starting point.

Conclusion

Investigating primate group phenomena (socio-spatial structure, interaction structure, reciprocity of affiliative relationships) by using simulation models, we based the implemented behavioral rules on existing models and an additional array of empirical data of primate social behavior and widely accepted hypotheses on primate emotion and cognition. We emphasize the importance of contrasting several potential explanations that implement simple or more elaborated behavioral or cognitive assumptions. This allowed us to identify multiple factors that may all affect socio-spatial group structure, i.e. individual variation in movement or perception properties. Moreover, this revealed that elaborated cognition (emotional bookkeeping) may result in specific alterations of group phenomena, i.e. individualized, partner-specific relations. While models may not prove the existence of specific capacities or mechanisms in the real animals, they may suggest possible (even counterintuitive) mechanisms to be further tested empirically. Additionally, models may serve as a tool to reveal gaps or inconsistencies in existing hypothesis. Therefore, we conclude that the models presented in this thesis provide a useful framework to investigate primate social complexity *in silico*, to yield useful new suggestions for studying primate social complexity *in situ*.

NL

Nederlandse Samenvatting

Het volledig begrijpen van de complexiteit van diergedrag binnen een sociale context vormt een uitdaging. Individuen maken deel uit van een (vaak complex) gestructureerd netwerk van talrijke interactiepartners die elkaar onderling in hun gedrag beïnvloeden. Indrukwekkende voorbeelden van complexe *ruimtelijke* groepsstructuur kunnen worden waargenomen in insectenkolonies, visscholen en vogelzwermen, waar de groep bijna als één organisme lijkt te ageren. In veel gevallen zijn de individuen in de groep op een bepaalde manier gerangschikt: volgens grootte, snelheid of andere eigenschappen. Groepen van dieren vertonen ook een *sociale* structuur, bijvoorbeeld een netwerk van affiliatieve (“vriendschappelijke”) banden en dominantierelaties. Deze sociale relaties kunnen over de tijd veranderen op basis van eerder uitgewisseld gedrag (zoals vlooiën of agressie). De ruimtelijke structuur van een groep (de posities van de individuen ten opzichte van elkaar) weerspiegelt vaak ook de sociale groepsstructuur en kan bijvoorbeeld dominantierelaties of affiliatieve relaties tussen de dieren weergeven. De zogenoemde *sociaal-ruimtelijke* groepsstructuur beschrijft deze samenhang. Interacties tussen de individuen beïnvloeden zowel de ruimtelijke alsook de sociale groepsstructuur, maar worden er tegelijkertijd ook zelf weer door beïnvloed. Zo kan de kans op interacties (of de kwaliteit ervan) afhangen van de ruimtelijke afstand en de sociale banden tussen de dieren. Deze wederkerige afhankelijkheden tussen individueel en groepsniveau, en tussen de dieren onderling, kenmerken een complex systeem en maken het ontrafelen van de onderliggende mechanismes van complexe groepsstructuren moeilijk.

Twee eigenschappen van groepen van primaten staan in dit proefschrift centraal. Het eerste deel van dit proefschrift onderzoekt mechanismes die de sociaal-ruimtelijke structuur van de groep beïnvloeden, in het bijzonder de ruimtelijke centraliteit van dominanten. Zo zijn bij een aantal primatensoorten dominante dieren vaker in het midden van de groep te vinden en dieren van lage rang meer aan de rand van de groep. Het tweede deel van dit proefschrift exploreert de mechanismes voor wederkerige, affiliatieve relaties bij primaten. Bij veel primatensoorten onderhouden individuen (vaak langdurige) affiliatieve banden met specifieke groepsleden. Deze zijn vaak wederkerig wat betreft de duur van vlooi beurten of de partnerkeuze. Empirisch onderzoek naar zulke complexe groeps patronen is niet altijd haalbaar gezien de ethische, financiële en methodologische restricties die gecontroleerde manipulatie van het gebruik van bepaalde gedragingen of cognitieve capaciteiten en het verzamelen van bijbehorende datasets belemmeren. Theoretisch onderzoek met behulp van computersimulaties biedt hiervoor een veelbelovend alternatief.

Computersimulatiemodellen kunnen worden gezien als een set van (probabilistische) regels, die de toestand van een systeem bepalen afhankelijk van zijn huidige staat. Veronderstelde hypothesen over de onderliggende mechanismes van bepaalde eigenschappen of patronen van het systeem worden vertaald naar modelalgoritmes, die dan gesimuleerd, en door systematische manipulatie van de parameters onderzocht kunnen worden. Dit biedt de mogelijkheid om te achterhalen of een hypothese niet in zich zelf tegenstrijdig is en kan kennishiaten in het theoretisch kader blootleggen. Alternatieve hypothesen kunnen worden vergeleken, parameterinstellingen zijn in zijn geheel en zonder problemen manipuleerbaar en relevante veranderingen in

het systeem zijn meetbaar. Bij zogeheten individu-gebaseerde modellen (*agent-based models*, ABM of *individual-oriented models*, IOM) ligt de nadruk op het gedrag van het individu en hoe interacties tussen individuen met bepaalde eigenschappen of gedragsregels kunnen resulteren in patronen op een hoger organisatieniveau, de groep. Cruciaal is dat deze groepspatronen in het model niet globaal gespecificeerd worden, maar door zelforganisatie als emergente eigenschappen ontstaan die puur resulteren uit de interacties tussen individuen. Wanneer zowel het gedrag van de individuen alsook de resulterende groepspatronen goed overeenkomen met de werkelijkheid, heeft een model (en dus de in het model geïmplementeerde hypothese) een grote verklarende waarde.

Er zijn meerdere mogelijke verklaringen voor de ruimtelijke centraliteit van dominanten. Deze verschillen in de aannames die worden gemaakt betreffende de cognitieve capaciteiten waarover de interacterende individuen beschikken, en reiken van zeer simplistisch tot hoog cognitief. Een van de hypothesen benadert het probleem vanuit een ultiem perspectief en beredeneert dat aan de rand van de groep een hoger predatierisico heerst, waardoor individuen met een voorkeur voor het (veilige) groeps midden zouden zijn geëvolueerd ('selfish herd theory', Hamilton, 1971). Vanuit een proximaal perspectief zijn het de dominante dieren die het beste aanspraak kunnen maken op hun voorkeur voor het midden van de groep. Onderzoek via computersimulaties heeft echter aangetoond dat een dergelijke voorkeur voor het midden van de groep niet noodzakelijk is om een soortgelijk sociaal-ruimtelijk groepsstructuur te genereren.

Het waarschijnlijk meest onderzochte individu-gebaseerde model van sociaal gedrag en de sociaal-ruimtelijke structuur van primaten (m.n. makaken) is het zogenoemde *DomWorld model* van Hemelrijk (2000). In dit minimalistische model ontstaat de groepsstructuur als een bijproduct van agressieve dominantie interacties. Na een dominantie interactie vlucht de verliezer (normaliter dus het dier van lagere rang) weg van de winnaar (normaliter het dominantere dier) en komt zo beetje bij beetje automatisch meer aan de rand van de groep terecht. In feite structureert individuele variatie in vluchtgedrag de ruimtelijke structuur binnen de groep.

Over het algemeen is het sociale gedrag van primaten echter veel uitgebreider en complexer dan in DomWorld (en andere modellen) is gerepresenteerd. Zo kunnen individuen in DomWorld pas op de nabijheid van een dominant dier reageren nadat er een confrontatie heeft plaats gevonden. Echte makaken, zoals de meeste andere primaten, kunnen daarentegen groepsleden en hun dominantierang al vanaf grotere afstand herkennen. Bovendien is preventie van agressie cruciaal. Omdat in deze minimalistische modellen entiteiten met eenvoudige gedragsregels al zeer complexe groepspatronen kunnen genereren, zou men het implementeren van meer ingewikkelde gedragsregels als overbodig kunnen beschouwen. Desondanks is het interessant om te onderzoeken, wat complexer gedrag van de individuen aan de groepspatronen zou kunnen toevoegen of hoe deze zouden kunnen veranderen. Dit is vooral relevant wanneer zowel het geïmplementeerde gedrag van de modelentiteiten, alsook de eruit ontstane groepspatronen meer overeenkomen met wat in werkelijkheid plaatsvindt. Een dergelijk model biedt dan een betere verklaring voor de onderliggende mechanismes van complexe groepspatronen bij primaten dan een minimalistisch model. In dit proefschrift hebben we dan ook modellen ontwikkeld, waarin we de modelentiteiten hebben uitgerust met meer op primaten lijkend gedrag.

Het eerste gedeelte van dit proefschrift (hoofdstuk 1-2) richt zich op manieren waarop veel primaten het risico op agressie (door dominantere dieren) ontwijken, zoals het mijden van dominanten en waakzaamheid tegenover dominanten. Mijden en waakzaamheid zijn waargenomen in verschillende primatensoorten en de frequenties van deze gedragingen zijn vaak omgekeerd evenredig aan dominantierang.

In hoofdstuk 1 introduceren we het *avoidance model*, waar het mijden van potentieel agressieve groepsleden bepaald wordt door twee parameters. De parameter *avoidance-dominance*

difference beschrijft het minimale verschil in dominantierang dat mijdgedrag teweeg brengt. De parameter *avoidance distance* beschrijft de ruimtelijke afstand tot een potentieel agressief individu dat mijdgedrag teweeg brengt. De kans op mijden van anderen varieert dus tussen de individuen binnen de groep en is omgekeerd evenredig aan dominantierang. Een klein *avoidance-dominance difference* en een grote *avoidance distance* karakteriseren een sterke mate van *voorzichtigheid* in het model. Verschillende gradaties van *voorzichtigheid* in het *avoidance model* werden vergeleken met een model zonder mijdgedrag, het *fleeing model* (overeenkomend met het DomWorld model). Het *fleeing model* bevestigde dat individuele variatie in vluchtgedrag kan resulteren in ruimtelijke centraliteit van dominanten (zoals eerder aangetoond in het DomWorld model, Hemelrijk, 1998b), zelfs wanneer de dominantiehiërarchie stabiel blijft over de duur van de simulatie. Grotere *voorzichtigheid* in het *avoidance model* versterkt deze sociaal-ruimtelijke groepsstructuur en resulteert ook in een grotere ruimtelijke spreiding van de groep. Deze patronen kunnen ook ontstaan wanneer er geen individuele variatie in vluchtgedrag is. Dit werd aangetoond in een model waarin wij voor individuele variatie in vluchtgedrag controleren (*avoidance with fleeing-control model*). Deze resultaten suggereren dat individuele variatie in het mijden van agressie een potentieel structurende factor is binnen groepen van primaten. Bij een zwakke mate van *voorzichtigheid* zijn de sociaal-ruimtelijke groepsstructuren in het *avoidance model* vergelijkbaar met het *fleeing model*. Echter, de twee modellen verschillen in de hoeveelheid en richting van dyadische ontmoetingen binnen de groep. Waar interacties in het *fleeing model* bijna gelijk verdeelt zijn over alle potentiële interactie partners, zijn er in het *avoidance model* meer interacties tussen individuen met vergelijkbare dominantierang. Met andere woorden, wanneer gedifferentieerde interacties met anderen niet alleen dichtbij maar ook op grotere afstand plaatsvinden, zijn sociale groepseigenschappen niet volledig te herleiden tot de ruimtelijke structuur. In hoofdstuk 1 is ook nog een uiterst simpel model onderzocht, het *velocity model*, waarin individuen *alleen* verschillen in hun snelheid (deze is in het model omgekeerd evenredig gemaakt aan dominantierang: de ranglaagste dieren verplaatsen zich het snelst) en *niet* in vlucht- of mijdgedrag. Verrassend genoeg resulteerde ook dit zeer eenvoudige model in ruimtelijke centraliteit van dominanten, d.w.z. de langzaamste individuen bevinden zich vaker dicht bij het midden van de groep. In het algemeen suggereert dit dat individuele variatie in verschillende typen bewegingen door de individuen sociaal-ruimtelijke groepseigenschappen kunnen structureren.

Primaten kunnen extra waakzaam zijn, door na het mijden van een potentiële agressor de afstand tot dit individu in de gaten te houden (*monitoring*), of door proactief rond te kijken (*scanning*) om de locatie van potentiële agressoren binnen de groep te bepalen. In hoofdstuk 2 vergelijken we het *avoidance model* (zonder extra waakzaamheid) met het *monitoring model* en het *scanning model*. In deze modellen is de geneigdheid voor *monitoring* en *scanning* gedrag omgekeerd evenredig gemaakt aan de dominantierang van een individu. Het blijkt dat individuele variatie in extra waakzaamheid de ruimtelijke centraliteit van dominanten en de ruimtelijke spreiding van de groep versterkt. Daarnaast is individuele variatie in *scanning* gedrag op zich al voldoende om ruimtelijke centraliteit van dominanten te genereren. Dit hebben we aangetoond in een model waarin de individuele variatie in vlucht- en mijdgedrag werd uitgesloten (*scanning control model*). Hoofdstuk 2 laat dus zien dat ook individuele variatie in verschillende vormen van waakzaamheid sociaal-ruimtelijke groepseigenschappen kunnen structureren. Individuele variatie in waakzaamheid had ook effect op de hoeveelheid en richting van dyadische ontmoetingen. In het *monitoring model* resulteerde de extra aandacht van subordinaten naar centrale dominanten in minder aandacht voor potentiële interactiepartners (andere ranglage individuen aan de rand van de groep). Hierdoor namen interacties tussen ranglage dieren af, terwijl de ruimtelijke structuur zeer vergelijkbaar was met het *avoidance model*. Analoot aan hoofdstuk 1, kunnen we concluderen dat sociale groepseigenschappen niet volledig te voorspellen zijn op basis van ruimtelijke structuur, maar ook kunnen afhangen

van de individuele variatie in waakzaamheid t.o.v. groepsleden. In het *scanning model* hadden individuen die vaak rondkijken een hogere kans om voldoende groepsleden waar te nemen, waardoor deze individuen (ranglage dieren aan de rand van de groep) minder snel geneigd waren om weer dichterbij de groep te komen. De grotere afstand tot groepsleden resulteerde vervolgens ook hier in minder interacties tussen ranglage dieren.

De modellen in hoofdstuk 1 en 2 tonen aan dat gedragingen die preventie van agressie faciliteren resulteren in een grotere ruimtelijke spreiding van de groep. Interessant genoeg zijn agressieve primaten vaak gekenmerkt door een grotere ruimtelijke spreiding. Onze modellen suggereren dat mijden en waakzaamheid dit patroon kunnen verklaren. Meer empirisch onderzoek is echter nodig om dit te bevestigen. Al met al laten de resultaten van hoofdstuk 1 en 2 zien dat individuele variatie in divers bewegings- (vluchten, mijden en zelfs snelheid) of waarnemingsgedrag (monitoring en scanning), de sociaal-ruimtelijke verdeling van individuen binnen de groep kan structureren. Wanneer de variatie in deze eigenschappen afhangt van sociale eigenschappen (zoals dominantierang), zullen groepsleden op een niet willekeurige manier binnen de groep gepositioneerd zijn, gerangschikt op de bepaalde sociale eigenschap (dominantierang). Met de modellen in hoofdstuk 1 en 2 hebben we individuele variatie in mijden en waakzaamheid als twee belangrijke structurende factoren voor groepen van primaten geïdentificeerd. Het structurend verband tussen deze gedragingen en groeps patronen is nog niet eerder aangetoond, noch empirisch noch theoretisch. Wij concluderen dat centraliteit van dominanten een robuuste eigenschap van primaten groepen lijkt te zijn, die door verschillende mechanismes onafhankelijk van elkaar kan ontstaan.

Het tweede deel van dit proefschrift (hoofdstuk 3-5) onderzoekt de mechanismes die ten grondslag liggen aan wederkerige, affiliatieve relaties binnen groepen van primaten. Ook hier lopen de verklarende hypothesen sterk uiteen wat betreft de benodigde onderliggende cognitieve capaciteiten die verondersteld worden. Individuen zouden bijvoorbeeld simpelweg een voorkeur kunnen hebben voor vlooipartners die bepaalde eigen eigenschappen delen (bijvoorbeeld leeftijdsgenoten of familieleden). Deze *symmetriegebaseerde reciprociteit* (zoals voorgesteld door de Waal and Luttrell, 1988 en Brosnan and de Waal, 2002) is cognitief gezien heel eenvoudig, maar evolutionair gezien gevoelig voor “valsspellers”. Bovendien hebben primaten vaak gedifferentieerde relaties met groepsgenoten van dezelfde leeftijd of familie, en deze relaties veranderen ook over de loop van de tijd. Als een cognitief zeer ingewikkeld mechanisme dat wederkerige relaties bij primaten zou kunnen verklaren wordt *berekende reciprociteit* gezien (*calculated reciprocity*, de Waal and Luttrell 1988), waarvoor eerdere gebeurtenissen met elke interactie partner exact zouden moeten worden bijgehouden. Echter, een soortgelijke strategie in het alledaagse leven toe te passen zou zelfs voor mensen een uitdaging zijn. Een alternatief mechanisme voor wederkerige relaties zou *attitudinal reciprocity* (de Waal, 2000; Brosnan and de Waal, 2002) kunnen zijn, waar het gedrag naar een ander individu bepaald wordt door het (kort daarvoor) ontvangen gedrag van dit individu. In tegenstelling tot *calculated reciprocity*, hoeft een individu hier niet alle details van eerdere interacties te onthouden, maar worden deze als het ware samengevat in een partnerspecifieke houding (*attitude*) middels emotionele reacties op eerdere interacties met de ander. Deze emotionele reacties bevatten geen complexe informatie (wie? wat? waar? wanneer?), maar alleen een emotionele waardering (positief/negatief) en kunnen daarom makkelijk worden samengevat. Vervolgens wordt deze (samengevatte) emotionele houding geassocieerd met de interactie partner. Dit proces noemt men *emotional bookkeeping* (Schino and Aureli, 2009).

Of wederkerig vlooiën en affiliatieve banden op lange termijn bij primaten daadwerkelijk door *emotional bookkeeping* gereguleerd worden is moeilijk te achterhalen door empirisch onderzoek en werd niet eerder onderzocht in simulatiemodellen. Een aantal simulatiemodellen heeft

laten zien dat wederkerig vlooien ook een resultaat kan zijn van de sociaal-ruimtelijke structuur binnen de groep en dat emotional bookkeeping niet per se nodig is (Puga-Gonzalez et al., 2014; Hemelrijk and Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). Gezien de belangrijke rol van emoties voor sociaal gedrag en het feit dat primatengedrag vaak niet puur door ruimtelijke nabijheid bepaald wordt (hoofdstuk 1-2), is het relevant om de toegevoegde waarde van emotional bookkeeping in deze context te onderzoeken. In het tweede deel van dit proefschrift (hoofdstuk 3-5) hebben we daarom verschillende model-versies vergeleken, waarin de individuen wel of niet gebruik maken van emotional bookkeeping (of verschillende gradaties ervan).

Om emotional bookkeeping in een model te implementeren, moet ook de onderliggende emotionele regulatie van gedrag gemodelleerd worden. Daarom hebben we een nieuw model ontwikkeld, het *EMO-model*, waarin gedrag binnen een sociale context gereguleerd wordt door emotionele processen. In het model wordt de emotionele toestand van een individu beschreven door een activerende, een aversieve en een attractieve component (respectievelijk *arousal*, *anxiety*, en *satisfaction*). De emotionele toestand wordt beïnvloed door sociale interacties en beïnvloedt zelf ook weer de geneigdheid van het individu om bepaalde gedragingen uit te voeren. Het ontvangen van agressie resulteert bijvoorbeeld in een verhoging van arousal en anxiety, wat vervolgens resulteert in agonistisch gedrag met verhoogde risicogevoeligheid en in een verhoogde kans op vlooien, waakzaamheid of actief gedrag (in plaats van rusten). Over de tijd nemen arousal en anxiety niveaus weer af tot een bepaald basisniveau. Vlooien resulteert in een snellere verlaging van arousal en anxiety en verhoogt bovendien het niveau van satisfactie. Over de tijd, wanneer er niet gevlooid wordt, neemt ook satisfactie weer af tot een bepaald basisniveau. Lage satisfactie verhoogt dan weer de kans op vlooien. Door dit soort terugkoppelingsmechanismen reguleren emotionele processen binnen het EMO-model zowel spontaan gedrag, alsook gepaste reacties op ontvangen gedragingen. Deze emotionele processen werken echter alleen op een korte termijn en beïnvloeden alleen de algemene (in plaats van partnerspecifieke) gedragskansen van een individu.

Een samenvattend *geheugen* van de emotionele reacties op eerdere sociale interacties (*emotional bookkeeping*) maakt het mogelijk om de waarde van groepsgenoten op langere termijn bij te houden. In het EMO-model associëren individuen partnerspecifieke emotionele attitudes met elk groepslid. Een *LIKE attitude* (affiliatieve attitude) representeert de affiliatieve waardering van een ander groepslid, gebaseerd op de hoeveelheid en duur van eerder ontvangen vlooien van dit groepslid. Met andere woorden, als gevolg van het feit dat individu A individu B vlooit, verhoogt de waarde van de LIKE attitude die individu B met individu A associeert. Vervolgens verhoogt dit de kans voor affiliatieve gedragingen (zoals naderen, affiliatieve signalen en vlooien) van individu B naar individu A. Over de tijd, wanneer individu B niet meer door individu A gevlooid wordt, neemt de waarde van de LIKE attitude langzaam weer af. Naast een LIKE attitude, associeert ieder individu ook een *FEAR attitude* (angstige attitude) met elk groepslid. In tegenstelling tot de LIKE attitudes, worden de FEAR attitudes in het EMO-model niet geüpdate, maar representeren de dominantie verhoudingen binnen de dyades, die over de tijd van een simulatie niet konden veranderen. Wel beïnvloeden ook FEAR attitudes het gedrag. Een hoge FEAR attitude (geassocieerd met een dominant groepslid) verlaagt de kans op agressie en verhoogt de kans op submissie naar dit (dominante) groepslid toe. Al met al beïnvloedt de emotionele toestand (*arousal*, *anxiety*, *satisfactie*) van een individu de algemene kansen voor verscheidene gedragingen op een korte termijn. De emotionele attitudes (*LIKE*, *FEAR*) daarentegen beïnvloeden gedrag op een partnerspecifieke manier en op een langere termijn.

In hoofdstuk 3 wordt de implementatie van de emotionele processen in het EMO-model onderbouwd, waarbij we ons baseerden op een omvangrijke set empirische data en literatuur

onder andere met betrekking tot (sociaal) gedrag van makaken (en andere soorten primaten), de emotionele regulatie van gedrag, de verschillende dimensies van het emotionele systeem en *emotional bookkeeping*. We zijn erin geslaagd om een representatief model te ontwikkelen dat structurele eigenschappen van makakengroepen op verschillende niveaus weerspiegelt. De algemene kansen op verschillende gedragingen werden zo geïmplementeerd dat de gemiddelde frequenties van elk gedrag overeenkomen met de empirische data. Andere eigenschappen van het model (zoals verschillen in gedrag en emotionele toestand tussen subordinaten en dominanten, of tussen dyades met klein of groot verschil in dominantierang) ontstonden daarentegen als resultaat van het samenspel van de verschillende geïmplementeerde processen, zonder dat deze eigenschappen zelf expliciet in het model geïmplementeerd werden. Naast de onderbouwing, de parametrisatie en de multi-niveau validatie van het EMO-model beschrijft hoofdstuk 3 hoe uit de op elkaar inwerkende processen de emergente eigenschappen binnen het model ontstaan. De volgende twee hoofdstukken laten zien dat het EMO-model een geschikt raamwerk is om sociaal gedrag met betrekking tot emotionele regulatie en *emotional bookkeeping* te onderzoeken.

Wanneer primaten beschikken over het vermogen tot *emotional bookkeeping*, kunnen zij kiezen uit verschillende potentiële vlooipartners afhankelijk van de partnerspecifieke attitudes tegenover deze individuen. Daarbij is er een voorkeur voor de meer geapprecieerde individuen (met een hogere LIKE attitude). In hoofdstuk 4 onderzoeken we hoe groot de voorkeur voor zulke individuen zou moeten zijn om een bepaalde mate van wederkerigheid in vlooi-gedrag te verkrijgen. Hiervoor hebben wij de parameter *LIKE-partner selectiviteit* (LPS) systematisch binnen het EMO-model geëxploreerd. LPS beschrijft de mate van selectiviteit voor groepsleden met een hoge LIKE attitude ten opzichte van individuen met een lagere LIKE attitude. De resultaten van onze studie tonen aan dat een sterke partner selectiviteit (hoge LPS) wederkerigheid in vlooi-gedrag versterkt. Het belangrijkste onderliggende mechanisme is de terugkoppeling tussen emotionele attitudes en gedrag. Omdat ranglage dieren vaak de nabijheid van ranghoge dieren mijden zijn er meer affiliatieve interacties tussen dieren met gering rangverschil. Hierdoor verhogen LIKE attitudes tussen deze dieren en wordt de aanvankelijk nog lage voorkeur voor dieren met gering rangverschil versterkt. Bovendien zijn affiliatieve interacties tussen dieren met een groot rangverschil vaak eenzijdig (ranglage dieren vlooiën dominanten) vanwege het hoge risico op agressie voor de ranglage dieren. Hierdoor ontwikkelen zich ook eenzijdige LIKE attitudes. Dieren met gering rangverschil mijden elkaar niet waardoor wederkerig vlooi-gedrag en wederkerige LIKE attitudes kunnen ontstaan die elkaar versterken.

Het EMO-model met dynamische LIKE attitudes (*dynamic attitudes model*) hebben we in hoofdstuk 4 vervolgens vergeleken met een cognitief eenvoudiger model (*fixed attitude model*). In het *fixed attitude model* zijn de LIKE attitudes niet gebaseerd op vlooi-interacties, maar op de (stabiele) rangafstand tussen de individuen. Het *fixed attitude model* representeert dus een alternatieve hypothese (namelijk op symmetrie gebaseerde reciprociteit) voor de regulatie van wederkerig vlooi-gedrag. Interessant genoeg werd er ook in het eenvoudigere *fixed attitude model* wederkerigheid in vlooi-gedrag versterkt, naarmate de selectiviteit voor dieren met kleine rangafstand toenam (hoge LPS). Meer algemeen suggereert dit dat selectiviteit voor bepaalde individuen (gebaseerd op veranderlijke interactiegeschiedenis of vaststaande eigenschappen) affiliatieve wederkerigheid kan versterken. Echter, alleen wanneer er gebruik werd gemaakt van *emotional bookkeeping* (*dynamic attitude model*) ontstonden er wederkerige relaties die zeer partnerspecifiek waren en niet op grond van rangafstand konden worden voorspeld. Ook in echte primatengroepen is er vaak variatie in affiliatieve relaties tussen dyades met dezelfde rangafstand (of andere vaststaande eigenschappen zoals familiebanden) te observeren. Dit suggereert dat wederkerige relaties in primaten daadwerkelijk via *emotional bookkeeping* kunnen ontstaan.

Over hoe lange tijd er met behulp van emotional bookkeeping iets kan worden bijgehouden en wat de verdere implicaties van deze tijdsduur zijn is nog niet eerder wetenschappelijk onderzocht. Intuïtief gezien zou men verwachten dat emotional bookkeeping over een langere termijn zou resulteren in stabielere, langdurigere relaties. In hoofdstuk 5 onderzoeken we deze vraag door de duur van de parameter *LIKE-HISTORY WEIGHT* (LHW) systematisch te exploreren. LHW beschrijft de snelheid van de afname van *LIKE* attitudes wanneer er niet gevlooid wordt. Een hoge LHW resulteert in een langer aanhoudend emotioneel geheugen van eerder vlooi gedrag. Voor elke setting van LHW hebben we ook verschillende settings voor partner selectiviteit (LPS) onderzocht. Emotional bookkeeping over een korte en, verrassend genoeg, ook over een lange termijn resulteerde in weinig variatie in *LIKE* attitudes. In deze settings werden eerdere vlooi-interacties of te snel “vergeten” (korte termijn), of ze werden voor alle interactiepartners te lang bijgehouden en niet snel genoeg “vergeten” (lange termijn). Wederkerige partnervoorkeur kon alsnog onder deze settings ontstaan wanneer partner selectiviteit (LPS) hoog genoeg was. Echter, de voorkeur voor bepaalde partners was niet consistent over lange periodes, omdat individuen vanwege de lage variatie in *LIKE* attitudes regelmatig van vlooi-partner wisselden. Emotional bookkeeping over een middellange termijn resulteerde daarentegen in hoge variatie in *LIKE* attitudes. In combinatie met hoge partner selectiviteit stelde dit individuen in staat om onderscheid te maken tussen regelmatige en incidentele vlooi-partners. Hierdoor zorgde deze setting voor een sterke terugkoppeling tussen gedifferentieerde emotionele attitudes en de verdeling van vlooiën, waardoor ook de interne representatie van ontvangen vlooiën (*LIKE*) en het daadwerkelijk ontvangen gedrag het meest overeen kwamen. Dit resulteerde in sterk wederkerige partner voorkeuren, die ook over langere periodes stabiel bleven. We concluderen dat emotional bookkeeping een goede verklaring zou kunnen zijn voor partnerspecifieke wederkerigheid op de lange termijn, verondersteld dat partner selectiviteit hoog genoeg is en emotional bookkeeping niet op korte of lange, maar op middellange termijn werkt. Er is echter meer empirisch onderzoek nodig om te verifiëren of primaten daadwerkelijk lang aanhoudende stabiele voorkeur hebben voor bepaalde vlooi-partners of dat er vaak van voorkeur gewisseld wordt.

Al met al hebben wij in dit proefschrift onderzocht hoe verschillende fenomenen op groepsniveau, met name centraliteit van dominanten en wederkerige, affiliatieve relaties, binnen groepen van primaten kunnen ontstaan. Hiervoor hebben wij bestaande modellen uitgerust met meer op primaten lijkend gedrag, waarbij we empirische data en verschillende hypothesen met betrekking tot emoties en cognitie bij primaten hebben geïntegreerd. Ons onderzoek benadrukt de relevantie van het vergelijken van verschillende potentiële verklaringen, die meer of minder geavanceerde cognitie of gedragsregels veronderstellen. Wij wijzen een aantal nieuwe factoren aan (individuele variatie in verschillende bewegings- en perceptie eigenschappen), die onafhankelijk van elkaar de sociaal-ruimtelijke groepsstructuur kunnen beïnvloeden. Daarnaast wijzen wij emotional bookkeeping aan als mogelijke verklaring voor langdurige, wederkerige partnervoorkeur. Modellen kunnen weliswaar niet aantonen of uitsluiten dat een onderzochte diersoort over bepaalde cognitieve vaardigheden beschikt. Desalniettemin concluderen we dat de modellen in dit proefschrift een relevant kader bieden om sociale complexiteit *in silico* te bestuderen, om zo nuttige nieuwe suggesties te genereren voor onderzoek van complexiteit bij primaten *in situ*.

R

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Curriculum Vitae

I was born on 3rd of November 1979 and grew up in a small suburb village of Berlin, in (back then) Eastern-Germany. After having finished school, I worked with a group of mentally handicapped people, as part of a “voluntary year of social service” program. Meanwhile, I was puzzling over whether it would make more sense to study Biology or Mathematics. In the end I could not decide between the two and moved to Greifswald (near the Baltic Sea) to study Biomathematics. At a certain point, I decided to come to Utrecht, the Netherlands as an exchange student. This would surely be a mind broadening experience and a good opportunity to improve not only my English, but also another foreign language I had started to learn, Dutch. After the exchange year at the Theoretical Biology group from Utrecht University I was convinced everything in Utrecht was just more *my way* than back in Germany. So I stayed in Utrecht to finish my studies. After graduating I grabbed the opportunity to work on a PhD research project at the Behavioural Biology group in Utrecht, of which this thesis presents the results.

