

I SPY WITH MY LITTLE EYE

*The presence and social application of visual
perspective taking in monkeys*

A.M. Overduin – de Vries.

© Anne Overduin – de Vries

Overduin – de Vries, Anne Marije

I spy with my little eye: *The presence and social application of visual perspective taking in monkeys.*

PhD dissertation, Utrecht University 2013

Cover photo: Anne Overduin – de Vries

Cover design: Nikki Vermeulen

Printing: Ridderprint, grafisch bedrijf, Ridderkerk, NL

ISBN: 978-90-5335-641-8

I spy with my little eye:

The presence and social application of visual perspective taking in monkeys.

Ik zie, ik zie wat jij niet ziet:

De aanwezigheid en sociale toepassing van Visueel Perspectief Nemen in apen.

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van doctor aan de Universiteit Utrecht op gezag van de rector magnificus, prof.dr. G.J. van der Zwaan, ingevolge het besluit van het college voor promoties in het openbaar te verdedigen op maandag 11 februari 2013 des middags te 12.45 uur

door

Anne Marije Overduin – de Vries
geboren op 7 oktober 1980
te Noordoostpolder

Promotor: Prof.dr. B.M. Spruijt

Co-promotor: Dr. E.H.M. Sterck

Dit proefschrift werd (mede) mogelijk gemaakt met financiële steun van het Biomedical Primate Research Centre (BPRC), Rijswijk, the Netherlands.

Table of Contents

CHAPTER 1: A general introduction to primate cognitive capacities in the visual domain	7
CHAPTER 2: Male long-tailed macaques (<i>Macaca fascicularis</i>) understand the target of facial threat	19
CHAPTER 3: Understanding the target of attention in common marmosets	29
CHAPTER 4: Long-tailed macaques (<i>Macaca fascicularis</i>) understand what conspecifics can see in a competitive situation	39
CHAPTER 5: Sneaky monkeys: an audience effect of male rhesus macaques (<i>Macaca mulatta</i>) on sexual behavior	49
CHAPTER 6: Sneak copulations in long-tailed macaques (<i>Macaca fascicularis</i>): no evidence for tactical deception	65
CHAPTER 7: Rhesus and long-tailed macaques show sexual behaviour at locations distant, not at locations hidden from the alpha-male	81
CHAPTER 8: Summary and Discussion	97
Nederlandse samenvatting	109
References	116
Dankwoord	126
Curriculum Vitae	128



1

A general introduction to primate cognitive capacities in the visual domain

Human and non-human primate intelligence

Because intelligence is one of the main features proposed to be substantially different between humans and other animals, knowledge of the evolution of human intelligence has great importance for the study of human evolution. An important element of human intelligence shaping many aspects of human behaviour is Theory of Mind (ToM), the ability to attribute mental states to oneself and others, and to understand that others have beliefs, desires, and intentions that are different from one's own (Premack and Woodruff 1978). ToM is made up of different underlying cognitive capacities differing in cognitive complexity. Most of the cognitive capacities underlying ToM do not stand on their own and basic cognitive capacities are necessary in order to allow other more complex capacities involving understanding other people's minds (Wellman and Gelman 1992).

To know more about the evolution of human intelligence, it is important to know which elements of human ToM are present in modern species of more or less closely related non-human primates. There are two approaches to study the connection between these elements, the first is based on the ontogeny of ToM in humans. Some ideas about the order in which separate elements may have evolved may be gathered by looking at the ontogeny of human intelligence since the stages of a child's cognitive development follow the same steps as the evolution of cognition (Piaget 1970, Dekleva

2011). Human children will first go through a phase where they attend to people's eyes, subsequently understand that other people attend to, reach for specific objects, before they can understand desires (Wellman and Gelman 1992). Similarly, during the evolution of human intelligence some features of ToM should have evolved and be present before others can evolve. The second approach is based on comparative knowledge of ToM and its precursors in non-human primate species. In this thesis we will focus on comparative studies of different species of non-human primates. Some basic elements of Theory of Mind may be present in primate species more distantly related to humans, such as for example New World monkeys, while more complex elements of ToM may be present in more closely related primate species, such as apes. Separate elements of ToM may require cognitive skills in different domains, and capacities in different domains may be equally complex. Additionally, advanced cognitive capacities may exist as emergent properties operating on a network of interrelated neuronal structures (Sterck and Begeer 2010). Therefore it may not be possible to put them all on one linear scale of increasing cognitive complexity. Nevertheless, these capacities are considered to differ in their cognitive complexity and we aim to discuss them from generally basic to more complex (Box 1). We will discuss cognitive capacities with the main focus on the visual domain. In this introduction, we first define the different cognitive capacities in the visual domain, in order of basic to advanced. We review evidence for their presence in primate species (Table 1). Next, we give an introduction to the proposed evolutionary history of these cognitive capacities. Following this, we speculate about the evolutionary benefits of these capacities, in particular in the social domain.

Elements of intelligence in non-human primates

A first cognitive capacity underlying ToM is *gaze recognition*. This requires the detection of eyes. Sensitivity to eyes is found in many animal species ranging from fish to humans (Emery 2000). Gaze recognition further requires an animal to discriminate between different gaze directions and may be based on operant learning. An individual may learn that if it sees both eyes of someone else during a certain behaviour it either benefits from or is punished by this individual. Subsequently, it learns to increase or decrease certain behaviours while being watched by others. This results in differences in behaviour when someone else's gaze is directed at oneself as compared to a gaze directed somewhere else, i.e. an audience effect. Such audience effects are found in many animal species, such as reptiles, birds, domestic dogs and primates (Emery 2000).

Second, the detection of a gaze which is not directed at oneself, i.e. averted gaze, may lead to *gaze following*. Gaze following behaviour may be a reflexive response or an individual may learn that if it follows someone else's gaze it often finds something interesting. If gaze following is based on this associative learning mechanism, it is considered a cognitively basic capacity, i.e. *low level gaze following*. Low-level gaze following is widespread among different primate genera (e.g. Lemur: Shepherd et al. 2006; Eulemur: Ruiz et al. 2009; but see Anderson and Mitchell 1999; *Callithrix*: Burkart and Heschl 2006; *Macaca*, *Cercocebus* and *Pan*: Tomasello et al. 1998) and is even found in some domestic non-primate species (Emery 2000).

Alternatively, gaze following is based on a cognitively more demanding mechanism of understanding that other individuals direct their attention at certain objects, i.e. understanding the target of attention. Individuals may follow gaze in a search

for the target of attention, i.e. *high level gaze following*. For both apes (Tomasello et al. 1999, Okamoto-Barth et al. 2007) and monkeys (Burkart and Heschl 2006, Amici et al. 2009, Goossens et al. 2012) there is evidence that gaze following is more than a reflexive behaviour, because they follow gaze geometrically, i.e. to a hidden location, thus extrapolating the direction of the gaze. For the apes, the evidence for high level gaze following is considered convincing. However, the results with monkeys can be explained through a simpler mechanism. First, subjects may have learnt a rule such as ‘move in the gazed direction in order to find something interesting’ (Amici et al. 2009). Second, in other studies, results should be interpreted with caution, since looking at the hidden location may be a result of elevated arousal from the facial expressions of the demonstrator and no significant results were obtained (Goossens et al. 2012). Third, results (Burkart and Heschl 2006) can be explained by reflexive co-orientation, because only few distracter objects were in the same direction as the target of attention, subjects were allowed to check two containers, and success rates were low (28-43 % correct with either eyes only or head and eye cues). Another indication that gaze following in monkeys can be more than reflexive comes from *Cercopithecus diana diana* monkeys, which expect to see a target of attention if they observe averted gaze of conspecifics (Scerif et al. 2004). However, this may be a conditionally learnt expectation. So far, the only unequivocal evidence for high-level gaze following is found in apes.

The fourth element of ToM; *Visual Perspective Taking (VPT)*, may be expressed in two different levels. *Level 1 VPT* allows individuals to understand which objects are visible from another viewpoint, including an understanding that objects that are seen may not be seen by other individuals and vice versa (Salatas and Flavell 1976, Flavell 1981). Although many different paradigms have been used to study VPT in non-human primates, not all paradigms unequivocally evidence VPT. Level 1 VPT is found in apes (Hare et al. 2000, Hare et al. 2006, Melis et al. 2006), Old World monkeys

Box 1: Definitions of ToM elements

Detection of eyes: react to a stimulus of two horizontally aligned circles

Gaze recognition: discriminating between at least two different gaze directions, e.g. between gaze at self and averted gaze.

Gaze following: after detection of someone else’s averted gaze, look in the same direction (Emery 2000).

Low-level gaze following: follow someone else’s gaze reflexively, or because following gaze often results in detecting interesting objects.

High-level gaze following: follow someone else’s gaze because you know the other is seeing something interesting.

Understanding the target of attention: understand that another individual’s gaze is directed at a certain target rather than just oriented somewhere in space.

Visual Perspective Taking (VPT)

VPT level 1: understand what other individuals can see, i.e. understanding line of sight

VPT level 2: understand that objects look different from different viewpoints.

Knowledge attribution: making inferences about what other individuals know.

Inferring intentions, and desires: understand that the behaviour of someone else has a certain goal (Dennett 1987)

Tactical deception: Acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent (Byrne and Whiten 1990).

Understanding false belief: Understand that other individuals may believe certain things that may differ from what you know is true.

(Flombaum and Santos 2005) and lemurs (Sandel et al. 2011). However, in order to ascertain the use of VPT in an experimental setting it is crucial that other simpler cognitive mechanisms are excluded. A simple mechanism that is not eliminated in all paradigms testing for VPT is that subjects may avoid seeing the eyes of a competitor when approaching contested food and this was not excluded in Old World monkey and lemur studies (Flombaum and Santos 2005, Hare et al. 2006, Sandel et al. 2011). Moreover, a paradigm that unequivocally evidenced VPT in apes (Hare et al. 2000) yielded negative results in New World monkeys (Hare et al. 2003, Burkart and Heschl 2007). Therefore, evidence for VPT is only solid for apes and not for Old World monkeys, New World monkeys or lemurs. *Level 2 VPT* includes an understanding of how objects may look different from different viewpoints (Salatas and Flavell 1976, Flavell 1981). Level 2 VPT has never been tested in non-human primates.

A fifth element, *knowledge attribution*, adds to the previous one that individuals understand that another individual knows about things it has seen, while it is unaware of events it has not witnessed. Experiments testing for knowledge attribution yielded positive results for both apes (Povinelli et al. 1990, Hare et al. 2001) and monkeys (Martcorena et al. 2011). Some of the results with apes (Povinelli et al. 1990) can be explained by conditional learning and were not reproducible if conditional learning was eliminated (Call et al. 2000). The results with monkeys can be explained by an expectancy to search for the object in the location where it actually is, without attributing knowledge (Martcorena et al. 2011). Additionally, the paradigm that yielded unequivocal positive results in apes (Povinelli et al. 1990) yielded negative results in Old World monkeys (Povinelli et al. 1991). Therefore, knowledge attribution is only unequivocally found in apes.

A fifth element of ToM includes *making inferences about someone else's intentions and desires*, and attribute goals to the behaviours of others (Dennett 1987). Apes are able to understand intentions of others since they reach for an object, which a human experimenter intends to grab but is out of reach (Hare and Tomasello 2004, Warneken and Tomasello 2006, Warneken et al. 2007). Additional evidence for understanding intentions comes from apes punishing individuals who purposely steal a contested food item, while not punishing individuals who got the food due to external factors and did not intend to steal it (Jensen et al. 2007). Moreover, chimpanzees who are confronted with an experimenter who fails to give them food exhibit fewer frustration behaviours and are less urged to leave the test area than chimpanzees confronted with experimenters unwilling to give the food (Call et al. 2004). This paradigm revealed similar results in a monkey species (*Cebus apella*: Phillips et al. 2009). The results in apes and monkeys were not attributed to simpler cognitive capacities. Therefore, both apes and monkeys seem capable of the attribution of intentions and desires.

A sixth element is *tactical deception*, where individuals actively withhold or change information from bystanders in order to deceive them. Tactical deception may include hiding objects or behaviour for others or misleading others by purposely giving certain signals in the wrong context. In order to evidence tactical deception it is important that the deceptive behaviour is indeed tactical and not learnt through operant conditioning. Apes tactically withhold information from human competitors by reaching for food through an opaque rather than a transparent tube and through a silent rather than a noisy tube (Melis et al. 2006). This behaviour is not likely to be the result from

operant conditioning, because subjects had no previous experience with the tubes and received no feedback on their accuracy during the experiment. In monkeys some deceptive behaviours are reported, which may indicate tactical deception (brown lemurs: Genty et al. 2008; spider monkeys: Amici et al. 2009; rhesus monkeys: Santos et al. 2006, Amici et al. 2009; and capuchin monkeys: Fujita et al. 2002, Amici et al. 2009, Wheeler 2009). However, the behaviour of lemurs (Genty et al. 2008) can be explained through operant conditioning during the experiment. Similarly the behaviour of spider, capuchin, and rhesus monkeys to refrain from opening a food containing box in the presence of a dominant (Amici et al. 2009) may be explained through daily encounters with dominants near food that often result in the dominant stealing the food. Deceptive behaviour in the form of predator alarm calls in absence of predators (Wheeler 2009) can also be explained as a result of conditional learning, since an individual that accidentally produces these calls may experience less competition for food. One of the behaviours displayed by capuchins that is difficult to explain by operant conditioning is that they spontaneously try to deceive a conspecific competitor by first opening a non-baited box before opening the baited one (Fujita et al. 2002). However, only one subject showed repetitive deceptive behaviour and the behaviours were not convincing, since the subject did not benefit from its deceptive behaviour and moved slowly to the baited box. More evidence for tactical deception comes from rhesus macaques, which prefer to steal a grape from a silent container when a human competitor does not watch the containers, while choosing at random if the competitor is watching the monkeys (Santos et al. 2006). This evidences that the silent approach is linked to the perceptual state of the competitor and, thus, conditional learning for this task seems less likely. Therefore, tactical deception is present in apes, and Old World monkeys, but evidence is less convincing for New World monkeys and lemurs.

The final most complicated element of ToM involves *understanding false believe*, where individuals understand that other individuals may believe something which differs from reality. For example, two individuals (X and Y) may witness a hiding event, subsequently, after the removal of individual X, the hidden object is relocated. Individual Y may understand that individual X believes the object is in the first hiding place, although individual Y knows that in reality it is somewhere else. Despite several attempts to evidence an understanding of false belief by apes (Call and Tomasello 1999, Hare et al. 2001, Kaminski et al. 2008, Krachun et al. 2009) and monkeys (Marticorena et al. 2011) there is no evidence of this capacity in non-human primates.

Based on the presence and absence of these cognitive capacities indifferent primate species (Box 1; Table 1), their evolutionary history can be deduced.

The evolution of primate cognition

To survey the evolution of human intelligence it would be best to do comparative analysis of components of ToM in modern primates, in conjunction with an accurate phylogenetic tree of the primate lineage. However, when searching data on the species level, the problem arises that only few species have been investigated for each capacity. In addition, the species under study differ between separate capacities. Therefore, it is easier to look at the presence of cognitive capacities related to ToM in the visual domain in the different primate clades: (1) great apes, (2) Old World monkeys, (3) New World monkeys, and (4) lemurs (Table 1). All four groups can be phylogenetically distinguished

	Lemurs					New World monkeys				Old World monkeys					Great apes		
	<i>Varecia variegata rubra</i>	<i>Lemur catta</i>	<i>Eulemur fulvus</i>	<i>Eulemur macaco</i>	<i>Eulemur mongoz</i>	<i>Callithrix jacchus</i>	<i>Saguinus oedipus</i>	<i>Cebus apella</i>	<i>Ateles geoffroyi</i>	<i>Macaca mulatta</i>	<i>Macaca fascicularis</i>	<i>Macaca arctoides</i>	<i>Cercocebus nemestrina</i>	<i>Cercocebus atys torquatus</i>	<i>Papio Ursinus</i>	<i>Pan troglodytes</i>	<i>Pongo pygmaeus</i>
reflexive gaze following		+ ¹	+ ²	+ ² , - ³		+ ⁴	+ ⁵			+ ⁶	+ ⁶	+ ⁶	+ ⁶	+ ⁷	+ ⁶	+ ⁸	
understanding the target of attention						c ⁴	c ⁹	c ⁹									
VPT	- ¹⁴	c ¹⁴		- ¹⁴	- ¹⁴	- ¹⁵	- ¹⁶			c ¹⁰				c ¹¹			
knowledge attribution																	
understanding intentions							+ ²⁶										
tactical deception					c ³²		c ^{33,34}										
false belief									+ ³⁵						+ ²⁰		
									- ²²						- ^{25,36-38}		

Table 1: cognitive capacities (on the left column) in non-human primate species (top row). Signs below species names indicate the results for that species concerning a specific cognitive capacities: (-) negative results; (c) controversial evidence; (+) unequivocal evidence. Shadings indicate the presence of cognitive capacities on the clade level: *dark grey*: at least one specie within the clade has unequivocal evidence; *light grey*: no unequivocal evidence, but at least one species has controversial evidence; *no shading*: only negative results or non tested species. Numbers in superscript indicate references: 1) (Shepherd et al. 2006); 2) (Ruiz et al. 2009); 3) (Anderson and Mitchell 1999); 4) (Burkart and Heschl 2006); 5) (Neiworth et al. 2002); 6) (Tomasello et al. 1998); 7) (Vick and Anderson 2003); 8) (Itakura and Tanaka 1998); 9) (Amici et al. 2009); 10) (Goossens et al. 2012); 11) (Scerif et al. 2004); 12) (Tomasello et al. 1999); 13) (Okamoto-Barth et al. 2007); 14) (Sandel et al. 2011); 15) (Burkart and Heschl 2007); 16) (Hare et al. 2003); 17) (Flombaum and Santos 2005); 18) (Hare et al. 2006); 19) (Hare et al. 2000); 20) (Melis et al. 2006); 21) (Povinelli et al. 1991); 22) (Marticorena et al. 2011); 23) (Povinelli et al. 1990); 24) (Call et al. 2000); 25) (Hare et al. 2001); 26) (Phillips et al. 2009); 27) (Warneken and Tomasello 2006); 28) (Warneken et al. 2007); 29) (Hare and Tomasello 2004); 30) (Jensen et al. 2007); 31) (Call et al. 2004); 32) (Genty et al. 2008); 33) (Fujita et al. 2002); 34) (Wheeler 2009); 35) (Santos et al. 2006); 36) (Call and Tomasello 1999); 37) (Krachun et al. 2009); 38) (Kaminski et al. 2008).

as separate clades with lemurs being the most primitive (The split between strepsirrhines and Simians was 50 million years ago) and great apes the most diverged clade (the split between humans and the common ancestor of chimpanzees and bonobos was 4.5 million years ago) (Byrne 2000).

Based on the distribution of cognitive capacities in these clades, we aim to reconstruct the evolutionary history of these capacities in the primate lineage. Capacities that are present in all four clades can be considered primitive. Because reflexive gaze following is present in all four groups of primates, it can be concluded that this cognitive capacity is a conserved characteristic within the primate lineage and that the common ancestor of lemurs and humans already possessed this capacity. In contrast, capacities of the next level of cognitive complexity, i.e. high level gaze following, VPT and knowledge attribution exist in apes, but are not unequivocally evidenced in lemurs, New World and Old World monkeys. Despite several attempts, no evidence of understanding false belief has been found in any of the non-human primates, and this cognitive capacity probably is unique for humans. Altogether, these cognitive capacities have been found consecutively from cognitively basic to advanced from lemurs to humans. This is consistent with a proposed general increase in cognitive complexity during primate evolution (Deaner et al. 2006).

In contrast, two capacities deviate from the expected pattern that cognitively basic capacities have evolved before cognitively advanced capacities: understanding intentions and tactical deception. Since understanding intentions is considered an advanced cognitive capacity, and the New World monkeys do not seem to possess seeing-related cognitive capacities at a similar or lower level (VPT, high level gaze following and knowledge attribution), it is rather surprising that evidence is found for this capacity in New World monkeys. Similarly, Tactical deception is also considered an advanced capacity compared to VPT, geometric gaze following and knowledge attribution, whereas evidence for the first but not for the latter capacities is found in Old World monkeys. On the one hand this may indicate that cognitive capacities evolved independently of each other, and that cognitively complex capacities in specific domains may have evolved before simpler cognitive capacities in other domains. Possibly, understanding intentions was important in the social life of the common ancestor of New World monkeys and apes, whereas understanding the visual perspective of others became only important after the split of the apes from the rest of the primates. Alternatively, moderately complex capacities such as understanding intentions, VPT and Geometric gaze following, may have evolved in a common ancestor of New World monkeys and humans. However, their presence may not have been shown, since the paradigms used thus far have not been able to establish their presence in lemurs, New World and Old World monkeys, and new tests are needed. In addition, many monkey species have not yet been tested. Therefore, in this PhD-thesis we test the presence and use of VPT-related cognitive capacities in an Old World monkey and draw some parallels with a New World monkey.

Social cognition

In order to comprehend the evolution of Visual Perspective Taking, it is important to establish the benefits of VPT and prerequisites of VPT in non-human primates. The complex cognitive capacities such as VPT that are characteristic for the primate lineage

and that define human intelligence are considered to depend on brain size (Jerison 1976, Reader and Laland 2002, Williams 2002), and more specifically to the size of the neocortex. The neocortex is a brain structure that is involved in many behaviours associated with intelligence, because it processes rational behaviour, perception of emotions, memory, perceptive and cognitive functions and organizes behaviour in present and future based on experiences in the past (Baumgartner 1983). Primates have larger brains than mammals of the same size (Jerison 1979) 50 to 80% of the primate brain consists of neocortex (Dunbar 1998). The best known hypothesis explaining the relatively large brains in primates is the social brain or Machiavellian intelligence hypothesis. This hypothesis states that species with more complicated social systems, where individuals regularly interact with a higher number of conspecifics, developed more advanced brain structures specifically in the neocortex (Byrne and Whiten 1988, Dunbar 1998). Although it is difficult to test the social brain hypothesis, because social complexity and brain complexity are difficult to measure, some comparative studies find support for the social brain hypothesis. First, neocortex size, is correlated with group size within primates, bats, carnivores, and (more controversially) in cetaceans (Reader and Laland 2002). Second, there is ample evidence that primate social systems are more complex than those of most other species (Dunbar 1998), and that primates have relatively larger brains than other animal species (Jerison 1979).

However, if social complexity has been the evolutionary pressure behind the development of cognitive complexity, it is important to show that cognitively complex capacities have benefits in a social context. Therefore, it is important to reveal whether non-human primates use their cognitive skills in their social behaviour. Moreover, knowing how primates employ VPT in their daily lives will benefit experimental tests on VPT in non-human primates by adjustment of experiments to their natural abilities.

Gaze following

Gaze following is an advantageous behaviour in group living primates. If an object is interesting for one individual, it may also be of interest to its group members. Gaze following enables an individual to locate objects that it had not noticed or that were out of its own visual field by following the gaze of group members. It has been demonstrated that averted eye cues facilitate the detection of objects by monkeys through “go no - go tasks”, where monkeys have to react to pictures on a computer screen (Fagot and Deruelle 2002). In a more natural setting, monkeys may locate food (Itakura and Tanaka 1998) or predators (e.g. Tomasello et al. 1998) by following the gaze of conspecific group members. Although primates may use vocal signals to communicate the presence of specific predators (Schel and Zuberbuhler 2012), gaze direction may reveal additional information about the specific location of the predator, which is crucial in order to flee in the correct direction. Thus, predation risk and living among group members, which may signal locations of important objects exert pressure on the evolution of gaze following.

Moreover, gaze following may enable group living primates to monitor social interactions between their group members. Although in many flocking animal species an individual’s visual scanning behaviour declines with group size when many eyes make light work (Pulliam 1973, Powell 1974), for primates a positive correlation between group size and visual scanning is found (Pulliam 1973, Powell 1974). This suggests that primates use visual scanning in order to keep an eye on group members rather than external

factors. Visual scanning may enable subordinate primates to keep track of the positions of dominants and potential aggressors in order to stay away from these individuals and avoid conflicts (Evers et al. 2012). Following the gaze of group members during visual scanning may facilitate the detection of these potentially dangerous group members.

Understanding the target of attention

A prerequisite to Visual Perspective Taking is understanding the target of attention of conspecifics, not yet full blown VPT, but more than reflexive gaze following. Understanding the target of attention requires animals to understand that other individuals do not just look somewhere in space, but that their attention is directed at a specific object. Understanding the target of attention of conspecifics is important for group living animals, as it may reveal crucial information about social relationships among group members. For example, if an individual observes an agonistic interaction between two other individuals, it may understand that the aggression of one individual is directed at a specific individual. This is crucial information for group living individuals, which show discriminative agonistic support (e.g. *Macaca sylvanus*: Carne et al. 2011). Especially in groups with complex structures the number of interactions is high. Thus, complex social structures exert pressure on the evolution of understanding the target of attention.

Visual Perspective Taking

The benefits of VPT in group living primates may be twofold: First, an individual may consider the visual perspective of group members if they want to hide objects, behaviours or themselves. Visual Perspective taking may be used by monkeys in order to reduce competition for food. Reduced competition may be achieved by choosing food items that cannot be seen by others (Flombaum and Santos 2005, Hare et al. 2000, 2006). Additionally, monkeys may use VPT in order to hide certain behaviours that risk punishment by group members. An example of such behaviour is sexual behaviour. Sexual behaviour in many multi-male multi-female group is skewed with most sexual behaviours performed by the highest ranking males (Altmann 1962). Low ranking males risk punishment if they perform sexual behaviour in view of higher ranking males. Therefore, subordinate males, and females that are willing to copulate with subordinate males may use VPT in order to hide their sexual behaviour for higher ranking individuals. Second, if an individual wants to send a visual message to a group member, it is crucial that the sender is able to see the signal. For example if a female is willing to copulate she may present her hindquarters to a male, and may pay attention to whether this male can see her by positioning herself in front rather than behind the male and by uttering vocal signals until the male is directing his attention towards the female. Thus, for group living primates with visual communication and competition for resources Visual Perspective Taking may be beneficial.

Visual perspective taking and hiding behaviour

Hiding is one of the main behaviours that may require Visual Perspective Taking. Hiding behaviour can include hiding an object, or hiding oneself for an audience. This thesis focuses on hiding oneself or hiding specific behaviour, namely sexual behaviour. However, such hiding behaviour may be based on different cognitive mechanisms that

may, or may not, require VPT. Thus in order to assess whether monkeys use VPT while hiding themselves or specific behaviour, it is important to distinguish between the following mechanisms (based on Gygas 1995)

- A. The monkey increases the distance between itself and the audience.
- B. The monkey moves close to an (opaque) object, without considering whether the audience is on the same side of the object or not
- C. The monkey positions itself with an (opaque) object interposed between itself and the audience.
- D. The monkey perfectly hides itself behind an opaque object including its limbs and tail.
- E. The monkey hides itself with an opaque object between itself and the audience, while keeping track of the audience, for example through a peak hole.

Mechanism A to C can be explained through simple operant learning, when individuals experience less punishment from the audience after performing behaviour at specific locations. Only mechanism D and E require VPT, because monkeys will have to distinguish their own visual perspective from their audience's. Hence depending on the specific hiding strategy used by monkeys we can tell how much cognitive complexity is used by the monkeys in natural hiding behaviour and whether hiding behaviour within complex social structures exert pressure on the evolution of Visual Perspective Taking.

Aims and overview of thesis

Because all existing paradigms that test for the existence of VPT in monkeys face with interpretational problems (see above), we developed a new paradigm and adjusted an existing paradigm (Hare et al. 2003). Chapters 2 to 4 experimentally investigated whether a New World and Old World monkey species demonstrate capacities of understanding where other individuals are looking at, and at which level.

Moreover, while many studies focus on the existence of VPT capacities in monkeys in experimental test situations, few studies have addressed the use of these capacities in natural behaviour of group living monkeys. In chapters 5 to 7, it is investigated by means of behavioural observations which cognitive capacities in the visual domain, namely audience effects, Visual Perspective Taking and tactical deception, are used in daily encountered social situations. In these three final chapters we focus on a natural hiding behaviour; sneaky mating, which is often observed in multi-male, multi-female groups, where high ranking males try to monopolize fertile females and where females and or lower ranking males try to escape from this monopolization. In chapter 5 and 6 we investigate whether sneaky mating is also present in our monkey groups and for which audience sexual behaviour is hidden. Subsequently in chapter 6 and 7 we search for specific mechanisms underlying the concealment of sexual behaviour for group members.

Chapter 2 addresses the question whether long-tailed macaques understand the target of attention of pictured conspecifics. Whereas Theory of Mind is possibly a uniquely human capacity, prerequisites like visual perspective taking (VPT) may be present in other species as well. Evidence for VPT has been found in apes, but is controversial for monkeys, and positive results may be explained by cognitively simpler capacities. We investigated whether monkeys understand the target of a conspecific's attention, a prerequisite to VPT, using a new paradigm, based on an expectancy violation paradigm. Subjects were exposed to pictures of scenes involving group

members. These pictures either represented congruent (agonistic signals follow dominance hierarchy) or incongruent (signals contradict dominance hierarchy) social situations. The only difference between pictures was the object of attention and facial expression of one of the pictured individuals. We expected that if the monkeys understand the target of attention of their pictured group member, they would look longer at incongruent than at congruent scenes.

Chapter 3 describes whether common marmosets understand the target of attention of pictured conspecifics. Understanding the target of attention of conspecifics is important for group living animals. In order to obtain information from social communication such as agonistic interactions, observing individuals must understand to which target the agonistic behaviour is directed. Understanding the target of attention is a prerequisite to Visual Perspective Taking and investigating this capacity in monkey species yields insight to the evolution of the underlying mechanisms of Theory of Mind. We used a new paradigm to determine whether monkeys understand the target of attention when looking at pictured social scenes. We investigated whether pair-housed marmoset monkeys show a higher interest in pictures representing threats to their cage mates than in pictures involving threats to unfamiliar conspecifics. We expected that if they would understand the visual perspective of the threatening monkey, they would be more aroused and interested in the picture if this individual threatened their cage mate than if it threatened an unfamiliar monkey

Chapter 4 focuses on Visual Perspective Taking in a competitive task in long-tailed macaques. Chimpanzees know what conspecifics have and have not seen and use this information to obtain food in a competitive situation with dominant conspecifics. The same paradigm with capuchin monkeys revealed that, unlike chimpanzees, they did not show an understanding of which food items were hidden for the dominant. Long-tailed macaques have been found to follow a conspecifics gaze around a barrier, and to follow a human gaze more often with a facial expression of fear than with a meaningless facial expression. This indicates that they do understand that the gazer is looking at something interesting. However, other explanations are possible. We investigated using a similar paradigm as with chimpanzees and capuchins whether long tailed macaques understand what conspecifics can and cannot see. We adjust the paradigm such that simple rules cannot account for our results. We expected that if monkeys understand the visual perspective of a conspecifics competitor they would preferentially approach a food item that could not be seen by their opponent.

Chapter 5 reports on the presence of an audience effect in sexual behaviour of rhesus macaques. Males and females have different sexual interests and subsequently may show conflicting sexual strategies. While dominant males try to monopolize females, promiscuity benefits females and subordinate males. One way to escape monopolization by dominant males is to copulate in their absence. We tested this inhibitory effect of males on the sexual behaviour of their group members in a captive rhesus macaques group with six sexually active males and seven sexually active females. We expected that high ranking individuals have an audience effect on lower ranking individuals' sexual behaviour.

In **Chapter 6** we investigate the presence of an audience effect in sexual behaviour of long-tailed macaques and systematically examined several cognitive mechanisms which may underlie sneaky mating. Sexual competition is highly prevalent

within multi-male multi-female primate groups and may lead to copulations in absence of potentially interfering bystanders. Such avoidance of bystanders may result from tactical deception or from simpler mechanisms such as taking advantage of encountered situations without bystanders, operant conditioning or a peripheral positioning of non-alpha males. We investigated which individuals are avoided as bystanders, how individuals react to the presence of bystanders and whether copulation partners separate themselves from the group in a tactical way. We observed a group of 15 female and seven male long-tailed macaques housed in three interconnected, but visually separated compartments. We expected that high ranking individuals have an audience effect on lower ranking individuals' sexual behaviour. Additionally we expected that if tactical deception is used to hide sexual behaviour, individuals coordinate their separation from the rest of the group.

Chapter 7 explores the cognitive mechanisms underlying sneaky mating in long-tailed and rhesus macaques. The monopolization of sexual interactions by primate alpha males does not necessarily benefit subordinate males and females. Therefore, subordinate males and females try to escape from this monopolization with alternative mating strategies such as sneaky mating. Although sneaky mating has been suggested to result from advanced cognitive mechanisms involving tactical deception, this has never been shown empirically. In our study we tested with observational data on two different macaque species which strategies are used to hide sexual behaviour from conspecifics. We tested whether macaques use distancing or opaque objects in order to hide sexual behaviour.

2

Male long-tailed macaques (*Macaca fascicularis*) understand the target of facial threat

A.M. Overduin - de Vries, F.A.A., Bakker, B.M. Spruijt, E.H.M. Sterck

Whereas Theory of Mind is possibly a uniquely human capacity, some of the underlying cognitive capacities, such as Visual Perspective Taking (VPT) may be present in other species as well. Evidence for VPT has been found in apes, but is controversial for monkeys and positive results in monkeys may be explained by alternative simpler cognitive capacities. Therefore, evidence for VPT in monkeys is weak. We investigated a prerequisite of VPT; understanding the target of attention in monkeys, using a new paradigm that is based on expectancy violation. We tested whether long-tailed macaques understand the target of attention within pictured social scenes involving conspecific group members. These pictures either represented congruent (agonistic signals follow dominance hierarchy) or incongruent (signals contradict dominance hierarchy) social scenes. The only difference between scenes concerned the looking direction, i.e. the target of attention, and the facial expression of the central monkey in the picture. Male subjects looked significantly longer at incongruent than congruent scenes, suggesting that they understand the target of attention of other individuals. Alternative explanations involving simpler mechanisms were excluded. The presence of this prerequisite of VPT in a monkey species opens up the possibility that the evolution of VPT took place in a gradually step like way.

INTRODUCTION

There is growing evidence that human cognition has evolved in a step like fashion and many aspects of human cognition are present in apes and monkeys (Taylor Parker and McKinney 1999). Although some studies report significant differences in cognition between monkeys and apes (Byrne and Whiten 1988, Byrne 1995, Barrett et al. 2003, Deaner et al. 2006), others argue that the differences found for some cognitive skills cannot be generalised for other skills (Amici et al. 2010), that differences found between taxa are due to differences in human contact (Tomasello and Call 1997) or that conclusions are based on too few subjects or species (Tomasello and Call 1997). In addition, several empirical studies argue against an ape-monkey dichotomy of cognition (Torigoe 1985, Amici et al. 2008, Amici et al. 2010). Thus, there is no overall clear-cut distinction in cognitive skills between monkeys and apes.

One facet of cognition, Visual Perspective Taking (VPT; understanding what others can see), is considered a prerequisite to understanding another individual's mental state (Theory of Mind) (Baron-Cohen et al. 1985). In apes the presence of VPT has been shown (Hare et al 2000, Brauer et al. 2005, Shillito et al. 2005, Okamoto-Barth et al. 2007). In contrast, for monkeys both positive (Flombaum and Santos 2005, Amici et al. 2009, Teufel et al. 2010, Goossens et al. 2012) and negative (Cheney and Seyfarth 1990, Kummer et al. 1996, Hare et al. 2003, Burkart and Heschl 2006) results exist, depending on the species and methods used.

A paradigm used to study VPT is gaze following, where individuals co-orient with the gaze direction of others. Gaze following is a widespread naturally occurring behaviour among primates ranging from prosimians to humans (Emery 2000). It can result from one of two mechanisms (e.g. Brauer et al. 2005): first, reflexive co-orienting comprising instinctive following of another individual's gaze; second, Visual Perspective Taking, where individuals voluntarily follow other's gazes, because they know they may see something. Four recent studies on gaze following in monkeys support the Visual Perspective Taking model. Monkeys show higher gaze following responses to human demonstrators (Goossens et al. 2008) or conspecifics (Teufel et al. 2010) with facial expressions than with neutral faces. This voluntary co-orienting implies an understanding that demonstrators with facial expressions may see something relevant. Moreover, monkeys were able to follow a human (Amici et al. 2009) or conspecific's (Goossens et al. 2012) gaze around a barrier and relocate to a position where they could look behind the barrier. This indicates that the gaze follower understands that the other individual is seeing something that was not visible for the individual itself. However, it is not clear whether the gaze follower has an understanding of what the gazer is looking at. Moreover, some results (Goossens et al. 2008, Teufel et al. 2010, Goossens et al. 2012) may be explained by higher arousal levels in subjects due to the facial expressions of the demonstrators. Although measurements of anxiety and general visual scanning did not reveal any difference between different conditions (Goossens et al. 2008, Goossens et al. 2012), this does not exclude that some sort of arousal may have caused a higher level of gaze following (Goossens et al. 2008, Teufel et al. 2010) or a higher chance of passing the barrier (Amici et al. 2009, Goossens et al. 2012). Additionally, although long-tailed macaques showed check-looking behaviour (Goossens et al. 2008), an indicator of VPT, this was absent in capuchins and spider monkeys (*Ateles geoffroyi*) (Amici et al. 2009).

Another paradigm that has successfully shown VPT in apes (Pan troglodytes Hare et al. 2000), but less successfully in monkeys (Hare et al. 2003, Burkart and Heschl 2007), is a setting where a dominant and a subordinate compete over food. Marmosets (*Callithrix jacchus*) assigned food as belonging to their opponent when the opponent had gazed at the food, and thus showed no VPT (Burkart and Heschl 2007). Similarly, results with capuchins (*Cebus apella*) were most consistent with reading the behaviour of the opponent (Hare et al. 2003). This behaviour reading is a simpler mechanism than VPT as it requires the perception of an opponent's gaze cue, and an operant conditioned rule. Operant conditioning may result in movement in the opposite direction of an opponent's gaze. Namely, choosing the non-cued direction will most of the time result in less punishment from the opponent and more success in obtaining food items than choosing the cued direction.

To prevent behaviour reading, researchers have used human experimenters as competitors (Kummer et al. 1996, Flombaum and Santos 2005) or attributed a guesser or knower state of mind to human experimenters (Povinelli et al. 1991). These studies yielded both positive (rhesus macaques (*Macaca mulatta*): Flombaum and Santos 2005), and negative (rhesus macaques: Povinelli et al. 1991, long-tailed macaques: Kummer et al. 1996) results. Nonetheless, simple rules that do not require visual perspective taking, such as "avoid the eyes of the human" (Povinelli et al. 1991, Kummer et al. 1996, Flombaum and Santos 2005), may explain the positive results. In addition, it may be more difficult for monkeys to understand a human's goals, intentions, and visual possibilities than those of a conspecific.

Although monkeys understand that a conspecific's gaze may help them find interesting objects, a central question remains whether they understand that another individual actually looks at a specific target. This is a prerequisite for VPT. Therefore, in this study we test whether long-tailed macaques understand the target of attention of others. We employ a new paradigm, using the well assessed facts that monkeys know the dominance hierarchy in their social group (review: Cheney and Seyfarth 1990, *Papio cynocephalus ursinus*: Cheney et al. 1995), that they can recognise group members from pictures (rhesus macaques: Parr et al. 2000, grey-cheeked mangabeys (*Lophocebus albigena*): Bovet and Deputte 2009, capuchins: Pokorny and De Waal 2009, Silwa et al. 2011), and that agonistic facial expressions are often unidirectional (van Hooff 1962, de Waal and Luttrell 1985), providing information about the target of attention. In this new paradigm, monkeys are confronted with pictures of social scenes involving three of their group members that are either congruent or incongruent concerning their group's dominance hierarchy. The pictures consisted of three monkeys in a row; the central monkey had a dominance rank in between those of the two flanking monkeys. The facial expression and gaze direction of the central monkey varied. For example, the central monkey looked aggressively at the higher-ranking monkey, representing an incongruent situation. Monkeys are expected to look longer at these incongruent than at congruent scenes (Kim and Spelke 1992, Cheney et al. 1995). The only differences between the pictures are the facial expression and gaze direction, and with that the target of attention of the central monkey. Therefore, we predict that only if monkeys understand the target of attention of the central monkey, a difference in looking time is found between congruent and incongruent scenes.

METHODS

Subjects

Subjects lived in three different groups: (A) a mixed sex group of 22 individuals, (B) a group of four males (C) a mixed sex group of six individuals. Since subjects participated on a voluntary basis, we tested respectively 13, four and five individuals. The three groups were formed from one social group for management reasons. From 30-06-2009 group B was split off from group A; on 10-05-2010, one individual was removed from group A; and from 08-10-2010 group C was split off from group A. Some individuals in group A and C were tested both before and after a group splitting. After the split, 21 subjects received pictures of current group members, while three individuals did not return in a social group, and received pictures of former group members. This research was approved by the Animal Ethical Committee of the Biomedical Primate Research Centre (DEC # 628) and complies with the Dutch legal requirements.

Hierarchy

Prior to testing, the dominance hierarchy of each group was established on the basis of submissive signals (Overduin-de Vries et al. 2012). Because of the high number of inconsistencies for juveniles, their dominance ranks were unreliable and we excluded pictures of juveniles from the stimuli. In group A, the adults' hierarchy was significantly linear ($h' = 0.95$, $p = 0.0001$). The hierarchy of group B and C was linear, but this was not significant due to the small group size (group B: $h' = 1$, $p = 0.38$; group C: $h' = 1$, $p = 0.39$) (de Vries 1998). However, since at least 7 interactions per dyad were observed with no inconsistencies, we assume linearity.

Experimental setup

Two experiments were run: "the BT (Bared teeth) experiment" and "the OM (Open mouth) experiment". They had the same procedure, but differed in the stimuli used. The experiments make use of the expectancy violation paradigm, which predicts that individuals look longer at unexpected (incongruent) than at expected (congruent) situations (Kim and Spelke 1992, Cheney et al. 1995).

Testing Procedures

On a test day, the subject was shown only one picture. After a subject entered the test room (10 m²) on a voluntary basis, it was encouraged to sit in front of the screen (HP Compaq, 19 inch) with a reward. Subsequently, a trial commenced by simultaneously playing a trivial sound, to attract the attention of the monkey to the screen, and showing a picture on the screen. The picture remained visible for one minute. The subject's responses were recorded with two video cameras (Sony, DCR-SR72).

If the subject failed to look at the screen during picture exposure, it was cued back in front of the television and the picture was shown again. If a monkey did not look at the picture after three trials, it received the same picture the next day. Once the subject had looked at a picture, that picture was never shown again to that subject.

Test Stimuli

The pictures were constructed using Photoshop (version CS2) and displayed three monkeys on a row, which were group members of the subject monkey. Each of the pictured monkeys measured approximately 5.5 x 3 inches. The central monkey had a dominance rank in between those of the flanking monkeys. All pictures had their outdoor cage as a background, suggesting that the three individuals were together in the same environment. By varying the facial expression and looking direction of the central monkey, a four-picture-set was created (Figure 1). In each experiment, subjects received one to three different four-picture-sets (each subject saw in each experiment 4 to 12 different pictures). Within each four-picture-set, the appearance of the flanking monkeys and the body of the central monkey were identical. The central monkey's head with a neutral or agonistic facial expression originated from a different photograph than its body. The central monkey directed its gaze either to the right or to the left, by randomly using mirrored images, balancing the proportion of mirrored images between conditions. The identity of the central monkey always differed between four-picture sets shown to one subject, and the flanking monkeys were changed as much as possible (i.e. in both the BT and OM experiment, only 2 subjects saw scenes containing flanking monkeys that they had seen in another configuration).

-The bared-teeth (BT) experiment.

The BT experiment tested whether monkeys recognise the incongruity of a dominant individual giving a submissive display towards a subordinate individual. The facial expression of the central monkey was either a neutral face or submissive bared-teeth display. The scene was incongruent when the central monkey gave the bared teeth display to the flanking lower-ranking monkey and congruent when it gave the bared teeth display to the flanking higher-ranking monkey.

-The open-mouth (OM) experiment.

The OM experiment tested whether monkeys recognise the incongruity of a subordinate individual giving a threatening display towards a dominant individual. Stimuli were similar to those used in the BT experiment, but showed a neutral face and a threatening open-mouth display (Figure 1). The scene was incongruent when the central monkey gave the open mouth display to the flanking higher-ranking monkey and congruent when it gave the open mouth display to the flanking lower-ranking monkey.

Data Analyses

The video recordings conveyed 25 frames per second. Looking times were measured by counting the number of frames a monkey was looking at the screen during the total 60 seconds that the stimulus was presented. The scoring observer was blind to the stimuli presented to the subject. The independent ratings of two observers for 10 different videos were significantly correlated (Pearson's product-moment correlation: $t = 23.5$, $df = 8$, $p = 1.1 \times 10^{-8}$).

The response of each individual was calculated by subtracting the individual's mean looking time for one to three congruent scenes from the individual's mean looking time for one to three incongruent scenes. Subjects from different groups were analysed together, however, if males and females significantly differed in their response, the subsequent



Figure 1: One example (of in total 15 variants) of a four-picture set used in the OM-experiment: (a) open mouth display towards dominant (congruent social scene); (b) open mouth display towards subordinate (incongruent social scene); (c) Neutral face towards subordinate (control scene); (d) neutral face towards dominant (control scene). Original stimuli were in full colour and were randomly mirrored

analysis was performed separately for the sexes. If there was no sex difference, subsequent analyses were conducted for males and females together.

The main test of this study was whether the subject's expectancy was violated when confronted with incongruent scenes and, thus, whether the response significantly differed from zero.

Furthermore, we investigated whether variation in stimuli pictures was related to variation in responses. The accuracy of the central monkey's looking direction was determined by assigning a number from one (imperfect gaze direction) to six (central monkey gazes perfectly at a flanking monkey). We had 38 unique four-picture sets (BT-experiment: $N = 23$, OM-experiment: $N = 15$), which could share one or two of the monkeys in the picture, but at least one of the monkeys was different. We calculated the mean looking time over all monkeys that had looked at that picture. Since sample sizes were small and not all data were normally distributed, non-parametric two-tailed statistical tests were used, with $\alpha = 0.05$.

RESULTS

BT-experiment

Within the bared teeth (BT) experiment pictures were shown of congruent and incongruent submissive displays. Male (mean = $2.0 \pm$ SD 5.6) and female (mean = $-0.2 \pm$

SD 3.6) responses (looking times for incongruent minus congruent scenes) did not differ significantly (Mann-Whitney U test: $U = 91$, $N_1 = 9$, $N_2 = 15$, $p = 0.277$). Therefore, data of males and females were combined. Subjects did not significantly differ in their looking time between congruent and incongruent images (Wilcoxon signed-ranks test: $t = 150$, $N = 24$, $p = 1$, Figure 2). Likewise, a comparison of the two control conditions, where the central monkey was looking with a neutral facial expression, did not give a significant difference in looking time (Wilcoxon signed-ranks test: $t = -0.829$, $N = 24$, $p = 0.407$).

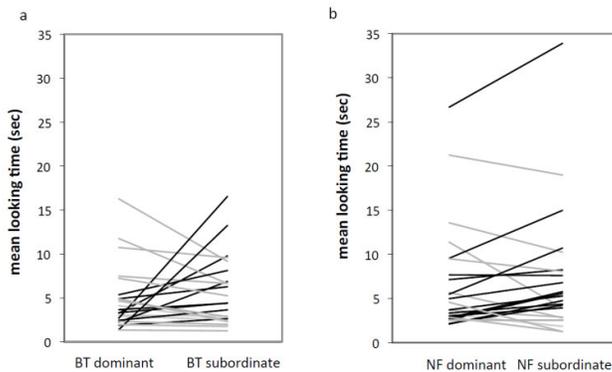


Figure 2: Looking times in the BT-experiment: (a) the incongruent (BT dominant) condition and congruent (BT subordinate); and (b) both control image conditions (Neutral face (NF) towards dominant or subordinate). Separate lines correspond to the responses of individual macaques. Solid lines indicate macaques that responded in correspondence with expectancy violation, whereas dotted lines indicate contradictory responses

OM-experiment

Within the open mouth (OM) experiment pictures of congruent and incongruent threat displays were shown. Males (mean=3.7 \pm SD 5.0) significantly differed in their response (looking times for incongruent minus congruent scenes) from females (mean= -2.4 \pm SD 4.6) (Mann Whitney U test: $U = 76$, $N = 20$, $p = 0.010$). Consequently, male and female data were analysed separately. Male subjects looked significantly longer at incongruent compared to congruent agonistic situations (Wilcoxon signed-ranks test: $t = 33$, $N = 9$, $p = 0.039$, Figure 3a). In contrast, females did not discriminate between congruent and incongruent scenes (Wilcoxon signed-ranks test: $t = 22$, $N = 11$, $p = 0.365$, Figure 3b). The control conditions revealed no significant difference in looking time between neutral gazes at dominant and subordinate individuals (Wilcoxon signed-ranks test: males: $t = 28$, $N = 9$, $p = 0.570$; females: $t = 25$, $N = 11$, $p = 0.520$, Figure 3c-d).

Gaze Accuracy

The gaze accuracy of the central monkey did not significantly affect subjects' responses in either condition and either experiment (Kendall correlation: BT congruent: $Z = -1.7688$, $t = -0.302$, $p = 0.077$, $N = 23$; BT incongruent: $Z = -0.686$, $t = -0.119$, $p = 0.493$, $N = 23$; OM congruent: $Z = -1.064$, $t = -0.182$, $p = 0.287$, $N = 15$; OM incongruent: $Z = 1.396$, $t = 0.290$, $p = 0.163$, $N = 15$). In addition, no significant differences in gaze accuracy were found between congruent and incongruent stimuli (Wilcoxon rank sum test: BT-experiment: $U = 299$, $N_1 = N_2 = 23$, $p = 0.317$; OM-experiment: $U = 110.5$, $N_1 = N_2 = 15$, $p = 0.949$).

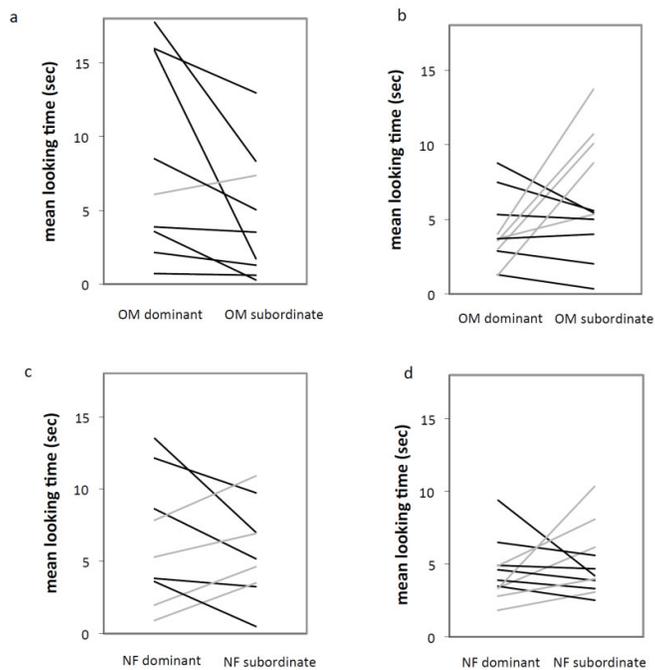


Figure 3: Looking times in the OM-experiment. The separate graphs represent male (a) and female (b) responses to the incongruent(OM dominant) and congruent(OM subordinate) scenes. Additionally, male (c) and female (d) responses to both control images (NF towards dominant and subordinate) are given. See for explanation of lines the legend of Figure 2

DISCUSSION

We tested for a prerequisite of VPT; understanding the target of attention, with a new expectancy violation paradigm involving pictured social scenes. Our results indicate that male monkeys look longer at pictured monkeys in incongruent agonistic scenes than those in congruent scenes. Since the only difference between the two types of pictures was the looking direction, and, thus, the target of attention of the central monkey, this shows that they perceive the incongruity of the target of the facial threat. However, since results were not uniform, neither for the two facial expressions nor for the two sexes of subjects, they need further discussion.

Contrasting with the OM-experiment, in the BT-experiment subject monkeys did not discriminate between congruent and incongruent submissive interactions. This was not expected, because bared-teeth displays are highly unidirectional (van Hooff 1962, Maestriperieri and Wallen 1997). In a similar long-tailed macaque group of our colony the bared teeth display was observed within 195 dyads, and only in one of these dyads the display was exchanged in either direction (Preuschoft 1995). The absence of an effect in our BT-experiment cannot be explained by a general lack of interest in submissive interactions, because bared-teeth displays increase gaze following behaviour, whereas open mouth displays do not (Goossens et al. 2008). An alternative explanation may be found in the consequences for the audience of a “wrong behaviour”. Whereas a threat to a dominant may cause aggression and affect the whole group, a BT to a subordinate probably only has minor consequences and thus may not affect third parties. Therefore, subjects may have been more attentive to the incongruence in the OM- than in the BT-experiment.

In the OM-experiment, we found a significant difference in response between male and female subjects. Whereas males showed more interest in incongruent than congruent aggression scenes, females did not. First, the difference cannot be explained by a difference in interest in aggressive situations. In our test, no significant difference in the time spent looking at the picture was found between male and female subjects for the congruent OM stimuli (Wilcoxon rank sum test: $U = 66$, $N_1 = 9$, $N_2 = 11$, $p = 0.2299$). Thus females seem to be equally interested in agonistic scenes as males. This is consistent with the involvement of long-tailed macaque females in aggressive behaviour (de Waal 1977, Sterck and Steenbeek 1997). Moreover, involvement in aggression by macaques is independent of sex (rhesus macaques: Reinhardt 1987). Second, the absence of significance in females was not due to higher general noise values in the female data, which may be caused by distraction of the female subjects. When looking at the time spent looking at each individual picture in the neutral face to dominant condition (the condition where we expect the least effect of expectancy violation), for females the standard deviation, a measure of noise, (BT: 71.3, OM: 69.0) was actually lower than that for males (BT: 131.8, OM: 122.2). Last, females may not understand the incongruity of pictured situations. However, this would contrast with baboon (*Papio ursinus*) females, that have increased interest in playbacks of fight sequences involving incongruent than congruent call sequences (Bergman et al. 2003). What may have caused more variation in female responses is that females pay more attention to the picture if the central monkey was a member of the same matriline (Wilcoxon signed rank test, $V = 0$, $N = 7$, $p = 0.016$). For males we could not test this, but variation in familiarity of the central monkey was higher for females than for males, since only two of the males received pictures where the central monkey was a family member compared to eight of the females. Therefore, variation in relatedness between the female subject and the pictured monkey may have caused variation in the data. Additionally, like human males macaque males may not pay more attention to gaze cues if the cue giver is a familiar, while human females do (Deaner et al. 2007). High variation in the results for females between trials within a condition may have blurred the differences between conditions.

In contrast with females, the results for males in the OM-experiment do indicate an understanding of the target of attention in the pictured social scenes. Several alternative explanations involving cognitive capacities simpler than understanding the target of attention can be precluded, because of the configuration of our stimulus pictures and the controls. First, associative learning of naturally occurring social situations where aggressive interactions of dominants only take place near a subordinate individual cannot explain the results obtained. Within our stimuli pictures, the proximity of a dominant or subordinate to a threatening monkey did not differ between picture conditions, and, therefore, could not be used by the subjects to discriminate between pictures. Second, the results cannot be explained by a higher interest of subjects in pictures where the central monkey is gazing at the dominant than where it is gazing at the subordinate, since subjects were not more interested in control pictures with neutral gazes at the dominant than at the subordinate. Third, since both congruent and incongruent scenes show an agonistic facial display, differences in arousal due to emotional content of pictures are not expected. Moreover, if arousal were different between congruent and incongruent pictures, this would actually show that they

understand the target of attention. In conclusion, the most plausible explanation of our results is that male subjects understand the target of attention of a pictured conspecific.

Understanding the target of attention of conspecifics is a crucial mental capacity required for VPT and Theory of Mind. Evidence for VPT has been found for all great ape species (Brauer et al. 2005), but is mixed for monkeys (Cheney and Seyfarth 1990, Kummer et al. 1996, Hare et al. 2003, Flombaum and Santos 2005, Burkart and Heschl 2006, Amici et al. 2009, Teufel et al. 2010, Goossens et al. 2012). Our study gives the first unequivocal evidence of this prerequisite of VPT in a monkey species. This finding suggests that understanding the target of attention of conspecifics is a conserved primate feature. Although additional research with other species is required to confirm this proposition, these results, in combination with earlier studies on monkeys (Flombaum and Santos 2005, Amici et al. 2009, Teufel et al. 2010, Goossens et al. 2012), imply that many more monkey species share capacities underlying Visual Perspective Taking with apes and humans. The presence of prerequisites of VPT in monkey species opens up the possibility that monkeys possess cognitive capacities underlying VPT and that the evolution of VPT took place in a gradually step like way.

ACKNOWLEDGEMENTS

We would like to thank all the staff at BPRC for their care of the subject animals and supporting the research. We are grateful to Coby de Wit, Esther den Heijer and Matthijs Graner for their help training and testing the monkeys. Anne Overduin – de Vries was supported by research grant from the BPRC.

3

Understanding the target of attention in common marmosets

A.M. Overduin - de Vries, B.M. Spruijt, E.H.M. Sterck

Understanding the target of attention of conspecifics is important for group living animals. In order to obtain information from social communication such as agonistic interactions, observing individuals must understand to which target the agonistic behaviour is directed. Understanding the target of attention is a prerequisite to Visual Perspective Taking and investigating this capacity in monkey species yields insight in the evolution of the underlying mechanisms of Theory of Mind. We used a new paradigm to determine whether monkeys understand the target of attention when looking at pictured social scenes. We investigated whether pair-housed common marmosets (*Callithrix jacchus*) show a higher interest in pictures representing threats to their cage mates than in pictures involving threats to unfamiliar conspecifics. Marmosets did not show a difference in interest between pictures with threatened cage mates and unfamiliar individuals. Therefore, we cannot conclude that common marmosets understand the target of attention of conspecifics, suggesting that common marmosets will not be capable of Visual Perspective Taking.

INTRODUCTION

Understanding the target of attention of conspecifics is important for group living animals, as it may reveal crucial information about the location of predators and food and about social relationships among group members. Gaze following, defined as “the ability of one individual (X) to follow the direction of gaze of a second individual (Y) to a position in space” (Emery et al. 1997), is used by many animal species to facilitate detection of targets (primates: Itakura and Tanaka 1998, dogs : Miklosi et al. 1998, ravens: Bugnyar et al. 2004, goats: Kaminski et al. 2005, geese: Kehmeier et al. 2011). It is not known whether subjects have expectancies of finding information when they decide to follow another’s gaze, since gaze following can result from different cognitive mechanisms. Gaze following may be an automatic response to look in the direction that others are looking at, i.e. “low-level” gaze following (Call et al. 1998), especially since it is already elicited within 100ms after a gaze cue onset (Shepherd et al. 2006). Alternatively, gaze following may be voluntarily controlled, based on a search for a specific target of attention, past distracter objects, or to hidden locations (e.g. behind screens) i.e. high-level gaze following. High-level gaze following requires an individual to understand that the gazer has a target of attention and this is, therefore, a precursor of Visual Perspective Taking (VPT) where individuals know what others can and cannot see. Because of being a precursor of VPT, investigating high-level gaze following in monkey species without evidenced VPT or ToM would give insight to the evolution of Theory-of-Mind-like abilities (Sterck and Begeer 2010).

Whereas apes have VPT (Tomasello et al. 1999, Hare et al. 2000, Brauer et al. 2005, Okamoto-Barth et al. 2007), evidence for its presence in monkeys is less convincing as both positive (Flombaum and Santos 2005, Burkart and Heschl 2006) and negative results (Kummer et al. 1996, Hare et al. 2003, Burkart and Heschl 2007) have been found. Since different studies involve different monkey species and different methods, it is impossible to attribute the differences in results to differences between species or methods. Many experimental paradigms have been developed to test high-level gaze following in monkeys, but they all face the problem that results can be explained by cognitively simpler mechanisms.

It is clear that apes can follow the gaze of a human experimenter geometrically, since they can follow gaze around barriers (Tomasello et al. 1999, Brauer et al. 2005). Gaze following around a barrier is probably more than low-level gaze following, because individuals follow the gaze past a distracter object, the barrier, to a hidden location searching for the target of attention of the gazer. Experiments with monkeys suggests that they poses similar skills in high-level gaze following, and that they can follow a conspecific’s gaze around a barrier (Amici et al. 2009, Goossens et al. 2012). However, subjects often have to move towards the target of attention in order to look around the barrier, and this movement can equally well be explained by a conditional learned association between moving in the gazed direction and finding an interesting object. Although apes can move to the opposite direction to look behind a barrier (Tomasello et al. 1999) evidence in monkeys is meagre (Goossens et al. 2012) and may have resulted from arousal in combination with the restricted possible directions to move. Additional evidence of high-level gaze following in monkeys comes from research with macaques that follow gazes of human experimenters more often when the gaze is

accompanied with a socially relevant facial (*Macaca fascicularis*: Goossens et al. 2008, *M. sylvanus*: Teufel et al. 2010). These studies indicate that individuals may understand that demonstrators with meaningful facial expression may see something relevant (the target), and that gaze followers may voluntarily control whether they follow gaze. However, the problem with this paradigm is that enhancement of gaze following responses by facial expressions maybe caused by higher salience of the gaze behaviour and by higher arousal of subject monkeys. Although measurements indicate that these alternative explanations do not account for the results, it is still possible that subjects were influenced by the facial expressions of the demonstrator but that it was not detectable with statistics. More evidence for higher forms of gaze following in monkeys comes from an experiment where common marmosets were able to follow a human's gaze towards one of nine containers (Burkart and Heschl 2006). This may prove geometric, i.e. high-level, gaze following rather than reflexive co-orienting, i.e. low-level, gaze following, because subjects choose the target of attention above chance levels despite the presence of several distracting objects (8 containers). However, if marmosets reflexively followed the human's gaze, it is questionable how much distraction was caused by the containers outside the human's field of vision. Moreover, since marmosets were allowed to check two of the containers, the proportion of correct choices in the first trials (31/41%) does not convincingly differ from what is expected if they reflexively follow the gaze of the human and choose a container randomly within their visual field.

An important difference between low- and high-level gaze following is that high-level gaze following requires an understanding of the target of attention of the gazer. Monkeys make inferences about someone else's target of attention, as they show signs of expectancy violation when a human is gazing at a specific target, yet reaches for another unattended object (Santos and Hauser 1999) or when pictured conspecifics with averted gazes appear to look away from a target object (Scerif et al. 2004, Horton and Caldwell 2006). However, these results can also be explained by associative learning. Monkeys often encounter conspecifics with averted gazes and they may have learned that gazing and acting is often in the same direction and that gaze following often result in finding an interesting object. Altogether, there is no unequivocal evidence that monkeys are capable of high-level gaze following.

We used a new paradigm (Chapter2) to investigate whether monkeys understand the target of attention when looking at pictured social scenes. First, we determined whether common marmosets distinguish pictures of a familiar, i.e. their cage mate, from pictures of an unfamiliar conspecific. A second test was based on an experiment where baboons were more interested in play backs of threat grunts towards relatives than towards non-relatives (Cheney and Seyfarth 1999). Likewise, common marmosets should be interested in social scenes where a group member is threatened, because they live in closely bonded family groups where joint territory defence occurs regularly (Koenig and Hartmut 1994). Within the new paradigm, we compare two conditions that both involve gazing at a target, but the facial expression of the gazer as well as the target of attention is varied. Facial expressions of gazers directed at specific targets may reveal social information. We hypothesized that if monkeys understand targets of attention, they would recognize the difference between pictured scenes where aggression is directed at a familiar individual and where an unfamiliar individual is threatened.

METHODS

Subjects and housing

Experiments were conducted with 24 pair-housed marmosets at the Biomedical Primate Research Centre in Rijswijk, the Netherlands. All individuals were mother-reared and originated from group-housed families. We had an equal number of males and females (Table 1). Cages measuring 75(l) x 70(w) x 188(h) cm, were arranged in same sex rooms and were provided with sawdust bedding and enrichment consisting of plastic baskets, wooden branches and garden hoses. Food containing enrichment (with fruit, porridge, or gum) was provided daily, while various temporally hanging objects were provided every week (Vernes and Louwerse 2010). Monkey chow and water were provided ad libitum. Two different groups of marmosets were tested (Table 1), the first group involved duo's which most of the time originated from the same group, occasionally were family members (2 dyads), but were never twins. Two subjects from different duo's were twin brothers, but they never saw each other's pictures. In the second group, duos always were twins. Cages were positioned side by side, preventing visible access to subjects in adjacent cages. Therefore, subjects from different cages could have seen each other only sporadically, when they are caught from their cage in a transparent box or tube for health checks or for participation in this experiment.

Experimental design

Monkeys were tested in a transparent test box (32l x 25w x 20h cm) that was placed in a test room where no other marmosets were present. Monkeys were separated from their home cage in two different ways. Subjects from group 1 were caught from their home cage using a transparent tube and placed in the test box for 30 minutes each time before commencing an experimental trial, while repeatedly treats (tiny marsh-mellow pieces) were provided. This way they habituated to the test situation in the 30 minutes preceding a test trial. In order to limit stress during catching and subsequent separation, in group 2 subjects received positive reinforcement training to walk in the test box voluntarily. During training, subjects habituated to transportation towards the test room, while remaining in the test box. Subjects from group 2 received one treat (bigger piece of marsh-mellow) after their transportation to the test room and immediately thereafter commenced with a trial.

The test box was situated at a distance of 97 cm from a television screen (19.5 inch), while a video camera underneath the television recorded the behaviour of the subject. Pictures were projected on the screen with a laptop, which was operated from an adjacent room. Simultaneously with the onset of a picture, a trivial sound was played to attract the attention of the subject towards the television.

Test stimuli

Two different experiments were conducted investigating whether marmosets: (1) recognize individuals from pictures; and (2) understand the target of attention of pictured conspecifics.

Experiment 1: Individual recognition

Here, it was tested whether individuals could recognize their cage mate from a picture. For this purpose, each individual was exposed to two separate pictures; (1) a picture of their cage mate; (2) a picture of an unfamiliar conspecific from the same sex and from the same room. It was expected that if individuals recognized their cage mate, they would spend more time looking at unfamiliar individuals than at their cage mate (c.f. Fisher-Thompson and Peterson 2004, Schell et al. 2011).

Experiment 2: Understanding the target of attention

In this experiment it was tested whether subjects recognize the target of attention of a pictured conspecific. Pictures in the second experiment consisted of three photographed monkeys in a row (Figure 1). The central monkey was always looking towards one of the flanking monkeys and the flanking monkeys both looked at the central monkey. The flanking monkeys were the cage mate and an unfamiliar individual from the same sex from the same room, the central monkey was also an unfamiliar individual. The display of the central monkey was either threatening (with raised tufts (Stevenson and Poole 1976), sometimes combined with open mouth (Digby 1995) and/or pilo-erection anterior (Stevenson and Poole 1976)), or neutral with normal tufts, closed mouth and no pilo-erection. The display and looking direction of the central monkey was varied systematically, such that each of the subjects received four conditions (Figure 1); (1) aggressive display towards the cage mate (2) aggressive display towards the unfamiliar individual; (3) neutral display towards the cage mate; (4) neutral display towards the unfamiliar individual. The position of the flanking monkeys (left or right of the central monkey) was randomized between conditions.

It was predicted that if monkeys recognize the target of attention in condition 1 and 2, monkeys would be more interested in the picture if their cage mate was

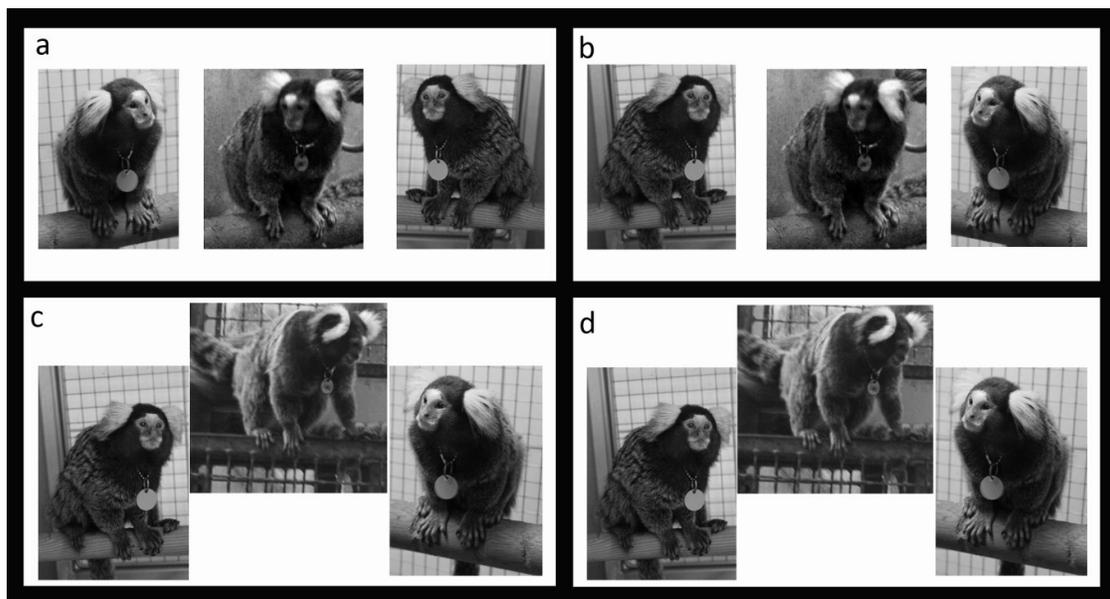


Figure 1: examples of stimuli of the four different conditions from the main experiment: (a) neutral display towards individual A, (b) neutral display towards individual B, (c) threat display towards individual B, (d) threat display towards individual A.

threatened on the picture than when an unfamiliar individual was threatened. Two control conditions (3 and 4) were implicated in the experiment in order to attribute a difference between condition 1 and 2 to a difference in the social information. If differences in looking time between condition 1 and 2 are caused by a difference in social information, we do not expect to find a similar difference between picture 3 and 4. However, if differences in looking time between condition 1 and 2 are due to gaze following and subsequent focussing on a more or less interesting target of attention, we expect to find a similar difference between condition 3 and 4.

The order of conditions in both experiments was randomized. Pictures from different conditions were presented for 30 seconds with 1-minute intervals between two pictures, resulting in a total time of two minutes for experiment 1 and five minutes for experiment 2. If subjects did not look at one of the conditions during the full 30 seconds of picture exposure, the experiment was repeated after an interval of at least 4 hours. Only first time exposures to specific picture conditions were included in the analysis. Subjects first completed experiment 1, before they entered experiment 2. The two experiments were done during different sessions, separated by an interval of at least 4 hours.

We controlled for the variation in stimuli characteristics between conditions, by using the same pictures in different conditions; i.e. the cage mate of individual A was used as unfamiliar for individual B, while individual B's cage mate was used as unfamiliar for individual A.

Analysis

The attention to the pictures by subject monkeys was calculated by counting the number of frames it spent looking at the television from a 25 frame/second movie in 'avi' format using QuickTime Player Version 10.0. We choose to do analyses on total looking times rather than the duration of first fixation or the frequency of fixations, because we think this is the best measure of expectancy violation. If an individual's expectancy is violated, it may show elevated attention by (1) check- looking more often (Scerif et al. 2004, Horton and Caldwell 2006), and or (2) increase the duration of fixation (Scerif et al. 2004, Steckenfinger and Ghazanfar 2009). The total looking time will increase if any of these behaviours increases, which is not true for the other two possible measurements. Videos were scored by an observer blind to the conditions. Looking times were log normally distributed, therefore, we used parametric linear models (LM) with the logarithm of the looking time as dependent variable and pictured condition as independent variable. Looking times may differ between sexes and groups, especially since the training methods differed between groups. To correct for the effect of sex and difference in training on our results, both factors, sex and group, were integrated as fixed factors in the model. All tests were done using the software package "R" (R Development Core Team 2009) Version 2.10. The "lm" function for linear models was used from the "stats" package. All tests are two-tailed with $\alpha = 0.05$.

RESULTS

Recognition of cage mates

Looking times did not significantly differ between pictures of cage mates and pictures of unfamiliar individuals (LM: coefficient = $0.32 \pm SD 0.2$, $t = 1.35$, $N = 23$, $P = 0.183$, Table 1).

Recognition of the target of attention

There was no significant difference found between pictures where a neutral face was directed at an unfamiliar individual than for pictures with neutral faces towards cage mates (LM: coefficient = $0.33 \pm SD 0.2$, $t = 1.98$, $N = 21$, $P = 0.055$, Table 1).

There was no significant difference in looking time between pictures with a threat display towards the cage mate or the unfamiliar individual (LM: coefficient = $0.03 \pm SD 0.2$, $t = 0.16$, $N = 22$, $P = 0.88$, Table 1).

Subject	Group	sex	Individual recognition	Understanding the target of attention	
			Condition 1-2	Condition 1-2	Condition 3-4
1	1	m	0.84	-9.68	-1.68
2	1	m	-1.44	6.72	0.64
3	1	m	1.80	-7.56	19.24
4	1	m	20.60	-0.32	0.04
5	1	m	-4.44	0.28	-5.32
6	1	m	-1.48	0.60	2.04
7	1	f	-0.36		
8	1	f	8.00	-18.56	9.04
9	1	f	-1.52		
10	1	f	7.92	6.84	1.04
11	1	f	9.72	-7.56	0.56
12	2	m	-5.80	0.16	3.32
13	2	m		0.56	-1.92
14	2	m	-2.72	5.28	0.40
15	2	m	-2.76	-3.64	1.20
16	2	m	5.40	4.16	2.56
17	2	f	0.76	2.36	
18	2	f	9.76	-2.48	4.64
19	2	f	9.00	-0.56	2.12
20	2	f	2.36	1.20	-0.56
21	2	f	0.16	0.92	-1.80
22	2	f	-4.68	-0.84	
23	2	f	4.28	-0.04	-0.24
24	2	f	1.88	-3.04	-1.12

Table 1: characteristics and responses of individual subjects in both experiments. Within the “individual recognition” experiment the difference in time spend looking (in seconds) is given for pictures of (condition 1) the cage mate minus (condition 2) an unfamiliar individual. Within the “understanding the target of attention” experiment, the difference in time spend looking (in seconds) is given for pictures of (condition 1) aggression directed at the cage mate minus (condition 2) aggression directed at an unfamiliar individual, and (condition 3) neutral face directed at the cage mate minus (condition 4) neutral face directed at an unfamiliar individual.

DISCUSSION

Marmosets individually recognize each other when confronted with real life individuals (Harrison and Tardif 1988). Recognizing life individuals is possible through three sensory

systems: olfactory, auditory and visually. Marmosets can recognize individuals by smell (Smith 2006) or vocalisations (Miller and Thomas 2012), but it is uncertain whether they can recognize individuals based on visual cues only. Results from our experiment comparing looking times at pictures from cage mates and unfamiliar individuals indicate that subjects do not recognize their cage mate from a picture. This may reflect an inability of marmosets to recognize individuals from visual cues only, corresponding with their arboreal life, restricting visual communication (Altmann 1967, Seyfarth 1987) or an inability of our methods to detect visual recognition.

The question of our second experiment was whether marmoset subjects understand the target of attention of a pictured conspecific. We found no evidence for this when comparing looking times for pictures with threat displays directed at either cage mates or unfamiliar individuals. Several explanations may account for these negative results. First, subjects may not be able to recognize individuals from pictures, congruent with their lack of differentiation between pictures of a familiar and an unfamiliar individual (see above). Second, it is possible that subjects did not recognize our stimuli as truly social scenes, since the pictures had several limitations. The use of pictures restricted the scenes to still 2D representations of scenes that naturally occur to the animals in animated 3D scenes. Furthermore, pictures were composed of three separate photographs with different backgrounds. Therefore, subjects could have interpreted pictures as three separate individuals, which were not able to interact with each other. In follow up studies this can be remedied by merging three separate monkey pictures and a single background picture into one fluent image (c.f. Chapter 2). Third, although baboons are more interested in situations where relatives are threatened than where unrelated individuals are threatened (Cheney and Seyfarth 1999), we do not know whether marmosets are differentially interested in scenes where relatives, cage mates or unfamiliar individuals are threatened since this has never been tested. Alternatively, different individuals may have different interests in social scenes. While some individuals may be more interested in situations where cage mates are threatened (c.f. baboons Cheney and Seyfarth 1999), other individuals may be more interested in scenes where unfamiliar individuals are threatened, because this may represent banishment of an unfamiliar intruder which they might want to join. Indeed, when unfamiliar individuals enter their territory, marmosets defend it with multiple individuals and may engage in a joint attack (Koenig and Hartmut 1994). Moreover, marmosets are more likely to act aggressively towards unfamiliar intruders than towards familiar ones (French et al. 1995). Therefore, there may be too much variation in looking times between subjects depending on their motivation to flee from a potential threat to their group or to join banishment of intruders. Finally, it is possible that marmosets do not understand what their conspecifics are looking at. This would contrast with previous results indicating that common marmosets are able to extrapolate human gaze towards a target of attention (Burkart and Heschl 2006). However, the proportion of correct choices in the first trial in Burkart and Heschl's study (31% from head and eye cues or 43% for eye cues only) were not particularly high, especially if you consider the fact that subjects were allowed to look in two out of nine containers and that only a few of these nine containers would be seen by subjects that reflexively co-orient with the demonstrator. Moreover, other studies of VPT in marmosets found negative results (Burkart and Heschl 2006). Hence, the evidence for high-level gaze following in marmosets is faint.

Summarizing, we find no results indicating that common marmosets understand the target of attention of conspecifics. Since this is a prerequisite for VPT, our findings suggest that common marmoset are not able to establish the visual perspective of a conspecific. This is partly congruent with outcomes form other studies on common marmosets (mixed evidence in Burkart and Heschl 2006, Burkart and Heschl 2007). Therefore, further investigations are needed to confirm the suggestion by Burkart and Heschl (2006) that common marmosets possess high-level gaze following.



4

Long-tailed macaques (*macaca fascicularis*) understand what conspecifics can see in a competitive situation

Overduin – de Vries, A.M.
Spruijt, B.M.
Sterck, E.H.M.

Visual Perspective Taking (VPT), an understanding of what others can see, is a prerequisite for advanced cognitive capacities like Theory of Mind. The presence of VPT in monkeys is a much-debated topic, and several different paradigms have been developed to test its existence. However, all face interpretational problems since results can be explained by simpler cognitive mechanisms than VPT. Therefore, we adjusted one method where two individuals compete for access to food, visible or invisible for the dominant competitor (Hare et al. 2000). The new set-up prevented monkey subjects to use two alternative mechanisms: behavioural reading or approaching the less accessible food. In most trials subjects retrieved only one food item and preferred the invisible food item. Surprisingly, they occasionally adopted an alternative strategy to obtain both food items, by first approaching the most at risk food item visible for their competitor. In contrast with previous research, our results cannot be explained by alternative simpler cognitive mechanisms, since behavioural reading was prevented by a one-way mirror between the dominant competitor and the food containing occluders, and accessibility was equal to both food items. Therefore, this is the first unequivocal evidence of VPT in a monkey species.

INTRODUCTION

The presence of advanced cognitive capacities in non-human primates is an intensively studied topic, since it reveals information about the evolution of human intelligence. One of the most important cognitive capacities in humans, Theory of Mind, is probably less well developed in other primates (Call and Tomasello 2008). Theory of mind (ToM) is the capacity to form concepts about the mental states of others. ToM consists of several building blocks that can be present in species that lack a full-blown ToM. One of the building blocks that is present in apes (*Pan troglodytes*: Hare et al. 2006, Melis et al. 2006), but less evident in monkey species, is Visual Perspective Taking (VPT), i.e. the ability to understand what another individual can see.

Three different paradigms have been developed to test for the existence of VPT in several monkey species (Hare et al. 2003, Scerif et al. 2004, Burkart and Heschl 2006, Burkart and Heschl 2007, Goossens et al. 2008, Amici et al. 2009, Goossens et al. 2012). All these paradigms face their own interpretational problems, since many of the results can be explained by simpler cognitive mechanisms than VPT. A first indication for the presence of VPT in monkeys is found in gaze following studies (Scerif et al. 2004, Burkart and Heschl 2006, Goossens et al. 2008). Gaze following is a prerequisite to VPT, and may result from a basic set of cognitive structures (Triesch et al. 2006). Gaze following may be the result of reflexive co-orientation and is present in many primate and other animal species (Tomasello et al. 1998, Itakura 2004). However, there is evidence that gaze following in monkeys is more than a reflexive co-orientation, because individuals show voluntary control of gaze following if they follow gaze more often when associated with certain facial expressions (Goossens et al. 2008, Goossens et al. 2012). That way, individuals may follow gaze because they make inferences about the gazers target of attention (Scerif et al. 2004, Goossens et al. 2008). This higher level of gaze following may include VPT. Alternatively, the reported increase in gaze following behaviours may have resulted from a higher arousal level due to the presence of agonistic facial expressions which resulted in increased visual scanning and a higher frequency of looks in the same direction as the demonstrator.

The second paradigm requires animals to follow someone else's gaze to a location hidden behind a barrier. Most of these tests comprise a movement in the same direction as the line of sight of the gazer (Amici et al. 2009), and the results can be explained by subjects moving in line with the gaze direction, which can be a conditionally learned mechanism. Indeed, marmosets move in the direction of the gaze instead of understanding which targets are behind a barrier and thus invisible to the gazer (Burkart and Heschl 2007). Few studies investigated whether monkeys can walk away from the location of the target of attention in order to look around a barrier, which more reliably proves an understanding that the gazer is looking at an object, which cannot be seen through the opaque barrier (Goossens et al. 2012). However, although similar studies with apes were performed in large enclosures (*Pan troglodytes*: (Tomasello et al. 1999) (wall condition), the monkey subjects had limited alternative directions to move (Goossens et al. 2012) and thus any movement would result in a movement to the other side of the barrier.

The third paradigm that is often used to study VPT is a setting where two individuals have to compete for visible and invisible food items. Although apes were able

to choose a food item that could not be seen by their opponent (Hare et al. 2000), similar experiments in monkeys revealed that they could only make the correct choice based on behavioural reading (Hare et al. 2003, Burkart and Heschl 2006). Dominant competitors may show attentional behaviour towards the visible object because they see this object and are motivated to approach it. Subsequently, subordinate subjects may avoid the object that is looked at by the competitor, because they avoid being looked at by the dominant or treat an object that is looked at by someone else as its property. Since monkeys were not able to make the correct choice after removal of the visual cues from the competitor, the monkeys apparently solved the task by behavioural reading instead of VPT.

Moreover, the absence of a capacity in two New World monkey species does not mean that all monkey species lack the capacity of VPT. In addition, the placement of the visual obstruction, either parallel or orthogonal with the dominant's shortest way to the food (Hare et al. 2000, Hare et al. 2003), may create differences in accessibility of the food items for the dominant, and this may have guided the subject's behaviour instead of VPT.

Therefore, we tested an Old World monkey species with an adjusted version of the food competition paradigm. During decision-making, we prevented subordinate subjects from behavioural reading while at the same time adding the visual presence of the dominant competitor, by using a one-way mirror between the dominant and the food. Additionally, we used occluders that not only consisted of opaque barriers, but also of transparent barriers in order to balance the accessibility of the visible and invisible food items for the dominant.

METHODS

Subjects

Three male and 11 female long-tailed macaques contributed to the dataset. All subjects were housed in one social group (the 'Haas' group) and were tested in part of their home cage. The group was located at the Biomedical Primate Research Centre in Rijswijk, the Netherlands, and originated from the 'Ethologystation', Utrecht University. The dominance hierarchy of subjects was determined on the basis of submissive behaviours (teeth baring and unprovoked avoidance). From the resulting matrix, the dominance hierarchy was obtained (de Vries 1998) using Matman 1.1 (de Vries et al. 1993), which was significantly linear ($h'=0.58$, $p=0.0096$) (de Vries 1995). Subjects were trained by positive reinforcement to be temporarily separated from their group members in part of their home cage. Outside testing hours, monkeys were fed fruit, vegetables or bread manually through the wire mesh in front of the test cage and monkey chow from a food container, which hung on the front of the test cage. During testing this food container was temporarily moved to another position in their home cage. Water was available at libitum. Monkeys received permanent environmental enrichment in the form of a sawdust bedding, ladders, tires, fire hoses, an outside swimming pool, and extra enrichment containing food was provided every other week (Vernes and Louwerse 2010).

Test cage and occluders

Two individuals, a subordinate subject and a dominant competitor, were separated into the test cage (485x70wx83hcm), which consisted of three compartments in a row (Figure 1). The central arena (245x83x70dcm) was subdivided in two sub-compartments by a wire mesh partition that prevented the subjects from accessing two food items simultaneously. Two favoured food items (either two small marshmallows or two in-shell peanuts, randomly alternated) were presented, each in one of two half open box-shaped occluders (28x15x15cm). Occluders consisted of an opaque bottom and top, a transparent (Plexiglas) side and an opaque (wooden) side (Figure 1). One of the sides (opaque or transparent) was always directed at the dominant competitor, while the other side (transparent or opaque) was directed at the partition, one box on either side of the partition. By either directing the opaque or transparent side of the occluder at the competitor, we varied the visibility of the food item for the competitor, while the accessibility was kept constant.

Subject and competitor were positioned in opposite compartments and separated from the central compartment by removable doors. To eliminate the possibility that a subject made a choice based on the competitor's behaviour towards the visible food item, we blocked the view of the competitor by placing a one-way mirror in the removable door that separated the competitor from the central arena. This set-up allowed the subject to see the competitor, and therefore from the subject's perspective it appeared as if the competitor could see the subject and the food containers, but in fact

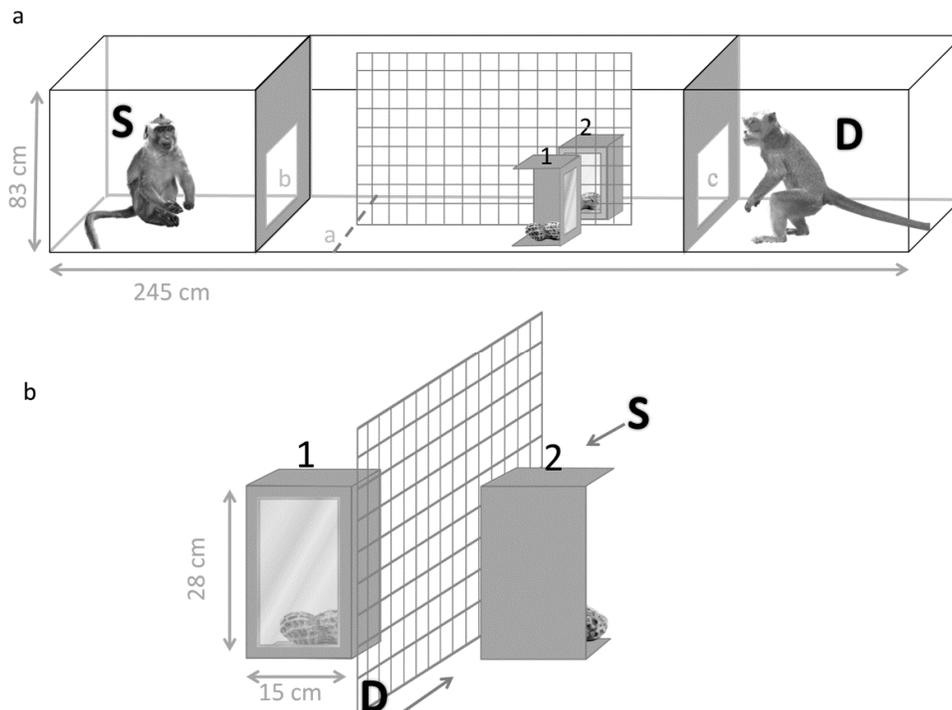


Figure 1: Schematic outline of (a) the complete test cage, and (b) a detail of the test cage including the occluders. Numbers 1 and 2 represent respectively the occluder with the visible food item (1), and the occluder with the invisible food item (2). Grey characters indicate (a) the imaginary line that subordinates had to cross before the dominant was released during test trials, (b) the transparent window in the door of the subordinate, (c) the window in the door of the dominant that was either a one-way mirror (during test trials) or transparent Plexiglass (during control trials). “S” indicates the position of the subject, while “D” refers to the position of the dominant competitor.

the competitor was not able to see the food items or the subject. Once the door of the competitor to the central compartment was opened, it was able to see the food item behind the transparent side of the occluder, from now on called the 'visible food', but not the food item behind the opaque side of the barrier, from now on called 'invisible food'. The position of the subject (left or right from the central arena) was randomized between trials.

Pilot experiment

During a pilot experiment before the main experiment, subjects were familiarized with the presence of two food items in the occluders and the competitive situation. The occluders were positioned such that the food item in one of the occluders was visible, while the food item in the other occluder was invisible from the competitor's perspective. A trial commenced by baiting the food containers and simultaneously making sure that the subject paid attention to the baiting process by conspicuously moving the food items and making noises. In trials where the competitor's view was restricted by the one-way mirror, no specific effort was made to attract the attention of the competitor. After baiting, the subject was released in the test arena. The competitor was released after the subject had made a choice, i.e. crossed an imaginary line (Figure 1). Subjects were tested for a maximum of three times in this setting.

In order to increase the competitive attitude of subject and competitor in pilot test sessions where the competitor's view was blocked by the one-way mirror and one of the occluders, control trials were included between each two consecutive test trials of the same subject. In control trials, both food containers were positioned with the transparent side towards the competitor, exposing both food items to the competitor. Additionally, the one-way mirror between the competitor and the central arena was replaced by transparent Plexiglas.

In the pilot experiment we experienced that subjects often obtained both food items, and therefore instead of giving the subjects a head start in the pilot experiment, in the main experiment subjects and competitors were released simultaneously during control trials. In between the pilot and main experiment, subjects were familiarized with the simultaneous release with their competitor by baiting both occluders visible for both individuals (without one-way mirror) and releasing subject and competitor simultaneously from opposite doors to the central compartment. This was repeated three times per subject before the main experiment commenced.

Main experiment

The purpose of the main experiment was to measure the preference of subjects for the visible or invisible food item (c.f. Hare et al. 2003, Burkart and Heschl 2007). All procedures of the main experiment were equal to the procedures of the pilot experiment, with one exception. During control trials in the main experiment, the subject and competitor were released simultaneously.

During test trials, subject's choices, the number of food items obtained by the subject, as well as the behaviour of both individuals was recorded on video (SONY DCR-

SR72E). If one of the food items dropped out of the test arena out of reach of both subject and dominant (N= 4), the trial was repeated after another control trial.

Subjects performed five test trials with, when possible, five different competitors, i.e. when five or more dominant individuals were present in the group. Higher-ranking individuals were tested with as many different competitors as possible, i.e. the second, third, fourth and fifth individual were tested with 1,2,3 and 4 different competitors. The alpha male and alpha female were paired as competitor with all other subordinate subjects. The remaining dominant individuals were included as competitor if submissive displays were observed unidirectional within the dyad, with one exception: tartufo, the fifth ranking individual, was coupled with era, the third ranking individual, while submissive behaviour (unprovoked avoidance) was once observed from the dominant to the subordinate and never the other way around. However, it was important to include the tartufo-era duo, since it was one of the only four possible dyads involving tartufo as subject. Moreover, aggressive behaviour within this dyad was exclusively observed from dominant to subordinate (4 times), and interactions with the individual that ranked in between era and tartufo confirmed the dominance of era over tartufo, supporting the inclusion of tartufo as subject with era as his competitor in our dataset.

Analysis

A generalized linear model (GLM) was performed with as dependent variable the binomially distributed choice of the subject monkey of either the visible or invisible food item. Several fixed and random factors were incorporated in the model.

Subjects may have had a preference for the food item in one of the compartments over the other, because in the front of the test cage two human observers were present during the test and monkeys were habituated to food provisioning in the front of the test cage. Additionally, we controlled for individual identity, because subjects may differ in their behaviour and competitors may have different effects on a subject's behaviour. Therefore, the position of the invisible food item (in the front or back compartment) and the identity of both individuals were included in the general linear model as random factors.

We aimed to measure the preference of subjects for one of two food items and expected that it would be most profitable to choose the invisible food item, in order to minimize competition with the competitor. However, subjects sometimes managed to obtain both food items before the competitor could reach the food. In these cases, where individuals aim to retrieve both food items, it would be more efficient to reach for the visible food first, to ascertain the possession of the most at risk food item and then later, when the competitor is already released, go for the food that the competitor is not aware of. Therefore, we hypothesize that a subject's first choice is dependent on the number of food items it aims to obtain. Because we cannot access the aim of monkeys, we took the number of actually obtained food items (2 or ≤ 1) as an estimate of the subject's aim, and this was included in the model as fixed factor. In a few trials (N=6), subordinate subjects did not retrieve any food item. However, they did approach one of the food items and thus had the intention of at least retrieving one food item. Therefore, trials where subjects did not retrieve any food items (N=6) were lumped with trials where subjects obtained only one food item. Note that in the trials where no food was

retrieved, subjects showed more variation in their choice, i.e. visible or invisible food, rendering our outcomes by including these cases conservative.

All statistical tests were two-tailed with α set at 0.05. All tests were done using the software package “R” (R Development Core Team, 2009) Version 2.10. The “glmer” function for generalized linear mixed models (GLM) was used from the “lme4” package.

RESULTS

In almost all trials (59/65), subordinate subjects succeeded in obtaining at least one food item. Once a food item was taken by the subject, it was never taken away by the competitor, and all obtained food items were consumed. When all subjects were analysed together without including the factor for the number of food items obtained, subjects tended to have a preference for the invisible food item (generalized linear mixed model: coefficient = $0.47 \pm \text{SD } 0.27$, $z = 1.76$, $P = 0.079$). Moreover, the number of food items obtained by the subject had a significant influence on the choice made between visible or invisible food items (generalized linear mixed model: coefficient = $-1.91 \pm \text{SD } 0.66$, $z = -2.89$, $P = 0.0038$). Subjects that retrieved ≤ 1 food item significantly more often chose the food invisible from the competitor’s perspective (71%) than the food item visible from the competitor’s perspective, whereas subjects that were able to retrieve 2 food items significantly more often first approached the food item visible from the competitor’s perspective (69%)(Figure 2).

Competitors could behave aggressively towards subjects. They were significantly more often aggressive to the subject when the subject chose the visible (48%) than the invisible (25%) food item (binominal test: $p = 0.018$)(Figure 3).

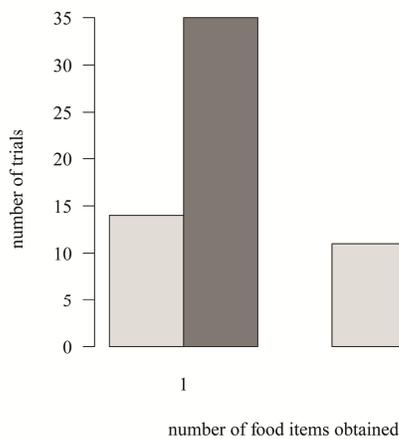


Figure 2: Number of trials where the invisible (darkgrey bars) or visible (lightgrey bars) food item was chosen by the subject in trials where the subject either obtained 1 or 2 food items.

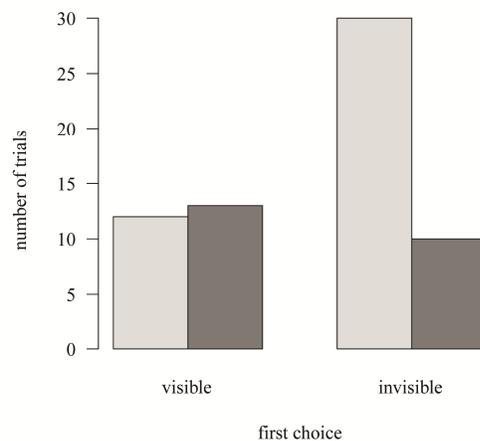


Figure 3: Number of trials where the competitor did (darkgrey bars) or did not (lightgrey bars) behave aggressively towards the subject in trials where the subject either chose to approach the occluder with the visible or with the invisible food item.

DISCUSSION

We investigated whether long-tailed macaques are able to judge what a conspecific competitor can see. Indeed, we found a trend that a subject had a preference for a food item that appeared invisible from the competitor's perspective over a food item that appeared visible from the competitor's perspective. Moreover, we found that some subjects were able to obtain both food items and we considered this an alternative strategy. When analysing the data while taking in account the different strategies, we found that subjects that obtained only one piece of food had a significant preference for the invisible food item, while subjects that obtained both food items had a significant preference to approach the visible food item first. Our results show that long-tailed macaques know what another individual can see and are capable of Visual Perspective Taking (VPT).

Choosing the invisible food item enabled long-tailed macaque subjects to obtain food that could not be noticed by the competitor and therefore reduces the chance of being robbed or punished by the competitor for obtaining the food it was interested in. In contrast, choosing the visible food item secures the possession of the most at risk food item and once the most at risk food was possessed, subjects had enough time to take the hidden piece, because the competitor was not aware of this food item. This strategy was also used by dominant chimpanzees in a similar setup, but where the roles of dominant and subordinate were reversed (Hare et al. 2000). Dominant chimpanzees probably adopt this strategy because they can claim both food items due to their dominance and they first ascertain possession of the most at risk food item. Indeed, dominant chimpanzees almost always obtained both food items. Similarly, our subordinate subjects may have used the strategy because they could get both food items if they were quick enough to grab the visible food before the competitor could. Therefore, probably the relative speed of both individuals is an important factor determining which of the two strategies is applied. Indeed, no individual obtained in all five sessions two food items and whether to use or not to use this alternative strategy is not only dependent on the subject, but also on the specific trial. Another factor influencing the effectiveness of the alternative strategy is whether dominant individuals show respect of ownership. Dominant long-tailed macaques have been shown to respect ownership of subordinates that continually inspect possessed objects (Kummer and Cords 1991). Within our setup, subjects could immediately consume the food item and probably because of respect of ownership, competitors did not try to 'steal' the food from the subject. It was, however, not fully respected by competitors that subjects took the visible food item in our setup, because aggression by the competitor towards the subject was often observed after retrieval of the visible food item. It is probably the risk of this aggression that caused most subjects to choose for the strategy to choose the invisible food item. Indeed, this strategy reduced the risk of aggression, since aggression was less often observed when individuals choose the invisible then when individuals choose the visible food item.

The choice of the subject in our setup was not based on a preference for the food item that was least accessible for the competitor. In previous research (capuchins: Hare et al. 2003, marmosets: Burkart and Heschl 2006) one food item was behind an opaque barrier making it not only less visible, but also less accessible for the competitor, while

the other, visible, food item only had a barrier to the side of the food item (Hare et al. 2003) or below it (Burkart and Heschl 2006), which less restricts dominant's accessibility during approaches. In our experiment the accessibility of the food item for the competitor was equal for both food items, because a transparent barrier was placed between the visible food item and the competitor. Therefore, our results provide unequivocal evidence of VPT in monkeys.

Moreover, our results cannot be explained by behavioural reading by the subjects. Capuchin monkeys and marmosets were only able to choose the correct food item if they were allowed to read the behaviour (attentional behaviour towards one of the two food items) of their competitor (Hare et al. 2003, Burkart and Heschl 2006). When the dominant was invisible during the decision of the subject, marmosets and capuchins were not able to make the correct choice. Within our setup, subjects saw their competitor while making a choice, but the competitor had no visual access to any of the food items before and during the choice of the subject and thus could not show elevated attentional behaviour towards one of the food items. Therefore, attention by the dominant did not direct the subject's behaviour.

The fact that our subjects were able to make the correct choice despite the absence of attentional cues by the competitor, while capuchin and marmosets were not (Hare et al. 2003, Burkart and Heschl 2007), can be explained by several differences between studies and species. First, while our subjects continuously saw their competitor, for capuchins and marmosets the competitive situation may not be obvious once the visual presence of the dominant competitor was removed during the choice of the subject. Therefore, capuchins and marmosets may have chosen randomly while our subjects preferentially choose the hidden food. Second, in our study the first strategy of preferably approaching the invisible food item was used more frequently than the alternative strategy, and subjects tended to have an overall preference for the invisible food item. In previous studies no results are provided about the number of food items obtained by the subject per trial. If the proportion of trials in which the alternative strategy is used was near 50%, no overall preference may be found. This would also explain why capuchins and marmosets when released simultaneously with the dominant still had a preference for the hidden food; they had no chance of obtaining both pieces and therefore did not use the alternative strategy. It is therefore crucial in this paradigm to consider the number of food items obtained by the subject. Third, marmosets and capuchins are monkeys with a different social structure from long-tailed macaques. While long-tailed macaques have a despotic dominance hierarchy (Thierry 2004), the other two species have relatively egalitarian dominance hierarchies (capuchins: de Waal 1997, marmosets: Schaffner and Caine 2000) and may therefore be less sensitive to competitive situations. Finally, both capuchins and marmosets are New World monkeys while long-tailed macaques belong to the Old World monkeys, and New World monkeys have less advanced cognitive skills indicated by a lower general intelligence, 'g', scores than Old World monkeys, although the difference is not significant (Reader et al. 2011). In order to investigate whether the reported difference between species is due to a difference in methods, social or cognitive abilities, it is important to test capuchins and marmosets and a despotic New World monkey such as *Cebus capucinus* (Bergstrom and Fedigan 2009) and/or egalitarian Old World monkey such as *Macaca nigra* or *Macaca tonkeana* (Sueur et al. 2011) with the current method.

Concluding, long-tailed macaques have a preference for food items that appear invisible from the perspective of a dominant competitor when they can obtain only one of two available food items, but adopt an alternative strategy of taking the visible food item first in order to achieve both food items. This is the first unequivocal evidence for Visual Perspective Taking in a monkey species. This indicates that this important precursor to Theory of Mind is not only found in apes, but also in at least some monkey species.

5

Sneaky monkeys: an audience effect of male rhesus macaques (*Macaca mulatta*) on sexual behaviour

A.M. Overduin - de Vries, J.J.M. Massen, B.M. Spruijt, E.H.M. Sterck

Males and females have different sexual interests and subsequently may show conflicting sexual strategies. While dominant males try to monopolize females, promiscuity benefits females and subordinate males. One way to escape monopolization by dominant males is to copulate in their absence. We tested this inhibitory effect of males on the sexual behaviour of their group members in captive group-living rhesus macaques. Copulations between females and non-alpha males almost exclusively took place when the alpha male was out of sight. Furthermore, the inhibiting effect was not unique for the alpha male. An upcoming non-alpha male also inhibited copulations of its group members, and three other non-alpha males inhibited female copulation solicitations. Females adjusted their behaviour to the presence of bystander males, as they initiated and accepted initiations more often in absence than in presence of bystander males. Although not significant, in males a similar pattern was found. The observed reduction in mating behaviour in presence of bystander males is in accordance with an “audience effect”, in which the behaviour is modulated in relation to the presence or absence of third parties. This audience effect may serve as an important mechanism to reduce (aggressive) interruptions of subordinate male copulations.

Published in 2012; *American Journal of Primatology* **74**: 217–228.

INTRODUCTION

Primate males in species with multi-male mating systems compete with each other and aim at preventing female promiscuity (Dixson and Anderson 2002). The most common male strategy is monopolization of females by higher-ranking males. These high-ranking males concentrate their sexual behaviour on receptive females by forming consorts (de Ruiter and van Hooff 1993, Berard et al. 1994, Alberts et al. 2006) and mate guarding. In addition, dominant males can disrupt copulations and consorts of subordinate males by chasing the female away from the subordinate male (Chapais 1983, Manson 1996), indicating that dominant males can monopolize access to females. According to the Priority of Access model, this results in a correlation between male dominance rank and mating success (Altmann 1962). In many species this correlation is found [for review: (Cowlshaw and Dunbar 1991); *Gorilla gorilla beringei*: (Robbins 1999); *Macaca fascicularis*: (de Ruiter and van Hooff 1993); *M. mulatta*: (Massen et al. 2012); *M. fuscata*: (Garcia et al. 2009); *M. sylvanus*: (Paul et al. 1993); *Mandrillus sphinx*: (Wickings et al. 1993); *Pan troglodytes*: (Klinkova et al. 2005, Boesch et al. 2006); *Papio anubis*: (Bulger 1993, Alberts et al. 2006)]. However, especially when females ovulate in synchrony and receptive females do not coordinate their movements (Ostner et al. 2008), males may fail to monopolize them for the full length of their fertile period, and the degree of monopolization can differ between species (reviewed in van Noordwijk and van Schaik 2004), populations (*Macaca fascicularis*: de Ruiter et al. 1992), subsequent years (*Macaca mulatta*: Berard et al. 1993, Smith 1993, Berard 1999) or may not even be found (*Macaca mulatta*: McMillan 1989, *Cebus apella nigrinus*: Alfaro 2005). This indicates that, especially in seasonal species where female synchrony is largest (Newton 1988), not only male dominance may determine the distribution of male access to receptive females, but that subordinate males can also copulate and father a substantial part of the offspring (van Schaik et al. 2004). One way for subordinate males to enhance their copulation opportunities is to minimize disruption of their copulations by copulating quickly and out of sight of high-ranking males.

Female choice can overcome the effect of male dominance (Soltis et al. 1997). In mammals female choice often results in promiscuity (Dixson 1998, van Noordwijk and van Schaik 2000). Although copulating with multiple males is costly for females when it results from male coercion (Smuts and Smuts 1993), or when there is a high risk on sexual transmitted diseases (Nunn et al. 2000, Thrall et al. 2000), female promiscuity is often beneficial for females. A major ultimate benefit concerns protection against infanticide (primates: Hrdy 1979; Janson 2000, mice: Cicirello and Wolff 1990, mammals: Ebensperger 1998). In primates, males that have copulated with a particular female refrain from attacking her subsequent offspring (Hausfater and Hrdy 1984) and even actively defend it (Buchan et al. 2003). In addition, promiscuity may benefit females by allowing cryptic female choice or sperm competition resulting in better quality offspring (Zeh and Zeh 2003), avoiding sexual harassment, provisioning of goods and services by sexual partners, and drive the number of males that defend the group (reviewed in: Engelhardt 2004, Wolff and Macdonald 2004). Promiscuity commonly represents a preferred female strategy, since females actively seek multiple copulation partners (Soltis 2002) and in many species females have evolved adaptations to improve their chances of

being promiscuous (Birkhead 2000). For instance, a number of Old World monkeys and apes have exaggerated swellings in the anogenital region around the time of ovulation (Dixson 1998). The duration of sexual activity is longer in species with exaggerated swellings (Nunn 1999), which increases the probability of copulating with more than one male. Besides, Catharine primate females have, compared to other mammals, extended sexually receptive periods that reduce male monopolization of females and facilitate female promiscuity (Engelhardt 2004). Female promiscuity can be indiscriminate (Nikitopoulos et al. 2005) or females may bias copulations toward particular males. This bias does not necessarily follow the male dominance hierarchy, since females may prefer novel over well-known males (*Macaca fuscata*: Inoue and Takenaka 2008), or males that have a social bond with them (*Papio cynocephalus anubis*: Smuts 1985, *Macaca mulatta*: Massen et al. 2012) or young males (*Macaca mulatta*: Smith 1994). Since these males are often subordinate, females have developed tactics to escape from monopolization by higher-ranking males, such as copulating out of sight of high-ranking males.

Sneaky copulations by a female and a subordinate male out of sight of the dominant male may result from high-level cognitive capacities, including visual perspective taking and tactical deception (Byrne and Whiten 1990). Alternatively, but not mutually exclusively, sneak copulations may result from an inhibiting effect that dominant individuals have on the sexual behaviour of their group members. One way of dominant males to hinder subordinate male mating success is to disrupt on-going copulations, which has been reported in at least 13 different primate species (Dixson 1998 p.72, tabel4.5). Disruption can involve aggression such as chasing or attacking copulating individuals (*Macaca mulatta*: Lindburg 1971, Chapais 1983, Ruiz de Elvira and Herndon 1986; *Pan troglodytes schweinfurthi*: Tutin 1979). Simple operant learning, combining sexual behaviour in close proximity of disrupting individuals with punishment, may then result in a simple rule such as 'freeze particular behaviour when in close proximity of the dominant' (Amici et al. 2009).

Such an inhibition of particular behaviour by the mere presence of a bystander is called an audience effect. In some contexts, such as predator warning, audience effects prevent a signaler from giving costly signals without having an audience to receive the signal (Wich and Sterck 2003). In other contexts, such as greeting (Laporte and Zuberbühler 2010), mother-infant interactions (Semple et al. 2009), and sexual behaviour, audience effects reduce conflicts with potentially aggressive bystanders (Townsend and Zuberbühler 2009). Whether an audience effect on sexual behaviour increases the reproductive success of subordinate males is dubious. On the one hand, an audience effect might lead to a higher rate of copulations by subordinate males in the absence of dominant disruptors and thus a higher incidence of successful copulations. On the other hand, the number of times a male can copulate per hour is limited and thus the total number of copulations by subordinate males may decrease by means of an audience effect. While, in a few primate species the copulation frequency is correlated with reproductive success (reviewed in: de Ruiter and van Hooff 1993), male mating success is also based on a number of other factors in a complicated interactive way; namely, consort behaviour, the timing of copulation relative to ovulation, female partner preferences, the number of female partners, and troop composition (Takahata et al. 1999). In conclusion, the most unequivocal benefit of an audience effect on sexual behaviour is to reduce the amount of energy loss due to unsuccessful mating attempts in

the presence of disruptors, and the amount of aggressive interactions between males and / or females (Townsend and Zuberbühler 2009).

Since disruption is always accomplished by an animal higher in rank than at least one of the animals in the consorting pair (Ruiz de Elvira and Herndon 1986), it is expected that higher ranking males inhibit copulations of lower ranking ones and not the other way around. Whereas disruption by males is common in rhesus macaques, female rhesus macaques rarely disrupt copulations (Dixson 1998 p.72, tabel4.5). Thus it is expected that in this species, mainly males would have an audience effect on the sexual behaviour of group members. During disruptions of copulations in rhesus macaques, females receive the brunt of aggression (Ruiz de Elvira and Herndon 1986, Manson 1996), which indicates that females would benefit from reducing interruptions. In contrast, for males no fitness loss is associated with the disruption of copulations (Berard et al. 1994). Apparently, males buffer disrupted copulations by finding enough opportunities to copulate. Therefore, it is expected that female, but not male rhesus macaques, pay attention to the presence of potentially disruptive bystanders.

Studies that report sneaky copulations in primates range from observations at a single field site (Kummer 1968, Soltis et al. 2001) to a large compilation of such anecdotal observations (Byrne and Whiten 1990), and some experimental data (Ruiz de Elvira and Herndon 1986, Gyax 1995, unpublished experiment mentioned in Kummer et al. 1996) Besides, audience effects, where the presence of particular individuals affects behaviour of group members, have been found in primate sexual behaviour. Female chimpanzees suppress their copulation calls when in proximity of high ranking females (Townsend et al. 2008). Similarly, female bonobos make their copulations calls less conspicuous when copulating with subordinate males (Clay et al. 2011). However, there are still crucial questions that remain unanswered. First, the conducted studies address effects by a number of dominants, not differentiating between the effects of specific individuals (e.g. the alpha male). Second, studies (cf. Ruiz de Elvira and Herndon 1986, Soltis et al. 2001) do not correct for time out of sight, and therefore cannot distinguish whether a decrease in time spent in sight of dominants or a decrease of sexual activity in view of dominants determines the observed decrease of copulations in view of dominants. Third, no studies investigated the separate contribution of males and females to initiate or accept sexual behaviour depending on the bystanders present.

The present study assesses whether certain males, in a socially living rhesus macaque group, inhibit sexual behaviour of group members. Rhesus macaques live in multi-male multi-female groups in which the alpha male fathers a large proportion of the offspring (19.4-30.0% Widdig et al. 2004). Nonetheless, rhesus macaques are seasonal breeders and when multiple females are in oestrus (some may be ovulating synchronously), high-ranking males cannot monopolize fertile females effectively (Altmann 1962, Massen et al. 2012). We examine whether the presence of higher-ranking males inhibits sexual behaviour of lower-ranking males. Additionally, we test whether males and / or females refrain from soliciting copulations depending on the bystanders present. These questions were studied with an observational set-up in a captive multi-male multi-female rhesus macaque group.

METHODS

Subjects

Observations were conducted on one group of 29 socially housed rhesus macaques in Rijswijk, the Netherlands. Seven adult females (>3.5 years Smuts et al. 1987) were included in this study (Table 1). Six males of the group were sexually active during the observation period (Table 1). Their ages ranged from three to 20 years. Rhesus macaque males are sexually mature from the age of 4.5 years (Smuts et al. 1987), but males can already fertilize females from at least the age of 3.4 years [calculated by subtracting the gestation length, 186 days (Wilson et al. 1988), from the lowest male age at infant birth, i.e. 3.8 years (Bercovitch et al. 2003)]. The group consisted of three unrelated matriline, which created the opportunity for all the subjects to have multiple unrelated sexual partners (Table 1). In addition, one copulation within a matriline was observed (Figure 2: in 1 out of 5 sibling dyads (hollo and monica); zero out of 5 mother-son dyads). Observations were performed from 19 October 2007 until 19 March 2008. Rhesus macaques have a marked mating season and copulations were only observed from 24 October 2007 until 22 February 2008. During the observation period a spontaneous rank reversal took place (on 21 December 2007), including a displacement of the alpha male. The alpha male showed signs of social defeat, i.e. he was completely passive and immobile for more than one day, behaviour that occasionally follows the loss of rank in alpha-individuals. If this state lasts for more than one day, individuals do not recover and

Monkey	Sexually active (potential partners ^a)	Age (years)	Rank in period 1	Rank in period 2
Females				
Burly	Yes (4/3)	9	1	1
Monica	Yes (4/3)	4.5	2	2
(Edwina ^{ab})	Yes (4/3)	2.5	3	3
Missie	Yes (2/2)	7.4	4	8
(Tinyc)	Only period 1 (2/2)	21.2	5	4
Fladder	Only period 1 (2/2)	6.6	6	5
Vlam	Only period 1 (2/2)	8.5	7	6
(Curly ^{c,d})	No (5/-)	20.5	8	10
(Fat ^{c,d})	No (5/-)	30.2	9	9
Isis	Yes (5/5)	7.2	10	11
Dragon	Yes (5/5)	3.4	11	7
Males				
Gibbon ^e	Yes (8/-)	20.3	1	-
Hollo	Yes (6/3)	3.4	2	4
Lewinsky	Yes (4/4)	4.4	3	1
Bush	Yes (4/4)	4.4	4	2
Sand	Yes (4/4)	3.4	5	3
Adam	Only period 2 (6/3)	3.3	6	5

Table 1: Females and males that were study subjects, their sexual activity, age at the start of the mating season, and relative dominance rank in period 1 and period 2. All females between brackets were excluded from the analysis; all males listed in the table were treated in the analysis both as bystander males and as males that were part of a copulating dyad.

^aNumber of potential partners during period 1/2 that were sexually active and nonkin (from another matriline).

^bToo young to reproduce.

^cMay be too old to reproduce.

^dDied during the second period.

^eDied before the second period.

are euthanized. Alpha 1 was the alpha male in period 1: from 24-10-2007 until 20-12-2007. Alpha 2 occupied the alpha position in period 2: from 02-01-2008 until 22-02-2008. Alpha 2 was already present during period 1 occupying dominance rank three. The data were analysed separately for the two periods. The total observation time for both periods was respectively 71.3 and 133.5 hours.

Housing Conditions and Experimental Cage

This study was performed making use of the normal housing conditions without hindering the animals' normal behaviour. Some adjustments were necessary to visually separate the inside (72 m² and 2.85m high) from the outside (260 m² and 3.1m high) enclosure (Figure 1). Two tunnels allowed the monkeys to walk freely between inside and outside enclosures, while visually separating both enclosures with non-see-through flexible plastic flaps. The inside and outside enclosures were further visually separated by blinding the windows in between, using frosted window foil. The inside enclosure consisted of three compartments separated by concrete walls with openings through which the monkeys could walk freely. To monitor two inside compartments with two video cameras; the third inside compartment was locked during the observations. The monkeys were fed monkey chow, complemented by fresh fruit, vegetables or bread on a daily basis. Water was provided ad libitum.

The cages were provided with sawdust and permanent environmental enrichment consisting of fire hoses, tires, ladders and a swimming pool. Extra enrichment containing food was provided at least every week (Vernes and Louwerse 2010). This research complied with protocols approved by the Animal Ethical Committee of the Biomedical Primate Research Centre and with the legal requirements of the Netherlands. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

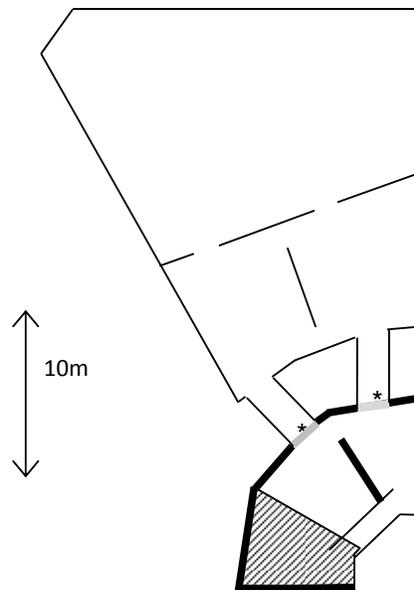


Figure 1: Schematic layout of the cage. Inside enclosures were surrounded by a concrete wall, indicated by bold lines, the outside enclosure by wire mesh, indicated by thin lines. Openings in the wall are indicated with a (*), these permitted monkeys to walk through but not see through as they were covered by plastic flaps. The striped area was an inside compartment only available to the monkeys outside observation hours.

Data Collection

Observations in the outside enclosure were conducted by one observer using Noldus The Observer 5.0 while two cameras (Sony, DCR-SR72) registered events in the inside enclosure. These videos were analysed by the same observer using Noldus The Observer XT 7.0. Data were collected twice a day in observation slots of 2 hours, the first observation slot was between 9:15 and 12:23 and the second between 13:21 and 16:24.

The presence of the focal animals in the inside or outside enclosure was recorded continuously during the outside observations. In addition, the presence of the alpha male in the inside enclosure was recorded during the analysis of the videos. During outside observations and video scoring all occurrences of sexual (Table 2) and dominance interactions were recorded with the main focus on sexual behaviour.

The dominance hierarchy of the group was determined during each of the two observation periods, on the basis of submissive signals, i.e. teeth-baring and unprovoked avoidance (to move away from a non-aggressive approaching animal). Teeth-baring is a good indicator of dominance rank (de Waal and Luttrell 1985), since it is a unidirectional submissive display in rhesus macaques and consistently reflects the relative status of adults independent of short-term contextual variation (van Hooff 1962, Maestripieri and Wallen 1997). Because teeth-baring alone did not yield sufficient data, unprovoked

Table 2. Sexual Behaviors of Rhesus Macaques (based on Altmann 1962, Manson 1996)

Copulation solicitations and reactions

Sexual presentation	- Female presents the hindquarters in the direction of a male
Lift female	- Male lifts a sitting female to standing position by pulling her upwards by her tail
Grasp waist	- Male places his hand on the rump of the female
Ignore female solicitation	- Male is not coming closer to nor trying to mount the female during the sexual presentation or within 10 sec after it stopped
Accept female solicitation	- Male mounts the female during or within 10 sec after a sexual
Ignore male solicitation	- Female remains seated while the male grasps waist, or she walks away from the male for more than an arm length, or she presents sexually to the male, but sits down again or walks away when the male tries to grasp the legs of the female with its hind legs
Accept male solicitation	- Female accepts that the male mounts her without one of the "ignore male solicitation" behaviors between the male solicitation and the mount

Copulation

Mount	- Male mounts the female by grasping her hind legs followed by one or more pelvic thrusts
Pelvic thrust	- Movement of the hips of the male while mounted
Copulation	- A series of more than one mount ^a . A copulation ends when the copulating dyad is more than an arm length away from each other for more than 5 min.

^aA criterion of more than one mount is taken to define a copulation, because single mounts often occur in a nonsexual context. Mount series outside the breeding season are generally single mounts between heterosexual or homosexual dyads and are less often accompanied by thrusting (Hanby and Brown 1974). Single mounts inside the breeding season seldom end in ejaculation (Manson 1996) (in the current study no ejaculatory pause was observed during a single mount).

avoidance behaviour between two individuals was added. From the resulting matrix, the dominance hierarchy was obtained (de Vries 1998) using Matman 1.1 (de Vries et al. 1993), and in both periods the dominance hierarchy was significantly linear (period 1: $h' = 0.40$, $P < 0.05$; period 2: $h' = 0.53$ $P < 0.001$) (de Vries 1995).

Data Analyses

The inhibiting effect of particular bystanders was studied on different aspects of sexual behaviour. We concentrated on the effect of male and not on female bystanders, since copulation disruption by female rhesus macaques is rarely reported (Dixson 1998 p.72, tabel 4.5) and less supported by theory (Niemeyer and Anderson 1983). First, the effect on copulations was determined. This was done for all possible bystander males, i.e. all males that were sexually active (Table 1). We predicted high ranking bystander males, but not low ranking bystander males, to have an inhibiting effect on the copulations of their group members (see above). However, we included lower ranking males in the analysis as bystander males, to get a complete picture which individuals did and did not have such an effect, and to investigate whether the monkeys leave the entire group or are sensitive to a particular bystander male in the audience. Second, the effect of the bystander male on the rates of female or male copulation solicitations was determined. Females solicit copulations with “sexual presentations”, while males solicit copulations both with “grasp waist” and “lift female” (Table 2). Third, copulation solicitations often preceded copulations, but could be rejected by the partner (Table 2). We tested whether females and males more often accepted copulation solicitations when a particular bystander male was out of sight than when he was in sight.

We calculated the rate of sexual behaviour in the presence and absence of a particular bystander male for both periods separately. With “present” we mean in the same enclosure as the copulating couple. Recall from the cage description that the two enclosures were visually separated from each other. Since the monkeys were able to move around freely, their time spent with a particular bystander male differed from their time without this particular bystander male. A simple comparison between the number of sexual behaviours with and without a high ranking bystander male could be biased by the fact that subordinate males spent less time close to higher ranking males. Therefore, we calculated, for both periods separately, the copulation rate for each female-male dyad across all time slots in which they were together in the same enclosure with the bystander male present $S(pr)$, and similarly across all time slots that they were together in the same enclosure, but in absence of the bystander male $S(ab)$. Subsequently, $S(ab)$ was subtracted from $S(pr)$ resulting in ΔS , which represents the size of the inhibiting effect by the presence of the bystander male. To analyze the inhibition of alpha males, we combined the data for both periods by calculating a mean ΔS for each female-male dyad. This larger dataset allowed us to carry out a general linear mixed model (GLMM) analysis with copulation rate as the dependent variable, presence of alpha male as fixed factor, and male and female identity as random factors. Subsequently, to disentangle the effect of both alpha males, we used a mean ΔS per female for each of the two periods separately and tested whether ΔS differed between the alpha present and absent condition using the paired t -test. A GLMM was not possible here because of the smaller dataset with incomputable degrees of freedom. Females, and not males, were chosen as

statistical units as we had more female than male subjects. The same procedure, using the *t*-test, was used for the effect of non-alpha males on copulation rates and for the effect of bystander males on female copulation solicitations and female acceptance of copulation solicitations. When studying the effect of bystander males on male copulation solicitation and male acceptance of copulation solicitations, males were used as statistical units. Since a few datasets significantly differed from a normal distribution (Shapiro-Wilk Normality Test, $\alpha \leq 0.05$, for small sample sizes of minimal $N=3$) and transformation of the data did not change this, we used the non-parametric equivalent Wilcoxon signed-rank test for these datasets. We executed two-tailed tests with $\alpha \leq 0.05$. Additionally, we mention trends with $P < 0.10$. All statistical tests were performed using the software package "R" (Ihaka and Gentleman 1996) version 2.7.1.

The analysis of the effect of the alpha males was based on more hours of observation than the analysis of the other males. For both alpha males, we simultaneously recorded events inside and outside and used both data sets for the analysis. The analysis of the other males was based only on the dataset we collected in the outside enclosures and thus approximately half as many observation hours, since recognition of individual males during entrance and departure was difficult from the videos recorded in the inside enclosure. Hence, the chance of finding an effect for non-alpha males was smaller than for alpha males.

RESULTS

Distribution of Copulations in the Group

During the first period, 34 copulations (31 involving non-alpha males), 103 female solicitations (94 involving non-alpha males), and 62 male solicitations (56 involving non-alpha males) were observed. During period 2, 90 copulations (52 involving non-alpha males), 268 female solicitations (217 involving non-alpha males), and 152 male solicitations (101 involving non-alpha males) were observed. Copulation rates were 0.88 and 0.67 copulations per observation hour in period 1 and 2 respectively. Alpha males showed aggressive interference of copulations in their view (alpha 1 interfered in 1 of 3 and alpha 2 in 4 of 8 copulations). Non-alpha males also interrupted copulations of their group members. In period 1 the 2nd ranking male interrupted 2 copulations and in period 2 the 3rd ranking male once interrupted a copulation. Also females interrupted copulations; the alpha-female and the 2nd ranking-female both interrupted copulations once in period 1. In period 2 the 1st, 2nd and 4th ranking females accomplished 9, 3 and 1 interruptions of copulations respectively. None of the other individuals interrupted copulations of group members. Aggression involved in interruptions was almost exclusively directed at an individual that was lower in rank than the aggressor, with one exception: the 2nd ranking female once directed her aggression toward the alpha male while he was copulating with the alpha female.

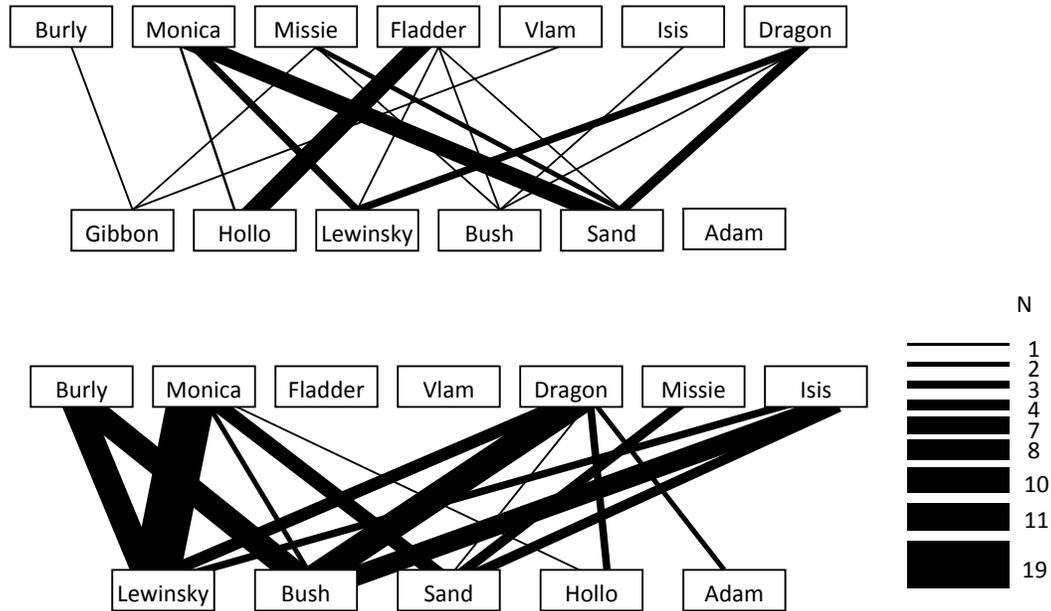


Figure 2. Distribution of copulations in the group in period 1 (top) and period 2 (bottom). The weight of the line corresponds with the number of copulations (N) within a particular copulating dyad. Females are listed at the top row of each scheme, males at the bottom. The names of the males and females are sorted from high (left) to low (right) dominance rank.

In general, males and females that copulated more than once during the mating season had more than one copulation partner (Figure 2). This was evident for both period 1 and 2 with the exception of the lowest ranking male (he only copulated twice, both times with the same female). The mean number of receptive females per day was $2.30 \pm \text{SD } 1.49$ in period 1 and $2.12 \pm \text{SD } 1.24$ in period 2. There were 7 instances (period 1 and 2 respectively 4 and 3 instances) of females copulating with two males on the same day. Females often behave receptively toward more than one male per day by sexually presenting toward, on average, $1.3 \pm \text{SD } 0.50$ males (period 1 and 2 respectively on average $1.28 \pm \text{SD } 0.50$ and $1.33 \pm \text{SD } 0.50$ males per day a female was sexually active). Alpha 1 was involved in nine percent (3 of 34) of the copulations in period 1. Alpha 2 was involved in 42 percent (38 of 90) of the copulations in period 2. Hence, alpha 2 monopolized a higher proportion of the copulations than alpha 1 (exact binomial test: $P < 0.001$).

High-ranking males had a significantly higher number of copulations than low ranking males in period 2, but not in period 1 (Spearman rank correlation: period 1: $r_s = -0.085$, $N = 6$, $P = 0.92$; period 2: $r_s = -1$, $N = 5$, $P < 0.05$). Female dominance rank was not related with the number of copulations (Spearman rank correlation: period 1: $r_s = -0.075$, $N = 7$, $P = 0.87$; period 2: $r_s = -0.16$, $N = 7$, $P = 0.73$).

The Effect of Bystander Males on Copulations

The presence of some bystander males may affect sexual behaviour of group members. The key result is that females copulate less often with non-alpha males in the presence

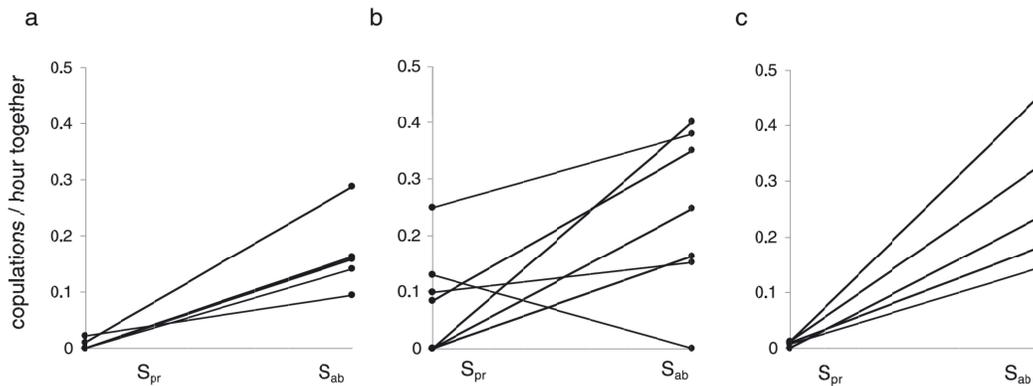


Fig. 3. The rate of copulations in situations with (S_{pr}) and without (S_{ab}) a particular bystander male's presence: (a) bystander male = alpha 1; (b) bystander male = third-ranking male in period 1; (c) bystander male = alpha 2. Each line in the figure represents a female; (a) $N = 5$, (b) $N = 7$, (c) $N = 5$.

than in the absence of an alpha male (GLMM: $F = 21.56$, $df = 1$, $P < 0.01$). In the first period, 28 of 31 copulations with non-alpha males occurred in absence of the alpha male. In the second period, 43 of 51 copulations occurred in absence of the alpha male. Per couple on average 0.23 and 0.73 copulations occurred in presence and 2.15 and 3.91 copulations in absence of alpha 1 and 2 respectively (Table 3).

During period 1, five females copulated with non-alpha males (the first and fifth ranking female exclusively copulated with the alpha male). Females copulated with non-alpha males significantly more often in the absence of than in the presence of alpha 1 (paired t -test: $T = 4.9$, $df = 4$, $P < 0.01$, Figure 3a). However, the alpha male was not the only male who inhibited copulations in period 1, since the presence of the third-ranking male also inhibited copulations of group members (paired t -test: $T = 2.6$, $df = 6$, $P < 0.05$, Figure 3b). Of the 28 copulations performed by other males than the third-ranking male, 17 were performed in his absence. Per dyad, on average 0.54 copulations were performed in presence of the third-ranking male and 1.31 copulations in his absence (table 3). Two males that were higher in rank than the third-ranking male copulated more often in his absence than in his presence although both males spent more time together with a female in presence than in absence of the third-ranking male. The alpha male was observed to copulate two out of three times in absence of the third-ranking male. The second ranking male copulated eight out of ten times in absence of the third-ranking male. None of the other bystander males in period 1 had a significant effect on copulations of females with other males during either of the two periods (paired t -test: $P > 0.195$).

During period 2, five females copulated with non-alpha males (the 3rd and 4th ranking females did not copulate). Also in this period, females started their copulations with non-alpha males significantly more often in the absence of than in presence of the alpha male (paired t -test: $T = 4.8$, $df = 4$, $P < 0.01$, Figure 3c). None of the non-alpha bystander males in period 2 had a significant effect on copulations of females with other males during either of the two periods (paired t -test: $P > 0.109$).

The Effect of Bystander Males on Copulation Solicitations

In period 1, females sexually presented significantly more often to non-alpha males when alpha 1 was absent than when he was present (paired *t*-test: $T = 3.2$, $df = 5$, $P < 0.05$, Figure 4a). However, in this period, the inhibition of female solicitation behaviour was not exclusive to the alpha male, since three out of five non-alpha bystander males significantly inhibited female copulation solicitations toward other males. These inhibiting males were the second (Paired *t*-test: $T = 2.8523$, $df = 5$, $P < 0.05$), the fourth (Wilcoxon signed-ranks test: $Z = 21$, $N = 6$, $P < 0.05$), and sixth ranking male (Wilcoxon signed-ranks test $Z = 26$, $N = 7$, $P < 0.05$). The third-ranking male had a trend of inhibiting female copulation solicitations (Paired *t*-test: $T = 2.5437$, $df = 5$, $P = 0.064$), and the fifth ranking male had no significant effect (Paired *t*-test: $T = 1.10$, $df = 5$, $P = 0.322$).

Similarly, in period 2 females solicited more often in the absence of than in the presence of alpha 2 (Wilcoxon signed-ranks test: $Z = 26$, $N = 7$, $P < 0.05$, Figure 4a). Additionally, the fifth ranking male had an inhibitory effect on the frequency of female solicitations in period 2 (Wilcoxon signed-ranks test: $Z = 21$, $N = 6$, $P < 0.05$). The remaining three males had no significant effect ($P > 0.136$).

Also for males we determined whether they changed their behaviour in the presence of a bystander male. In both periods non-alpha males tended to solicit copulations more often in presence than in absence of the alpha male (paired *t*-test: period 1: $T = 2.6$, $df = 3$, $P = 0.083$; period 2: $T = 2.7$, $df = 3$, $P = 0.074$) (Figure 4b). None of the non-alpha bystander males had a significant effect on the copulation solicitations of other males in both periods ($P > 0.119$).

Table 3: Mean (and range) of the number of copulations and time spent in presence and absence of each possible bystander male in both periods

Period 1				
rank	# copulations / couple		time spent (hours/couple)	
	presence	absence	presence	absence
1	0.23 (0-1)	2.15 (1-7)	31.3 (27.3-35.2)	12.7 (7.1-19.7)
2	0.53 (0-2)	0.93 (0-4)	5.0 (1.0 -10.4)	3.3 (0.9-7.6)
3	0.54 (0-4)	1.31 (0-5)	14.7 (11.9-17.2)	9.5 (7.3-15.8)
4	0.92 (0-5)	1.17 (0-4)	6.7 (1.9 -12.4)	3.7 (0.9-8.1)
5	0.81 (0-3)	0.82 (0-4)	5.5 (2.2 -9.7)	3.9 (0.6-7.9)
6	0.69 (0-2)	1.23 (0-5)	3.9 (2.6 -5.9)	3.2 (0.5-12.6)
Period 2				
rank	# copulations / couple		time spent (hours/couple)	
	presence	absence	presence	absence
1	0.73 (0-2)	3.91 (1-9)	86.5 (80.2-99.1)	17.2 (13.7-19.9)
2	0.40 (0-1)	2.60 (1-6)	4.1 (2.3-6.5)	5.0 (1.9-8.4)
3	1.20 (0-5)	2.90 (1-9)	3.7 (2.4-6.4)	5.6 (2.3-9.2)
4	1.08 (0-3)	3.00 (0-7)	3.2 (1.9-5.0)	6.1 (2.3-10.8)
5	0.93 (0-6)	2.93 (0-9)	3.4 (1.4-5.6)	5.8 (0.6-10.0)

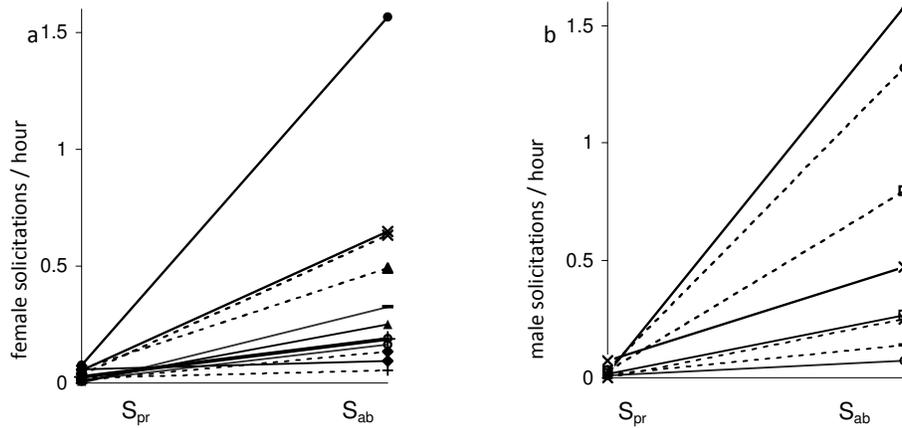


Figure 4: The rate of copulation solicitations by females (a) and subordinate males (b) in situations with (S_{pr}) and without (S_{ab}) the alpha male present. Solid lines represent period 1, while dotted lines represent period 2. Similar symbols are used for the same individual in both periods.

The Effect of Bystander Males on Acceptance of Copulation Solicitations

In period 1, six of seven females received copulation solicitations from non-alpha males. These females accepted solicitations from these males equally often in the absence of and in the presence of the alpha male (paired t -test: $T = -1.767$, $df = 5$, $P = 0.138$, Figure 5a). Also, none of the other bystander males in period 1 had an effect on females accepting copulation solicitations from males ($P > 0.604$).

In period 2, all seven females received copulation solicitations by non-alpha males. Females tended to accept solicitations more often in the absence of than in the presence of the alpha male (paired t test: $T = 2.6$, $df = 6$, $P = 0.073$, Figure 5a). None of the other males in period 2 had an effect on females accepting copulation solicitations from other males ($P > 0.578$).

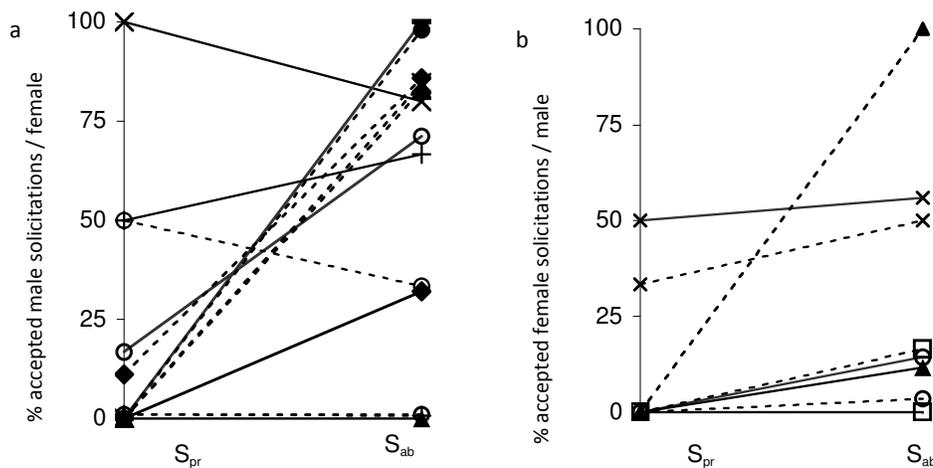


Figure 5: The proportion of copulation solicitations accepted by females (a) and males (b) in situations with (S_{pr}) and without (S_{ab}) the alpha male present. Solid lines represent period 1, while dotted lines represent period 2. Similar symbols are used for the same individual in both periods.

Also for males, we determined whether they adjusted their acceptance of female copulation solicitations to the presence of bystander males. Males tended to accept copulation solicitations from females more often in absence than in presence of alpha 1 (paired *t*-test: $T = 2.5$, $df = 3$, $P = 0.088$) and alpha 2 had no significant influence on the acceptance of copulation solicitations by males (Wilcoxon signed-ranks test: $Z = 10$, $N = 4$, $P = 0.125$) (Figure 5b). None of the non-alpha males had a significant inhibiting effect on male acceptance of female copulation solicitations in both periods ($P > 0.200$).

DISCUSSION

We investigated the mating pattern of female and male rhesus macaques, a primate species with a promiscuous mating pattern. Our results show that females and non-alpha males copulate at higher rates and show sexual solicitations and tend to accept these solicitations more often in the absence than in the presence of the alpha male. These audience effects may not be limited to the alpha males, but were also found in some non-alpha males.

Since females gain potential benefits from promiscuity and non-alpha males also aim to copulate, but the alpha male monopolizes females, females and non-alpha males may avoid copulating in presence of the alpha male. Such an inhibition of sexual behaviour by the mere presence of an individual can be categorized as an audience effect. In primates, audience effects have been shown in different contexts such as greeting (Laporte and Zuberbühler 2010), predator warning (Wich and Sterck 2003), mother infant interactions (Semple et al. 2009) and in sexual contexts (Townsend and Zuberbühler 2009). Adding to the literature on audience effects in sexual contexts, our results show that indeed female rhesus macaques copulate with non-alpha males more often when the alpha male is temporarily absent. This is in line with our prediction and agrees with previous findings (Ruiz de Elvira and Herndon 1986, Kummer et al. 1996). Since we, in contrast to Ruiz de Elvira and Herndon (1986), corrected the number of copulations in the presence and absence of the alpha male for the actual time each dyad spent in these conditions, our analysis precludes that effects like subordinates avoiding or being chased away by dominant individuals were responsible for the results, but shows that the rate of copulations was affected. However, whether the audience effect represents a shift of sexual behaviour resulting in a higher rate of sexual behaviour by females and subordinate males in the absence of the alpha-male, or represents a reduction of sexual behaviour because sexual behaviour by females and subordinate males is reduced in presence of the alpha male, remains unclear.

Our data suggest that the audience effect is not unique for the alpha male, since also non-alpha males had an inhibiting effect on the rate of sexual behaviour of their group members. In period 1 the third-ranking male had a significant inhibiting effect on copulations of group members. On the one hand, this result is tentative, as this male later became the alpha male, and thus his ascending trajectory may have caused his audience effect. On the other hand, three other non-alpha males that were not rising alpha males also inhibited female solicitations to males. Although the inhibiting males were not necessarily the highest-ranking males, which is not in line with our prediction, at least it is clear that some non-alpha males inhibit sexual behaviour of females.

Copulating out of view of non-alpha males may prevent interruption of copulations by males other than the alpha male (Chapais 1983, Ruiz de Elvira and Herndon 1986, Berard et al. 1994, Manson 1996, Overduin-de Vries et al. 2012). What's more, the third-ranking male also inhibited copulations of even higher-ranking males, including the alpha male. Although this seems counterintuitive, because alpha males often consort females and chase away other males (de Ruiter and van Hooff 1993, Berard et al. 1994, Alberts et al. 2006), also the sexual behaviour of the alpha male can be interrupted by other males (Ruiz de Elvira and Herndon 1986). Despite alpha male consorts, rhesus macaque alpha males are in some groups not the most frequent copulating males (this study) or not even responsible for most of successful copulations (Duvall et al. 1976). Therefore, it may be as important for an alpha male as for other males to reduce interruptions of copulations. Nevertheless, since alpha males are able to consort females during their fertile phase, it may be less relevant for them if they have a few copulations disrupted. Notwithstanding, even for alpha males, preventing disruptions reduces energy loss due to unsuccessful copulations and aggression based injuries. Thus, future research should consider a possible audience effect of non-alpha males on all other individuals in the group, including an effect on higher-ranking males.

In contrast with previous research which rarely reports copulation disruption by female rhesus macaques (Dixon 1998 p.72, tabel4.5), our study revealed that females were responsible for more disruptions of copulations than males. This contrast may be due to the dominance position of our alpha female, which was higher than the alpha male in period 2. However, this does not explain why two other females displayed a considerable amount of disruptions. Therefore, it would be worthwhile to study an audience effect of females on rhesus macaque sexual behaviour.

Male and Female Coordinated Responses to the Audience

Potentially, both subordinate males and females involved in a copulation may benefit from hiding the copulation. However, when copulations of subordinate rhesus macaque males with females are disrupted, it is mostly the female that experiences the brunt of the aggression (Ruiz de Elvira and Herndon 1986, Manson 1996). Therefore, mainly females are expected to benefit from hiding their copulations with subordinate males. In contrast, male rhesus macaques that are disrupted during copulations do not have reduced fitness compared to undisrupted males (Berard et al. 1994). Thus based on the literature, it is predicted that females, but not males, adjust their behaviour to the presence of an audience. Indeed, when ignoring the trends, females, but not males, more often solicit and accept solicitations to copulate in the absence than in the presence of bystander males. However, when trends are considered meaningful, males were found to solicit and accept more solicitations in absence than in presence of the alpha male in both periods. Therefore, the absence of a significant audience effect on male sexual behaviour may be due to our low number of males, and consequently the low statistical power, rather than the absence of an effect. This suggests a benefit of hiding sexual behaviour for both partners involved in a copulation. Alternatively, females may benefit, while males have an indirect benefit when females are more willing to copulate in occluded conditions and this may result in a male sensitivity to the audience.

Audience effects on sexual behaviour are expected when alpha males cannot well monopolize females and females have the option to mate promiscuously (see introduction). Therefore, audience effects will co-occur with indicators of female promiscuity such as seasonal breeding, which complicates monopolization for the alpha male (Emlen and Oring 1977), exaggerated swellings, which increase the duration of sexual activity (Nunn 1999), and extended female receptive periods, which obscure female fertility (Heistermann et al. 2001). Moreover, for an audience effect, a clear dominance hierarchy and disruptions of copulations may be required. Indeed, rhesus macaques have all these characteristics (promiscuity (Small 1990); a clear dominance hierarchy (Miller and Murphy 1956) and disruptions of copulations (Ruiz de Elvira and Herndon 1986, Manson 1996)) and exhibit audience effects (this study). Similarly, chimpanzees also largely fit these characteristics (promiscuity (Hasegawa and Hiraiwa-Hasegawa 1990); clear female dominance hierarchy (Wittig and Boesch 2003) and disruption of copulations (Tutin 1979)) and show audience effects (Townsend and Zuberbühler 2009). However, whether audience effects depend on one or on a particular combination of features remains to be studied.

In conclusion, several audience effects on sexual behaviour of rhesus macaques were found. First, the rate of sexual behaviour of female and subordinate male rhesus macaques is higher in the absence of than in the presence of the alpha male. Second, also the presence of some non-alpha bystander males reduced the rate of sexual behaviour. Third, one non-alpha bystander male had an audience effect on higher-ranking males's sexual behaviour including the alpha male. Furthermore, females altered their sexual behaviour in response to an audience effect, while for males it is less certain. This indicates that females, but possibly not males, benefit from hiding their copulations. Altogether, monopolization by the alpha male may be opposed by a relatively high rate of sexual behaviour from females with subordinate males in his absence, but also by a relatively low rate of sexual behaviour by females with the alpha male in the presence of some non-alpha males.

ACKNOWLEDGEMENTS

We are grateful to all animal caretakers of BPRC for their daily help with the animals and adjustments of the cages. Statistical advice from Han de Vries improved our analysis. We benefited from helpful discussions with Annet Louwerse to adjust the design to the home cages and behaviour of the animals. We thank Benjamin Wilson for proof reading our manuscript and five anonymous referees whose comments improved our manuscript.

6

Sneak copulations in long-tailed macaques (*Macaca fascicularis*): no evidence for tactical deception

A.M. Overduin - de Vries, C. U. Olesen, H. de Vries, B.M. Spruijt, E.H.M. Sterck

Sexual competition is highly prevalent within multi-male multi-female primate groups and may lead to copulations in absence of potentially interfering bystanders. Such avoidance of bystanders may result from tactical deception or from simpler mechanisms such as taking advantage of encountered situations without bystanders, operant conditioning or a peripheral positioning of non-alpha males. We investigated which individuals are avoided as bystanders, how individuals react to the presence of bystanders and whether copulation partners separate themselves from the group in a tactical way. Our observations of a group of 15 female and seven male long-tailed macaques housed in three interconnected, but visually separated compartments, revealed that both males and females can interrupt sexual behaviour and that bystanders of both sexes were avoided during copulations (n=256). The strength of the effect of bystanders tended to decrease with the dominance rank of male bystanders, but did not depend on the dominance rank of female bystanders. The audience effects of non-alpha individuals did not depend on the strong audience effect of the alpha male in combination with proximity with the alpha male. The effects that we found for separate bystanders suggest that sexual competition concerns rank dependent male-male competition and rank independent female-female competition. Additionally, both male and female copulation partners paid attention to the presence of bystanders and conducted fewer copulation solicitations in their presence. The timing of a male and female's separation from the group suggests that exploitation of the peripheral position of non-alpha males, and not tactical deception, may cause these audience effects.

Published in: 2013; *Behavioral Ecology and Sociobiology* **76**: 101-111.

INTRODUCTION

Many animal species live in multi-male multi-female groups. Within these groups, high ranking males typically have priority of access to fertile females (Altmann 1962), which is reflected by a correlation between mating success and male rank in many animal groups (for review: Cowlshaw and Dunbar 1991; for different species e.g.: *Macaca* species: de Ruiter and van Hooff 1993, Paul et al. 1993, Garcia et al. 2009, Massen et al. 2012; *Marmota flaviventris*: Huang et al. 2011; *Capra ibex*: Willisich et al. 2012), but not all (e.g. *M. fascicularis*: de Ruiter et al. 1992, *Porphyrio porphyrio melanotus*: Lambert et al. 1994, *Crocota crocota*: Engh et al. 2002). Subordinate males and females do not necessarily benefit from increased mating success of dominant males and use several alternative reproductive tactics (Berard et al. 1994, Soltis et al. 2001, Alfaro 2005) to increase the reproductive success of subordinate males and enhance female promiscuity. One of these tactics resulting from sexual competition is sneak copulation, involving sexual behaviour in absence of competitors. Sneak copulations have been reported in multiple animal species, including birds (Davies 2000), seals (de Bruyn et al. 2011) and ungulates (Hogg 1987, Willisich and Neuhaus 2009). Studies in primates that report sneak copulations range from observations at a single field site (Kummer 1968, Soltis et al. 2001) to a large compilation of these anecdotal observations (Byrne and Whiten 1990), and experimental data (Ruiz de Elvira and Herndon 1986, Gyax 1995, Kummer et al. 1996, Overduin-de Vries et al. 2012).

Non-human primates are our closest animal relatives and are proposed to share some complex cognitive capacities with humans, including tactical deception (Byrne and Whiten 1992). Sneak copulations in primates may be an example of tactical deception (Byrne and Whiten 1992), yet it is not known which cognitive mechanisms actually lead to the hiding of sexual behaviour. The reported hiding behaviours (Ruiz de Elvira and Herndon 1986, Byrne and Whiten 1990, Gyax 1995, Overduin-de Vries et al. 2012) may have resulted from four cognitively distinct mechanisms. Tactical deception is the cognitively most complex mechanism and comprises active avoidance of a particular competitor (Byrne and Whiten 1992). Second, sneak copulations may result from passively taking advantage of an encountered situation where the competitor is absent (Byrne and Whiten 1992). Third, operant conditioning, an even less advanced cognitive process, may result in inhibition of sexual behaviour near former punishing individuals. Last, subordinate males often reside in the periphery of the group (*Cebus apella*: Janson 1990, *M. fuscata*: Hayakawa 2007), and when females approach these males, copulations automatically take place at locations distant from the often centrally positioned alpha male. This mechanism is simpler than the former strategy as it does not require recognition of the absence of potentially punishing individuals. Above all, in order to label sneak copulation an example of tactical deception, evidence is needed that “the hiding is tactical and not simply an opportunistic response to being left alone by chance” (Byrne and Whiten 1992, p.613) or the consequence of simple conditioning or general positioning of non-alpha males.

To investigate the cognitive mechanisms underlying sneak copulations, it is necessary to determine which individuals are avoided as bystanders during copulations and on which grounds. Regardless of the cognitive mechanism underlying sneak copulation, an important benefit of hiding sexual behaviour is avoidance of harassment,

raising the focus on harassers. Harassment of copulations is a tactic that is often used by high ranking males to reduce mating success of their group members for the benefit of their own mating success (Dixson 1998 p.72, tabel 4.5),. Whether male harassment results in interference of the copulation before an ejaculation can occur depends on the relative ranks of the males involved (Niemeyer and Chamove 1983) and is more often used by high-ranking than by low-ranking males (Chapais 1983). Moreover, although less frequently reported than harassment by males, females may also harass copulations of group members (Niemeyer and Chamove 1983). Yet, harassment by females only rarely results in actual termination of copulation, and ejaculation generally still occurs (Niemeyer and Anderson 1983). The function of female harassment is more ambiguous than male harassment and less investigated. Harassment by females may function to test male mating quality (Niemeyer and Chamove 1983), to limit future competition over resources by reducing the number of births in the group (Niemeyer and Anderson 1983), and to reduce competition for access to benefits given by male copulation partners, such as agonistic support (Buchan et al. 2003). Female harassment may be rank dependent, since the alpha female is often the most frequent harasser (*Macaca arctoides*: Gouzoules 1974, *M. mulatta*: Wilson 1981). To sum up, based on the reported observations of interfering behaviours, it is expected that high-ranking males and females are avoided as bystanders during sexual behaviour.

Although some empirical studies confirm the avoidance of potential harassers (Ruiz de Elvira and Herndon 1986, Soltis et al. 2001), the effect of specific individuals is usually not determined, since most studies examined the combined effect of multiple individuals on hiding copulations and did not discriminate which individuals did and which did not influence the occurrence of copulations. Although in a previous study we found that in rhesus macaques the presence of the alpha male and some other high-ranking males individually inhibited copulations of their group members (Overduin-de Vries et al. 2012), it is not clear whether females have the same effect. Moreover, while we found that females reduce their sexual behaviour in the presence of a potential harasser (Overduin-de Vries et al. 2012), it is not clear whether males do the same.

Another central question when studying the cognitive mechanisms underlying sneak copulation is whether the male, the female or both partners involved in the copulation are paying attention to bystanders. Because of the costs associated with interferences, both males and females may be motivated to hide their copulations from potentially interfering bystanders. Disruption of copulations may have consequences for the reproductive success of lower ranking males. In *Macaca arctoides*, interruption of copulations results in a significant shortening of the pair-sit behaviour (Bruce and Estep 1992), which impedes positioning of the copulatory plug, and increases susceptibility to sperm competition (Dixson and Anderson 2002). Additionally, males may experience injury or energy loss from female harassment, since female harassment is mostly directed at the male (*M. mulatta*: Wilson 1981). Likewise, females risk injury from interferences since they are often the target of aggression after interferences by males (e.g. *M. mulatta*: Ruiz de Elvira and Herndon 1986, Manson 1996). Thus, both male and female copulation partners are expected to pay attention to the presence of these bystanders and to act accordingly.

This study was designed to investigate (1) which individuals in a social long-tailed macaque group inhibit sexual behaviour of their group members and whether this

inhibition is linked with the bystander's interference behaviour, sex, rank or proximity to the alpha male; (2) whether both males and females separately adjust their rate of copulation solicitations to the presence of potentially harassing bystanders; (3) whether sneak copulations result from peripheral positions of subordinate males; and (4) whether the individuals involved in a sneak copulation separate themselves from the rest of the group in a tactical way: i.e. whether the first individual's separation from the group is shortly followed by the second individual.

METHODS

Subjects

Observations were conducted on one group of 27 socially housed long-tailed macaques (the 'lixa group') at the Biomedical Primate Research Centre in Rijswijk, the Netherlands, formerly housed at the 'Ethology station', Utrecht University. Long-tailed macaques of this colony are non-seasonal breeders, consistent with other captive long-tailed macaque colonies (Honjo et al. 1978), but different from most wild populations (Kavanagh and Laursen 1984). Long-tailed macaques often live in multi-male multi-female groups of six to 58 individuals (van Schaik and van Noordwijk 1985) where alpha males try to monopolize fertile females and father the majority of infants (de Ruiter and van Hooff 1993, Engelhardt 2004), but females are promiscuous and actively approach non-alpha males to copulate (Nikitopoulos et al. 2005). Females copulate with more than one male during their fertile phase (Engelhardt 2004) and copulate outside ovarian cycles in order to confuse paternity (Engelhardt et al. 2007).

Fifteen (> 3.5 years) females and seven (>6.5 years) males were included in this study (Table 1). The remaining five monkeys in the group were under the age of 1 year and therefore sexually immature. In total eight females were pregnant or lactating during our observations (Table 1). Eight of the females had been given contraceptives (implanon

Table 1: Table 1 Study subjects. Information of subjects name, rank and age (in years). Additionally, for females their reproductive status and presence of hormonal implant is provided, while for males their origin (natal or non-natal) is provided.

Females	Rank	Age	Reproductive status	Hormonal implant
voila	1	11.5	Pregnant	No
silva	2	7.3	Lactating	No
fossa	3	3.5	Pregnant	No
sepia	4	12.0		Yes
riva	5	8.0		No
virginia	6	15.9	Lactating	Yes
tremaa	7	11.7	Lactating	Yes
foetsie-ba	8	11.0		Yes
mokka	9	8.2	Lactating	No
baklava	10	10.1	Lactating	Yes
goa	11	15.1		Yes
taiga	12	10.1		Yes
yukka	13	15.9		No
kaa	14	24.1		Yes
karamba	15	12.3	Pregnant	No
Males	Rank	Age	Natal?	
nacho	1	13.5	No	
bolero	2	13.6	No	
potato	3	26.6	Yes	
pesto	4	6.8	Yes	
rokoko	5	6.5	Yes	
voodoo	6	7.11	No	
bamboo	7	15.1	No	

implants; generic name: Etonogestrel). Since four of the males were non-natal and the group consisted of three unrelated matriline, all subjects had the option to show sexual behaviour with multiple unrelated sexual partners (mean \pm SD = 6.5 ± 0.5 (for female subjects), and 13.9 ± 1.6 (for male subjects)).

Housing

Three visually separated compartments were used during the observations. Two inside enclosures measured together 72 m^2 , 3m high, while an outside enclosure measured 209 m^2 , 3m high. Some adjustments (c.f. Overduin-de Vries et al. 2012) ensured the visual separation of the inside and the outside enclosure (Fig. 1). Two inside compartments were visually separated from each other by a concrete wall, the third inside compartment was locked and not available to the monkeys during the observations. Monkeys were able to walk freely between these compartments through tunnels and openings in the walls.

This study was performed making use of the normal housing conditions without hindering the animals' normal behaviour. The monkeys were fed monkey chow, complemented by fresh fruit, vegetables or bread on a daily basis. Water was provided ad libitum. The inside enclosure had a sawdust bedding and environmental enrichment, consisting of fire hoses, tires, ladders and an outside swimming pool was permanently available. Extra enrichment containing food was provided every other week (Vernes and Louwse 2010). This research complied with protocols approved by the Animal Ethical Committee of the Biomedical Primate Research Centre and with the legal requirements of the Netherlands.

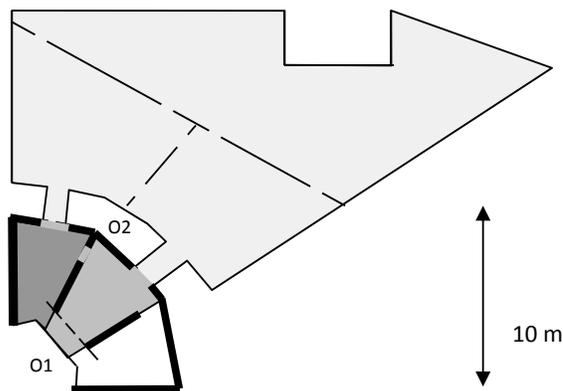


Figure 1: Schematic layout of the cage. Enclosures were surrounded by a concrete wall, indicated by bold lines, and wire mesh, indicated by thin lines. Openings in the wall are indicated with an asterisk; these permitted monkeys to walk through, but not see through as they were covered by opaque plastic flaps. This way, three visually separated compartments were created indicated by different shadings. Blank areas were not used by the monkeys during observation slots. O1 and O2 represent the positions of observers.

Observations

Observations were performed from 9 November 2009 until 19 March 2010 in two-hour slots (total observation time = 106 hours). Observations were balanced between morning and afternoon sessions. Two observers simultaneously recorded the presence of the focal animals in the two inside and one outside enclosure using The Observer 5.0 (Noldus 1991). The two observers communicated between inside and outside enclosures through walkie-talkies to validate the identity of individuals moving between compartments. A bystander was designated 'present' if the bystander was in the same enclosure as the dyad involved in a sexual interaction. All

occurrences of sexual and dominance interactions were recorded with the main focus on sexual behaviour (c.f. Overduin-de Vries et al. 2012). The recorded sexual behaviours included: copulation solicitations: sexual presentation (females), lift female and grasp waist (males); copulations: mount with thrusting; and other sexual behaviours: inspect, touching genitals (Angst 1974). In addition, interferences in sexual interactions were recorded. Interference was defined as an aggressive behaviour towards one or both partners involved in a sexual interaction, but it did not necessarily lead to interruption of the sexual interaction. A female was considered proceptive on a given day if she sexually presented at least once. The dominance hierarchy of the group was determined on the basis of submissive behaviours (teeth baring and unprovoked avoidance). From the resulting matrix, the dominance hierarchy including all adult individuals was obtained (de Vries 1998) using Matman 1.1 (de Vries et al. 1993), and the dominance hierarchy was significantly linear ($h' = 0.55$, $p < 0.0001$) (de Vries 1995). Subsequently, the males and females were ranked within each sex with the most dominant animal assigned rank one.

Data Analysis

We determined the inhibiting effect of bystanders on copulations and on copulation solicitations. Each adult individual (male and female) was treated as bystander. First, the effect of each bystander's presence on copulation rate was determined. Second, the effect of each bystander on the rates of female or male copulation solicitations was determined.

We calculated the rate of sexual behaviour (c.f. Overduin-de Vries et al. 2012), i.e. for copulations or for solicitations, in the presence and absence of a particular bystander using the Observer XT 7.0 (Noldus 1991). Since the monkeys were able to move around freely, their time spent with a particular bystander differed from their time without this particular bystander. A simple comparison between the number of sexual behaviours with and without a high ranking bystander male can be biased by the fact that subordinate males avoid the presence of high ranking males also during non-sexual behaviour. Therefore, we calculated the rate of sexual behaviours per hour for each female-male dyad across the summed time in which they were together in the same enclosure with the bystander present $S(pr)$, and similarly across the summed time that they were together in the same enclosure, but in absence of the bystander $S(ab)$. In order to correct for the variation between dyads, for each dyad these rates were centred around zero by subtracting for each dyad the mean of $S(ab)$ and $S(pr)$ from $S(ab)$ and $S(pr)$.

Finally, we analysed whether males and females coordinate their movements preceding a sexual event to avoid the alpha male, the individual that is expected to have the strongest audience effect. For each dyad that was observed to engage in sexual behaviour in the outside compartment, the intervals (in seconds) between the male and female going outside, from now on called 'latencies', were compared between episodes with and without a sexual event following their movement from the inside to the outside compartment when the alpha male was inside, further termed 'movement outside'. Only movements outside were taken into account, because we had the impression that the majority of the group was most of the time inside and that individuals went outside to

Sneaky mating in long-tailed macaques

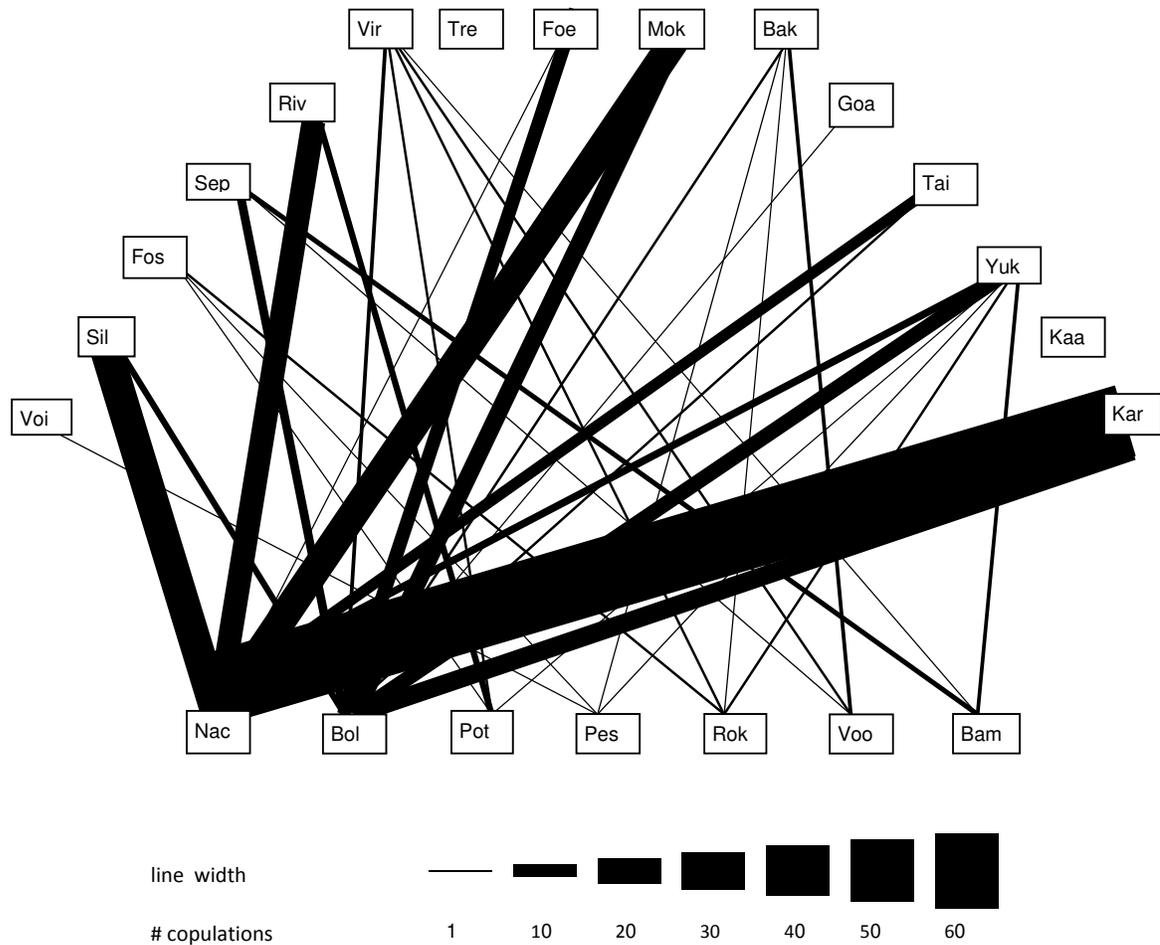


Figure 2: Distribution of copulations in the group, males on the bottom line and females in the arch are ordered according to dominance rank from high to low ranking from left to right. The width of the lines between individuals indicates the number of copulations observed for each dyad

separate themselves from the group. Latencies were calculated in two conditions: with and without sexual behaviour in the outside compartment by the male-female dyad. For each dyad these latencies were centred around zero by subtracting the mean latency of dyad d from dyad d 's latencies in both conditions.

Permutation tests were conducted (1) to investigate whether sexual behaviour was more often observed in the absence than in the presence of a bystander and (2) to investigate whether latencies were shorter before a sexual event than before a non-sexual event. To control for variation between dyads, permutations were conducted within dyads; that is, for each dyad the observations were put in a random order, thus, assigning each observation randomly to one of the two conditions. Permutation tests included 10000 sets of random permutations, under the null hypothesis that all observed copulation/ solicitation rates, or latencies were randomly distributed over both conditions; with or without audience (for sexual behaviour rates) or with or without sexual behaviour (for latencies). This created a null distribution of the mean difference between two conditions (from now on called "Mean Randomly obtained Difference": MRD), The proportion of times that the MRD was greater than or equal to the absolute

Mean Observed Difference (MOD) yields the right-tailed p -value P_r . This value was multiplied by two to obtain the 2-tailed p -value. The MOD, representing the observed difference between copulation rates or solicitation rates in and out of view of the bystander, is an indicator of the strength of the audience effect of a particular bystander.

In order to disentangle the effects of certain characteristics of bystander individuals on the strength of the audience effect, we ran linear models (LM), with as dependent factor the MOD and as independent factors the bystander's dominance rank, proximity to the alpha male, and proceptivity. Proximity to the alpha male was calculated by summing the number of hours spent in the same compartment as the alpha male. To diagnose the presence of multicollinearity we calculated the variance inflation factor for each of the predictors. These VIFs varied between 1.17 and 1.35, which are well below 5, and thus do not indicate serious multicollinearity. Inspection of the residuals showed that these were homogeneously distributed across the different predictor values and they did not deviate significantly from normality (Kolmogorov-Smirnoff test: p between 0.58 and 0.99)

All statistical tests were two-tailed with α set at 0.05. All tests were done using the software package "R" (R Development Core Team, 2009) Version 2.10 The "lm" function for linear models was used from the "stats" package, while the "sample" function for permutations was used from the "base" package. The sharper Bonferroni procedure for multiple testing (Hochberg 1988) was applied to test the audience effects of multiple males and females, with the family-wise error rate set at 0.05. Additionally, for single tests we report trends with p between 0.05 and 0.10.

RESULTS

Copulation, copulation solicitation and interference behaviour

Out of the 256 observed copulations, 126 involved non-alpha males. Male copulation solicitations ($N = 488$) involved non-alpha males 367 times. Female solicitations ($N = 222$) were directed towards non-alpha males 92 times. In general, males and females that copulated more than once during the mating season had more than one copulation partner (Fig. 2). There were two females that only copulated once. The mean number of proceptive females per day was $2.57 \pm \text{SD } 1.54$ (range: 1-6). There were 22 observed instances of a female copulating with more than one male on the same day. These instances included seven different females and fifteen of these instances included copulations with the alpha male. On a day a female was proceptive, she occasionally behaved proceptively toward more than one male, by sexually presenting toward, on average, $1.13 \pm \text{SD } 0.36$ (range: 1-3) males.

The number of copulations was significantly correlated with male dominance rank (Spearman rank correlation: $\rho = -0.857$, $N = 7$, $p = 0.024$). Female dominance rank was not related with the number of copulations (Spearman rank correlation: $\rho = 0.102$, $N = 15$, $p = 0.72$). There was no significant difference in the number of copulations between pregnant or lactating females and other females (Mann-Whitney test: $U = 18.5$, $N = 7, 8$, $p = 0.29$). Likewise, there was no significant difference in the number of days a female was proceptive between the group of lactating and pregnant females and other females (Mann-Whitney test: $U = 35$, $N = 7, 8$, $p = 0.45$). Females with hormonal implants

copulated significantly less often (Mann-Whitney test: $U = 45.5$, $N = 7, 8$, $p = 0.049$) and were proceptive on fewer observation days (Mann-Whitney test: $U = 49.5$, $N = 7, 8$, $p = 0.014$) than females without implants. Because in subsequent pair-wise comparisons investigating bystander effects, females were their own control, existing differences in sexual behaviours between the different reproductive stages are automatically controlled for.

In total, 8 sexual interactions ($N > 710$) of which 4 involved copulation ($N = 256$) were interfered. The alpha male showed four cases of aggressive interference in sexual interactions, while 8 out of 10 copulations in his view were not interfered. Non-alpha males, namely both the 2nd ranking and 3th ranking male, also interfered sexual interactions of group members. Also females interfered in sexual interactions; the 9th and 15th ranking-female both once interfered in a sexual interaction. None of the other individuals was observed to interfere sexual interactions of group members. The alpha male directed his aggression during interferences towards either the male (2 times), or both partners (2 times) involved in the sexual interaction. The two interferences by non-alpha males concerned aggression to both copulating partners, whilst interferences by females both times were directed towards the female. Aggression involved in interferences was almost exclusively directed at an individual that was lower in rank than the aggressor, with one exception: the 15th ranking female once directed her aggression toward the 9th ranking female that was copulating with the 2nd ranking male. On four occasions the harasser (one female, three times the alpha male) copulated with the interfered opposite-sexed individual afterwards.

Bystander effects on copulations

The presence of a particular bystander male may affect sexual behaviour of group members. The key result is that dyads of females and non-alpha males copulated significantly less often in the presence than in the absence of the alpha male (Table 2). The majority of the copulations (116/126) with non-alpha males occurred in absence of the alpha male. Each non-alpha male copulated on average $19.33 \pm \text{SD } 28.8$ times in absence and $1.67 \pm \text{SD } 3.2$ times in presence of the alpha male.

Although the alpha male had the strongest audience effect (with the highest MOD), he was not the only male that inhibited copulations, since the presence of the second, fourth, fifth and sixth ranking male also significantly inhibited copulations of group members (Table 2). The MOD of copulation rates of non-alpha males was neither dependent on rank nor on the bystander's proximity to the alpha male (Table 3). However, in this model, the alpha male was excluded, because his own proximity to himself is not a meaningful measurement. When including the alpha male to the model and eliminating the non-significant factor "proximity to the alpha male" we increase our limited sample size and improve our model. In this model, rank does significantly affect the audience effect strength (Table 4, Fig. 3a)

Out of the 15 females in the group, nine had a significant audience effect on the copulations of their group members (Table 2). The MOD was not dependent on the rank of the bystander female (Fig. 3b), or with proceptivity of bystander females, or with the bystander's proximity to the alpha male (Table 5).

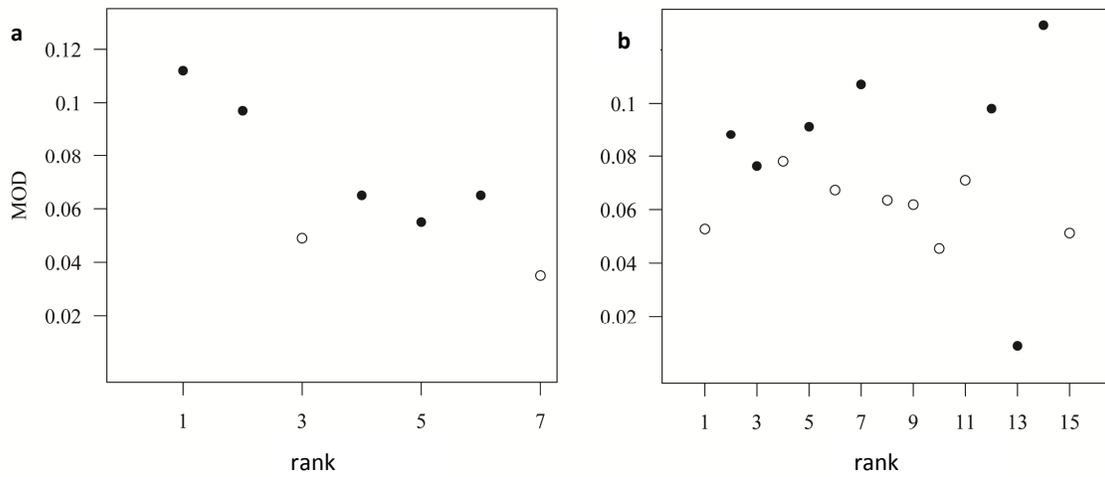


Figure 3: The audience effect strength (MOD) in copulation rates between absence and presence of (a) a particular bystander male or (b) a particular bystander female. Bystanders are represented on the x-axis by their dominance rank number from 1 (highest ranking) to 7 or 15 (lowest ranking). Filled dots represent data points from bystanders with significant audience effects, open dots represent bystanders without significant audience effects

Table 3 Results from the linear model with as dependent variable the audience effect strength of bystander males (mod) and as independent factors the dominance rank of the bystander male and its proximity to the alpha male

	coefficient	SE	T	P
intercept	0.08	0.07	1.27	0.29
dominance rank	-0.008	0.005	-1.61	0.21
proximity to alpha male	0.0003	0.002	0.18	0.87

Table 4 Results from the linear model with as dependent variable the audience effect strength of bystander males (mod) and as independent factor the dominance rank of the bystander male

	coefficient	SE	T	P
intercept	0.11	0.01	7.67	< 0.001
dominance rank	-0.01	0.003	-3.22	0.023

Table 5: Results from the linear model with as dependent variable the audience effect strength of bystander females (mod) and as independent factors proceptivity and dominance rank of the bystander female and its proximity to the alpha male

	coefficient	SE	T	P
intercept	0.11	0.19	0.57	0.58
dominance rank	2.8×10^{-5}	1.9×10^{-3}	0.02	0.99
proceptivity	-1.6×10^{-3}	1.1×10^{-3}	-1.48	0.17
proximity to alpha male	-4.4×10^{-4}	3.8×10^{-3}	-0.12	0.91

Bystander effects on copulation solicitations

Non-alpha males invited copulations significantly more often in the absence than in the presence of the alpha male (Table 2). Additionally, the 2nd and 7th ranking male significantly inhibited male copulation solicitations within their view (Table 2). Moreover, all but three (rank 8, 13 and 15) females had a significant audience effect on male copulation solicitations (Table 2).

Females sexually presented significantly more often to non-alpha males when the alpha male was absent than when he was present (Table 2). None of the other males significantly influenced female solicitation behaviour (Table 2). Additionally, 9 out of 15 females significantly inhibited female copulation solicitations of other females (Table 2).

Peripheral positioning

Subjects spent more time in the two inside ($90.9 \pm \text{SD } 11.5$ hours) than outside compartments ($17.6 \pm \text{SD } 11.5$ hours) (Wilcoxon signed rank test: $V = 0$, $N = 22$, $p < 0.001$). The monkeys spent an equal amount of time in either of the two inside compartments (Wilcoxon signed rank test: $V = 170$, $N = 22$, $p = 0.17$). Males tended to spend more time outside ($26.5 \pm \text{SD } 16.3$ hours) than females ($12.8 \pm \text{SD } 4.9$ hours) (Mann-Whitney test: $U = 26$, $N = 7, 15$, $p = 0.066$). Males spend fewer hours in proximity to the alpha male (mean = $39.7 \pm \text{SD } 5.2$) than females (mean = $49.1 \pm \text{SD } 2.3$) (Mann-Whitney test: $U = 1$, $N = 6, 15$, $p < 0.001$). Whereas the alpha male had a higher copulation rate inside (1.6 copulations/hour) than outside (0.48 copulations/hour), non-alpha males tended to have higher copulation rates outside ($0.39 \pm \text{SD } 0.67$ copulations/hour) than inside ($0.15 \pm \text{SD } 0.25$ copulations/hour) (Wilcoxon signed rank test: $V = 19$, $N = 6$, $p = 0.094$).

Separation from the group

In episodes with a sexual interaction outside, the latency (the intervals between the male and female of a dyad going outside) was on average $379 \pm \text{SD } 550$ seconds, compared to $559 \pm \text{SD } 804$ seconds when no sexual interaction occurred outside (Fig. 4). Although the average latency in episodes with sexual behaviour was shorter than in episodes without sexual behaviour, the difference was not significant (permutation test: $p = 0.15$). In episodes without sexual behaviour, males were significantly more often the first of the dyad to appear outside (exact binomial test: male first = 1130/1667, $p < 0.0001$). In the episodes where a sexual behaviour occurred outside, males tended to be the first of the dyad to be outside (exact binomial test: male first = 58/97, $p = 0.07$). There was no significant difference in the proportion of times that the male was outside first between episodes with and without sexual behaviour (Fisher's exact test: $N = 1761$, $p = 0.12$).

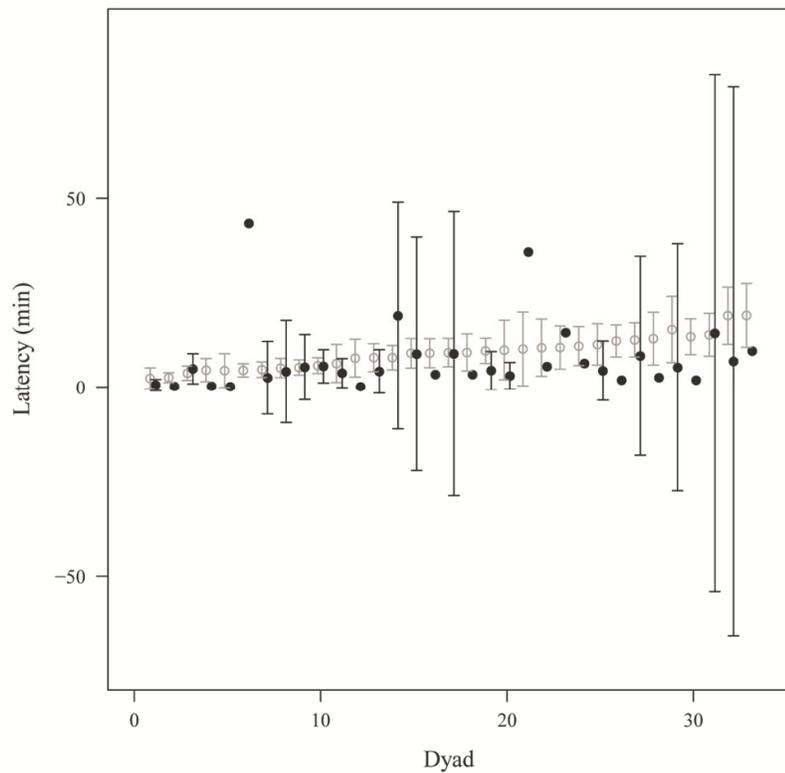


Figure 4: The latency between the movement of a male and female partner to the outside compartment for events with (black lines filled circles) and without (grey lines open circles) sexual interactions. Dyads on the x-axis are ranked according to the latency during events without sex. Error bars indicate 95% confidence intervals.

DISCUSSION

In order to label sneak copulations an example of tactical deception, it has to be shown that hiding is tactical (Byrne and Whiten 1990) and, furthermore, to investigate cognitive mechanism underlying sneak copulations it is necessary to determine which individuals are avoided as bystanders and on what basis. We investigated whether the presence of group members affected sexual behaviour of group living long-tailed macaques, how certain characteristics of bystanders relate to their inhibiting effect, and how individuals reacted to the presence of particular group members. Moreover, we investigated whether movements to the outside compartment are synchronized between male and female copulation partners to sneak away from the remainder of the group.

Our study confirms that male long-tailed macaques, by their mere presence, significantly inhibit copulations of group members in their view. The alpha male has a strong audience effect and reduces the number of copulations within his view. Additionally, four other males inhibited the occurrence of copulations within their view. Their audience effects were not a side effect of the alpha male's audience effect mediated by proximity of bystander males to the alpha male, indicating that it is indeed the bystander male itself that has an audience effect. The motivation to avoid males as bystanders during sexual

behaviour may be harassment. Although the observed rate of interference was low, it may not be representative of the actual risk of interference (cf. difference between risk and rate of predation (Hill and Dunbar 1998) or infanticide (Janson and Schaik 2000)), since effective avoidance of potential harassers will decrease the number of interferences in a group. Indeed, we found ample evidence that dyads avoid bystanders during copulations. This suggests that the potential risk of interference by a particular bystander causes an audience effect of this individual.

The alpha male in our study was the most frequent harasser, but non-alpha males also interfered in copulations. This is consistent with other primate species where interferences are more frequently observed by higher than by lower ranking males (*M. fuscata* Stephenson 1975, *M. mulatta* Wilson 1981, *Macaca arctoides* Niemeyer and Chamove 1983). In line with this, the audience effect strength tended to be higher in high- than in low-ranking males. Yet this effect of male rank disappeared when the alpha male was left out of the analysis, rendering it unclear whether the effect of dominance rank is important for audience effects between non-alpha males. However, the difference in audience effect strength between alpha and non-alpha males is evident. The absence or lower audience effect strength of lower ranking males may result from their reduced influence on particular dyads. Possibly, copulating dyads involving high-ranking individuals did not pay attention to the presence of males that were relatively low in rank. This can be due to the direction of interference, which is commonly directed from a higher ranking towards a lower ranking individual (this study; Chapais 1983). In summary, our data provide evidence for an avoidance of several bystander males as potential harassers during copulations. This is consistent with rhesus macaques, that also show audience effects of alpha and non-alpha males on sexual behaviour of group members (Overduin-de Vries et al. 2012). The variability of audience effect strengths among males of different dominance ranks suggests that male audience effects result from dominance-based male sexual strategies such as interference.

Females also significantly inhibited copulations of their group-members. Similar to the effect of non-alpha males, the audience effect of females is not a by-product of the alpha male's audience effect in combination with female proximity to the alpha male, since females with different proximities to the alpha male did not differ in their audience effect strengths. Females also aggressively disturb copulations (Niemeyer and Chamove 1983, Overduin - de Vries et al. 2012), and hiding copulations from females may also function to prevent interferences. The strength of a female audience effect was not related to the dominance rank of the female. This is in line with the dominance rank of the females that interfered copulations: one was middle and the other low ranking. Our results contrast with the hypothesis that mainly dominant females are avoided because of their potential to interfere copulations (*M. arctoides*: Gouzoules 1974; *M. mulatta*: Wilson 1981) (*M. arctoides*: Gouzoules 1974, *M. mulatta*: Wilson 1981). Alternatively, the hypothesis that the function of interferences by females is to test male quality (Niemeyer and Chamove 1983) predicts that a female's potential to interfere copulations may depend on a female's willingness to copulate. However, there was no significant relation between female proceptivity and audience effect strength, refuting this hypothesis. Altogether, many females were avoided during copulations, and avoidance of a particular female was not based on her dominance rank, her proceptivity or proximity to the alpha male. Since no particular female characteristic was found to determine a females

audience effect strength and many females had an effect, it is possible that all females are potential harassers and benefit from interfering copulations, supporting the hypotheses that females prevent competition for future resources (Niemeyer and Anderson 1983) or for non procreative benefits given by male copulation partners, such as agonistic support (Buchan et al. 2003), or for parental investment (Soltis 2002). If this is true it indicates that female audience effects result from general female-female competition.

Analysis of the female initiatives to copulate revealed that they react to the presence of the alpha male and most other females, yet do not react to the presence of subordinate males. Also male copulation solicitations were inhibited by the alpha male and all but three females, and in addition by two lower ranking males. Altogether, the audience effects on both male and female solicitations show that both sexes pay attention to the presence of bystanders during copulation solicitations and adjust their behaviour accordingly. This suggests a benefit for both partners to hide their sexual behaviour, which is in line with the proposed costs of being interfered for both males (Wilson 1981, Bruce and Estep 1992) and females (Ruiz de Elvira and Herndon 1986, Manson 1996), such as the costs of receiving aggression and the reduced reproductive success due to interfered copulations. Alternatively, only one individual of the copulating dyad obtains direct benefits while the other obtains an indirect benefit when its partner is more willing to copulate in occluded conditions.

Because both partners adjust their sexual behaviour in the presence of bystanders, there is a possibility that hiding copulations is a coordinated behaviour between both partners involved in the copulation. Namely, if it is a coordinated movement, sneaky mating may be the result of tactical deception; i.e. both partners are "tactically getting left behind" (Byrne and Whiten 1992, p. 613). We determined whether there is evidence for a coordinated movement to the outside compartment to avoid the alpha male, which was most of the time inside. Although the latency in episodes with sexual behaviour was shorter than in episodes without sexual behaviour, this difference was not significant. Therefore, we have no evidence for tactical deception. However, we cannot firmly exclude tactical deception either, since the data were in the direction expected under the tactical deception hypothesis and additional data collection might reveal a significant effect.

Alternatively, bystander effects may result from conditional learning. Because of the low incidence of interferences in our study it was impossible to statistically link bystander effects with interference behaviour by a particular bystander. Despite the low incidence of interferences, it is possible that a few incidences of punishment in the past have resulted in a conditioned inhibition of sexual behaviour in the presence of certain individuals. Aggression-accompanied interference has been frequently reported (Gouzoules 1974, Wilson 1981, Chapais 1983, Niemeyer and Chamove 1983, Ruiz de Elvira and Herndon 1986, Manson 1996, Dixson 1998) and thus may be the underlying mechanism to bystander effects.

Moreover, sneak copulations may result from the general peripheral positioning of non-alpha males. Indeed, in our study males occupied peripheral positions during non-sexual events, since they tended to reside more often in the (less occupied) outside compartment than females, spend less time in proximity of the alpha male, and were more often the first of a dyad moving outside. Moreover, before a sexual event males

tended to be the first outside as well, and non-alpha males, in contrast with the alpha male, copulated more often outside than inside. This suggests that sneak copulations may simply result from the peripheral positioning of non-alpha males. Yet the rate of sexual interactions was significantly higher in the absence than presence of bystander males, in particular of the alpha-male. This enhanced incidence of sexual interactions suggests that, in addition to the opportunity created by the peripheral position of non-alpha males, dyads also exploit such a situation.

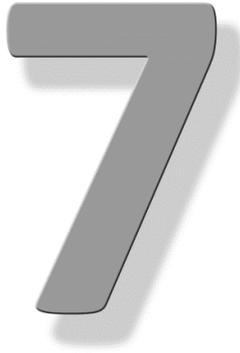
Altogether, the simplest explanation of our results is that copulations in absence of the alpha male result from exploiting the peripheral positioning of non-alpha males. Since bystander effects based on the spatial composition of the group do not require high cognitive mechanisms, they may be found in a wide array of species. It would be interesting to investigate whether similar effects of bystanders exist in species or groups where individuals occupy different dominant ranks and where the Priority of Access model does not predict mating success, such as spotted hyenas (*Crocuta crocuta*: Engh et al. 2002), harbour seals (*Phoca vitulina*: Coltman et al. 1999) and pukeko (*Porphyrio porphyrio melanotus*: Lambert et al. 1994).

In conclusion, males and females both can harass copulating pairs, both have an audience effect and both inhibit the occurrence of sexual behaviour of their group members of both sexes. The audience effects of non-alpha individuals were not just a side effect of sitting close to the alpha male, and, therefore, represent a true avoidance of potential harassers. Bystander effects express male-male competition and female-female competition, indicating that both are important factors in the sexual dynamics of long-tailed macaques. Reducing sexual competition does not seem to be a result of employing tactical deception. Rather, our results suggest that long-tailed macaque males and females copulate sneakily because they exploit the peripheral position of non-alpha males. Investigating these mechanisms in non-primate species would give more information on whether this effect depends on primate social cognitive capacities or whether it is a broader effect which exists in many species with comparable multi-male multi-female mating systems.

ACKNOWLEDGEMENTS

We would like to thank Nick Stolk for his contribution to the data collection, three anonymous reviewers for the thoughtful comments and the animal caretakers for their care for the monkeys. This research was funded by the Biomedical Primate Research Centre, Rijswijk, the Netherlands.





Rhesus and long-tailed macaques show sexual behaviour at locations distant, not at locations hidden from the alpha-male

A.M. Overduin - de Vries, B.M. Spruijt, E.H.M. Sterck

In multi-male multi-female groups, monopolization of sexual interactions by alpha males does not necessarily benefit subordinate males and females. Therefore, subordinate males and females try to escape from this monopolization by sneaky mating. Although in primates sneaky mating has been suggested to result from tactical deception, this has never been empirically shown and simpler cognitive mechanisms may guide this behaviour. Five different cognitive mechanisms of increasing cognitive complexity consistent with either no, level 1 or level 1.5 tactical deception may guide hiding behaviour. We studied which strategies are used to hide sexual behaviour by observing captive groups of two different macaque species (*Macaca mulatta* and *M. fascicularis*). Although temporary hiding locations in the form of opaque screens had been provided to the monkeys, sexual behaviour sporadically took place near one of these structures and copulations were not systematically hidden from the alpha male. However, females from both macaque species increased their distance from the alpha male and from other females during sexual interactions, exploiting the peripheral positioning of subordinate males. Additionally, non-alpha *M. mulatta* males significantly increased and *M. fascicularis* males tended to increase their distance from the alpha male during sexual interactions. Therefore, the increased distance during sexual behaviour cannot be explained by the rank dependent peripheral spatial positioning of non-alpha males alone. Concluding, sneaky mating results from both male and female individuals actively increasing the distance from the alpha male and female bystanders, consistent with level 1 tactical deception.

INTRODUCTION

Many animal species live in multi-male multi-female groups, where theoretically high-ranking males have priority of access to fertile females (Altmann 1962). Indeed, in many animal groups a higher incidence of copulations in dominant males is found (for review: Cowlshaw and Dunbar 1991; *Capra ibex*: Willish et al. 2012; *Gorilla gorilla beringei*: Robbins 1999; *Macaca fascicularis*: de Ruiter and van Hooff 1993; *M. mulatta*: Massen et al. 2012; *M. fuscata*: Garcia et al. 2009; *M. sylvanus*: Paul et al. 1993; *Mandrillus sphinx*: Wickings et al. 1993; *Marmota flaviventris*: Huang et al. 2011; *Pan troglodytes*: Klinkova et al. 2005; Boesch et al. 2006; *Papio anubis*: Bulger 1993; Alberts et al. 2006). However, in other groups there is no relation between dominance rank and mating success of males (*Crocuta crocuta*: Engh et al. 2002; *Cebus paella nigritus*: Alfaro 2005; *M. mulatta*: McMillan 1989, Dubuc et al. 2011; *M. fascicularis*: de Ruiter et al. 1992; *Phoca vitulina*: Coltman et al. 1999; *Porphyrio porphyria melanotus*: Lambert et al. 1994), and subordinate males employ sneaky copulations to counter dominant male monopolization (Kummer 1968, Ruiz de Elvira and Herndon 1986, Byrne and Whiten 1990, Gygas 1995, Kummer et al. 1996, Soltis et al. 2001). Whereas monopolizing alpha males may punish or disrupt lower ranking males and their female partners for copulations in his view, sneaky copulations may prevent punishment and disruption by the alpha male. Accordingly, female and subordinate male long-tailed macaques and rhesus macaques copulate more often in the absence than in the presence of specific individuals, in particular of higher ranking ones (Ruiz de Elvira and Herndon 1986, Gygas 1995, Overduin-de Vries et al. 2012), suggesting that they hide their copulations from these individuals.

In primates, sneaky mating may be interpreted as tactical deception (Byrne and Whiten 1990); “acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the benefit of the agent”. Within tactical deception three levels are distinguished. Level 1 is nothing more than the above definition. Level 1.5 adds to the above that an individual understands what another individual can see, i.e. Visual Perspective Taking (VPT). Level 2 additionally includes understanding deception (Byrne and Whiten 1990). Deception is not considered tactical if the act was based on a coincident rather than an act with the goal of benefiting from the deception. Therefore, hiding sexual behaviour may result from five different behavioural strategies with or without tactical deception from cognitive basic to complex (Gygas 1995).

The first strategy of *exploiting peripheral positions* concerns sexual behaviour at locations distant from high-ranking males. Peripheral positioning of non-alpha males results from non-sexual behaviour, such as fleeing or avoidance behaviour (Evers et al. 2011). Females willing to copulate approach these peripheral non-alpha males (Kaufmann 1965, Drickamer 1974, Berard et al. 1994, Inoue and Takenaka 2008, Dubuc et al. 2011). This strategy does not involve tactical deception because the peripheral positioning is not based on the goal of achieving benefits from hiding sexual behaviour.

The second hiding strategy concerns *creating peripheral positions*. Individuals willing to copulate actively increase their distance from bystanders. Animals may learn by trial and error that copulations at larger distances from specific bystanders are less often

disturbed, resulting in an audience effect, namely inhibition of sexual behaviour in the proximity of certain bystanders. If an individual consequently uses this strategy and it is clear that distancing is specifically linked to obtaining benefits from concealed copulation, this may involve tactical deception level 1.

The third strategy concerns *sexual behaviour near opaque objects*. Sexual behaviour is preferably performed close to opaque objects irrespective of whether the audience is on the same side or not. Similar to the second strategy, this strategy may result from trial and error learning, if they experience less punishment when copulations are occasionally behind the opaque object. If an individual consequently uses this strategy and it is clear that the approach of opaque objects is specifically linked to obtaining benefits from concealed copulation, this may involve tactical deception level 1.

The fourth strategy concerns *sexual behaviour behind an opaque object*. Individuals position themselves on one side of an object, while the audience is on the opposite side. Again, this strategy may be learned by trial and error and result in a simple rule “avoid seeing the audience while involved in sexual behaviour”. If an individual consequently uses this strategy and it is clear that hiding behind the object is done with the goal of concealing sexual behaviour, this may involve tactical deception level 1.

The fifth strategy concerns *true intentional hiding*. Individuals hide themselves including distal body parts while occasionally monitoring the audience through peek-holes. This strategy can involve level 1.5 tactical deception, since an individual must understand the visual perspective of the audience.

All five strategies may effectively hide sexual behaviour, although for the first three strategies sexual behaviour is either performed at distant locations from bystanders (strategy 1 and 2) or close to opaque objects (strategy 3), and it depends on chance whether the subject is actually hidden from bystanders or not. Therefore, the fourth strategy will be more effective, but requires learning a slightly more complex rule than the first three strategies, and is, thus, more cognitively demanding. However, the most effective strategy is the fifth strategy of *true intentional hiding*, but this requires more cognitive complexity in the form of VPT.

There is some evidence that monkeys may possess VPT. In an experimental setup, spider monkeys (*Ateles geoffroyi*) and capuchins (*Cebus apella*) followed a human’s gaze directed at a position behind a barrier (Amici et al. 2009). Similarly, long-tailed macaques (*M. fascicularis*) were able to follow and interpolate the focus of a conspecific’s gaze behind a barrier (Goossens et al. 2012), suggesting an understanding of the direct line of sight. Moreover in chapter 4 we show that long-tailed macaques know what their group members can see, i.e. VPT in a food competition paradigm. However, there is little evidence that this ability is used by the monkeys in hiding behaviour. A few experiments with opaque screens have been conducted to investigate the strategies used to hide sexual behaviour (Gygax 1995); unpublished experiment mentioned in (Kummer et al. 1996)). In one of these experiments, the monkeys first showed indications of hiding, but soon stopped hiding because the alpha male had no physical access to the copulating dyad (Kummer et al. 1996). In the second study, where the alpha male had continuously physical access to the whole group, low ranking and middle ranking long-tailed macaque males prefer to copulate near opaque structures over transparent structures (Gygax 1995). However, opaque structures were preferred by low-ranking males during non-sexual events (for middle ranking males the data of non-sexual events are not provided).

Although a preference for a position near a screen over positions without screens was specifically linked to sexual behaviour, it is not clear what property of the screens was responsible for this preference; restricted visibility, restricted accessibility, or elevated locations. Moreover, half of the screens (and in particular the screens that were used most by the monkeys) were positioned such that one side of the screen was always near the edge of the enclosure, making it possible that subordinate males only occupied positions behind the screens because they preferred peripheral positions. In conclusion, the monkeys prefer to sit near opaque objects, but whether this preference is linked to hiding behaviour, based on the restricted visibility, accessibility, peripheral position or whether they differentiate between the audience side and the other side is not clear. To discriminate between different strategies underlying hiding of copulations, it is necessary to determine whether monkeys have an increased preference for opaque structures during sexual compared to non-sexual behaviour, and to determine their preference for opacity, restricted accessibility, peripheral position or the side which is invisible for bystanders.

The purpose of the present study is to evaluate what behavioural strategy is used by macaques when hiding sexual behaviour. Additionally, we investigated for which bystanders sexual behaviour is concealed, and whether the effect of a particular bystander is linked to certain characteristics of this bystander such as rank or proximity to the alpha male. Two groups of captive rhesus macaques and two groups of captive long-tailed macaques were studied in their home cages. All groups contained multiple unrelated sexually mature males and females. The groups were provided with several screens varying in properties of visibility, accessibility and the presence of peek-holes allowing discrimination between strategy 3, 4 and 5. The spatial position and inter-individual distances of the monkeys were recorded during sexual and non-sexual events in order to separate preferred positions between different contexts, enabling discrimination of strategy 1 and 2.

METHODS

Subjects

Two groups of rhesus macaques (group 1 and 2) and two groups of long-tailed macaques (group 3 and 4), all housed at the Biomedical Primate Research Centre, Rijswijk, were included in this study. Group 1 to 4 consisted of respectively 30, 25, 27 and 33 individuals, including 10, 10, 15 and 16 adult females and 7, 4, 7 and 5 adult males. Sexually immature monkeys younger than 3.5 years for females (*M. mulatta*: Smuts et al. 1987; *M. fascicularis*: youngest mother 4 years (Smuts et al. 1987, van Noordwijk and van Schaik 1999) or 3 years for males (*M. mulatta*: youngest father 3.8 years (Bercovitch et al. 2003); *M. fascicularis*: youngest father 3.5 years (Rowell 1977)) were excluded from the analysis. Each subject contributed to the dataset as a potential part of a sexual dyad and as a possible bystander individual. Within each group the hierarchy was determined based on submissive behaviours using Matman 1.1 (de Vries et al. 1993). In all four groups the dominance hierarchy was significantly linear (group 1 to 4 resp.: $h' = 0.53, 0.50, 0.55, 0.82$, $p = 0.0006, 0.0001, 0.0004, 0.0001$ (de Vries 1995). After rearrangement

of the matrix, each individual was assigned a dominance rank number from 1 (highest ranking) up to 22 (lowest ranking mature individual in largest group).

Housing

The rhesus and long-tailed macaques were housed in similar cages. The cages consisted of interconnected inside and outside enclosures. During the observations exclusively outside enclosures were available for the monkeys (Figure 1 provides the outside cage of group 4). The outside enclosures measured for group 1 to 4: 260, 270, 218, 502 m². Compared to groups 1 to 3, group 4 had approximately a double sized enclosure (i.e. group 4 used two connected outside enclosures), because after the observations of the first three groups we aimed to exclude the possibility that the screens were not used because of the limited maximum possible distance between a copulating couple and the alpha male. All outside enclosures were 3.1m high and were subdivided in several sub-compartments with wire mesh.

Outside compartments had a sand bedding and were furnished with multiple sitting beams, which allowed the monkeys to sit on various height levels without being hidden. Additionally, enclosures were provided with permanent enrichment consisting of fire hoses, tires, ladders and a swimming pool (Vernes and Louwerse 2010). Monkeys were only fed in the inside enclosure, outside observation

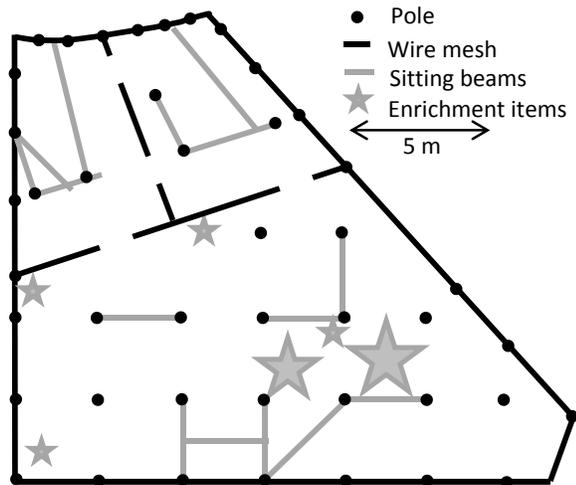


Figure 1: Scaled map of the outside enclosure of group 1. The poles indicated in the figure were used as reference points in order to map the positions of the rhesus macaques.

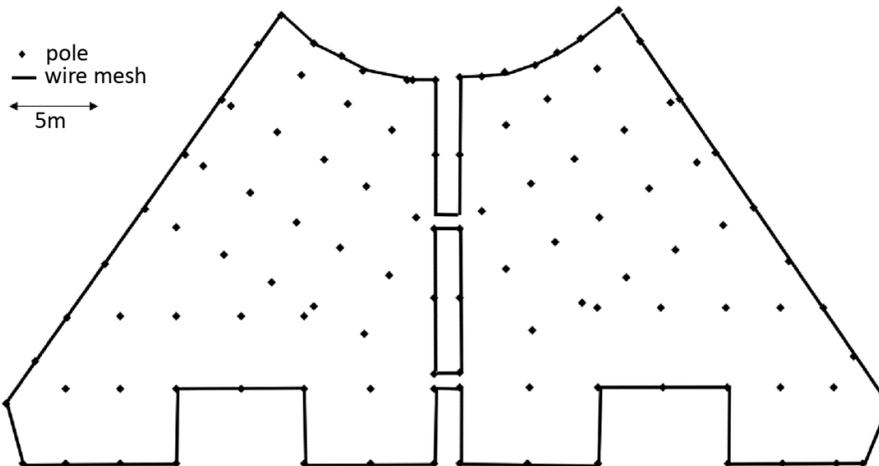


Figure 2: Scaled map of the outside enclosure of group 4. The poles indicated in the figure were used as reference points in order to map the positions of the long-tailed macaques.

hours. However, water was available ad libitum in the outside enclosure.

Observations

Groups were observed during different periods: group1: 25-11-2008 to 17-02-2009; group 2 25-11-2008 to 24-02-2009; group 3: 02-02-2010 to 01-04-2010; and group 4: 18-02-2011 to 15-04-2011 by five different observers (group 4 was observed by two observers simultaneously). Sexual behaviours (sexual present, lift tail, grasp waist, mount and copulate) were recorded ad libitum. For long-tailed macaques mounts were scored if a male mounted a female, but thrusts less than three times, whereas copulations involved 3 or more thrusts. The remainder of the behaviours for both species were conform the ethogram of our previous study (cf. Overduin-de Vries et al. 2012). One to two observation sessions of maximally two hours each were conducted per day, resulting in respectively 160, 192, 142 and 73 hours of ad libitum sampling for the 4 study groups.

Screens

All groups had access to 2 screens at the same time, one on each side of the enclosure, precluding monitoring both sides of both screens simultaneously by one bystander monkey. Screen type, and number of possible screen positions differed between monkey groups. Within *M. mulatta* groups, in order to discriminate between location and visibility, the locations of the screens were daily rotated between eight possible locations. Screens consisted of two U-profile plastic poles, which were positioned vertically and partially dug into the ground. Between the two poles two plates of wood or Plexiglas were mounted on top of each other. By varying the application of wood and/or Plexiglas per screen, four different types of screens were created: a) full opaque, b) bottom see through, top opaque, c) bottom opaque, top see through, d) full see through. The total size of the screens was 1.2 m width x 1.3 m high. These screens were used from 25 November 2008 to 9 February 2009 in group 1 (42 observation days) and from 25 November 2008 until 07-01 2009 in group 2 (21 observation days). Since the screens were never used by the monkeys in either group, we decided after this period to replace the screens in group 2 for two fully opaque wooden screens measuring 2.8 m width x 1.13 meter high. These screens remained permanently in the cage during the remainder of the observations, from 12 January 2009 until 24 February 2009 (31 observation days).

In group 3, each of the two screens rotated between three possible positions. Since the former experiments with rhesus monkeys revealed no use of the screens at all, we chose to only use the most concealing screen type: the full opaque screen. The screens measured 3.0 m width x 0.8 m high and were hung from the ceiling approximately 2 m above ground level. Each of the screens was equipped with a sitting beam on each side of the screen. In addition to the beams attached to the screens, several elevated beams were provided without screen.

For group 4, similar screens were used as for group 3. Because in group 3 the screens were never used, we decided to include another screen type that allowed monkeys, when hiding behind the screen, to monitor their group members on the other side of the screen. This new peek-hole screen type had the same size as the screens in

group 3, but had 51 holes of 5 cm diameter, positioned in three horizontal rows between 0.25 and 0.50 cm from the bottom of the screen. The positioning of the holes allowed the copulating monkeys to hide most of their body, while they could peek through one of the holes. Both screen types; one fully opaque screen and one peek-hole screen, rotated daily between six possible positions, assigning positions randomly with the concession that there was always one screen on each half of the cage.

Recording positions

To calculate inter-individual distances, we took scans from the position of all the animals in the group. We started our observations in group 1 and 2, where positions of animals were recorded by means of a scaled map with all the sitting beams and toys drawn in scale as a reference. In these first two rhesus macaque groups we used two different scan types: (1) 'general scans' of the general positioning of animals, and (2) 'sex scans' of the positions of animals while involved in sexual behaviour. General scans were taken at the start and end of each observation session. During general scans the positions of all individuals in the group were recorded, while during sex scans in group 1 and 2 only the positions of the sexual partners and the alpha male were recorded.

In order to obtain more quantitative data of group spacing through the full length of observation sessions, in the subsequent observations on the long-tailed macaques (group 3 and 4) we collected additional scan data by taking general scans each half hour. Moreover, for the observations of group 3 and 4 we adjusted our methods of taking scans. Positions of the animals were recorded by noting down for each individual the nearest pole of the enclosure. Each cage contained several vertical poles spaced at 0.22 poles/m². The enclosures of group 3 and 4 contained 58 and 110 poles. Distances between all combinations of two poles were calculated based on measurements from a scaled map (Figure 1). This method allowed recording the positions of all animals in the group also during sexual scans. This created the opportunity to analyse not only the effect of the alpha male, but also of other individuals.

Additionally, a third scan type was added in group 3 and 4; the 'matched control scan'. This was done to control for the difference in activity levels between general scans and sexual scans, with most general scans representing resting stages including many animals in close proximity of each other. Matched control scans of all individuals were taken 5 minutes after a sexual behaviour was recorded, balancing activity levels between sexual and matched control scans. When simultaneously with a matched control scan, a sexual behaviour was observed, the matched control scan was disregarded, since it did not reflect non-sexual behaviour. This way, the number of sex scans that was compared with matched control scans (group 3: $N=216$; group 4: $N = 201$) was slightly smaller than the number of sex scans compared with general scans (group 3: $N=217$, group 4: $N= 208$).

Inter-observer reliability of taking general scans (not sexual scans, because it takes to much time to get enough sexual scans for statistical analysis) was checked during a two-hour observation in group 4 by two observers simultaneously. For this purpose general proximity scans were made every five minutes. When the exact poles for all adult subjects in 24 scans were compared between both observers, the agreement was marginal ($\kappa = 0.64$, index of concordance = 0.66). However, if scoring two adjacent poles is counted as an agreement (which corrects for situations were an

individual is sitting equally distant between two poles) the agreement was amply sufficient (index of concordance = 0.82).

Analysis

In Group 1 and 2 inter-individual distances were calculated by measuring the distance on the scaled map. In Group 3 and 4 this was done by calculating the distance between two poles. Inter-individual distances were compared between sexual and non-sexual events by comparing (1) sexual scans with general scans and, for group 3 and 4, also comparing (2) sexual scans with matched control scans. In Group 1 and 2 the distance of the mating individuals from the alpha male during general scans and sexual scans was compared. For Group 3 and 4 a mean distance was calculated with each possible bystander individual during each of the three scan types separately. From sexual scans and matched control scans only the distances from the bystanders to each of the individuals involved in the sexual interaction (sexual scans) or that had been involved in a sexual interaction 5 minutes before (matched control scan) were included.

The strength of the effect of a particular bystander, further named the “audience effect strength”, was calculated by subtracting for each individual the distance towards the bystander during general scans from the distance towards this same bystander during sexual scans, and taking a mean over all individuals involved in sexual behaviour, resulting in the mean observed difference (MOD)(cf. Overduin – de Vries et al in press).

Since the methods of Group 1 and 2 were exactly the same, the data of Group 1 and 2 were analysed as one dataset. However, because the methods and species of Group 3 and 4 were different from those of Group 1 and 2, and the surface of the cage in Group 4 was double that of Group 3, the datasets of Group 3 and 4 were separately analysed.

All tests were conducted using the software package “R” (R Development Core Team, 2009) Version 2.10. All statistical tests were two-tailed with α set at 0.05. Additionally, for single tests we report trends with p between 0.05 and 0.10. When audience effects of multiple individuals within one group were analysed, alpha values were adjusted according to the sharper Bonferroni procedure for multiple testing (Hochberg 1988), with the family-wise error rate set at 0.05.

RESULTS

The use of screens

Individuals seldom copulated near opaque screens. In group 1, two out of 575 sexual interactions of non-alpha males took place within two meter distance from a screen. Of these two interactions, one was on the opposite side from the screen than the alpha male and, thus, out of the alpha male’s field of vision. In group 2, one out of 80 sexual interactions with non-alpha males took place within 2 meters from a screen, and was out of the alpha male’s field of vision. In group 3, seven out of 69 sexual interactions between females and non-alpha males took place on the beam attached to a screen. Three of these were out of the alpha male’s field of vision. In group 4, four out of 277 sexual

interactions were on the beam attached to a screen. One of these interactions was out of the alpha male's field of vision. Altogether, sexual interactions near screens did not occur significantly more often at the hidden side (6) than on the side visible to the alpha male (8) (binomial test: $p=0.79$). The frequency of sexual interactions near screens, 14 out of 1001 interactions, was too low for subsequent analysis on differentiation between screen types.

Distance

Group 1 and 2

-Comparing sexual scans and general scans

During general scans, male rhesus macaques were positioned at a significantly larger average distance from the alpha male (mean: $6.83 \pm \text{SD}1.43\text{m}$) than females (mean: $5.23 \pm \text{SD}1.21\text{m}$) (Kolmogorov-Smirnov test: $D = 0.56$, $N_1 = 9$, $N_2 = 20$, $p = 0.02$). During sexual scans, females were at significantly larger distances from the alpha male (mean: $9.57 \pm \text{SD}2.53\text{m}$) than during general scans (Wilcoxon signed rank test: $V=2$, $N = 18$, $p = 0.00003$). Likewise, males were at significantly larger distances from the alpha male during sexual scans (mean: $10.85 \pm \text{SD} 1.44$) than during general scans (Wilcoxon signed rank test: $V = 0$, $N = 9$, $p = 0.004$).

Group3

-Comparing sexual scans and general scans

During general scans, male long-tailed macaques were positioned at larger distances from the alpha male (mean: $8.94 \pm \text{SD} 1.03$) than females (mean: 7.42 ± 0.80) (Kolmogorov-Smirnov: $D = 0.73$, $N_1 = 15$, $N_2 = 6$, $p = 0.01$). During sexual scans, females were at significantly larger distances from the alpha male (mean: $11.59 \pm \text{SD} 3.40\text{m}$) than during random scans (Wilcoxon signed rank test: $V = 116$, $N = 15$, $p = 0.0004$). For males, the results were in the same direction; during sexual scans the average distance of all six non-alpha males to the alpha male was larger (mean: $12.18 \pm \text{SD} 4.25\text{m}$) than during general scans, however, this difference was not significant (Wilcoxon signed rank test: ($V = 18$, $N = 6$, $p = 0.16$).

Other individuals than the alpha male also influenced the position of group members during sexual behaviour. When distances were calculated for the 3rd and 5th ranking bystander female, the distance from females during sexual scans was larger than during general scans (Wilcoxon signed rank test: 3rd female: $V = 103$, $N = 14$, $p = 0.0004$; 5th female: $V = 102$, $N = 14$, $p = 0.002$). None of the other (female and male) bystanders significantly influenced the positions of non-alpha males or females during sexual behaviour. The audience effect strength, MOD, of a (female and non-alpha male) bystander on the positions of females during sexual behaviour (the mean observed difference in distance towards a particular bystander) significantly depended on the proximity of the bystander to the alpha male (glm: coefficient= $-0.46 \pm \text{SD} 0.13$, $t = -3.51$, $p = 0.003$) and tended to be lower for low- than high-ranking bystanders (glm: coefficient = $-0.04 \pm \text{SD} 0.02$, $t = -1.79$, $p = 0.09$).

Table 1: Audience effects of the alpha males of rhesus macaques (RM) and all adult individuals in long-tailed macaque (LM) groups, comparing sexual scans with general scans. Statistics of the Wilcoxon signed rank test (*N, P, V*) are provided in column 4-6 for female subjects and 9-11 for male subjects. *P*-values smaller than the Bonferroni corrected alpha value (column 7 and 12) are marked (*). Results for alpha males are underlined

species	group	Female subjects					Male subjects				
		bystander	N	P	V	Bonferroni corrected α	bystander	N	P	V	Bonferroni corrected α
RM	1&2	<u>alpha</u>	<u>18</u>	<u>0.00003*</u>	<u>2</u>	<u>0.050</u>	<u>alpha</u>	<u>6</u>	<u>0.004*</u>	<u>9</u>	<u>0.050</u>
LTM	3	sil	15	0.0004*	103	0.002	tre	7	0.031	27	0.002
		<u>nac</u>	<u>15</u>	<u>0.0004*</u>	<u>116</u>	<u>0.002</u>	sep	7	0.047	26	0.002
		fos	14	0.002*	102	0.003	sil	7	0.047	26	0.003
		voi	14	0.005	95	0.003	bam	6	0.063	20	0.003
		foe	14	0.005	95	0.003	pot	6	0.094	19	0.003
		kaa	14	0.005	95	0.003	yuk	6	0.094	19	0.003
		mok	14	0.009	93	0.003	<u>nac</u>	<u>6</u>	<u>0.156</u>	<u>18</u>	<u>0.003</u>
		tre	14	0.011	92	0.003	foe	7	0.156	23	0.003
		riv	14	0.011	92	0.004	mok	7	0.156	23	0.004
		bam	15	0.015	102	0.004	kar	7	0.156	23	0.004
		kar	15	0.020	90	0.004	vir	7	0.219	22	0.004
		yuk	14	0.030	87	0.005	fos	7	0.297	21	0.005
		sep	14	0.035	86	0.005	voi	7	0.297	21	0.005
		pot	15	0.055	84	0.006	goa	7	0.310	21	0.006
		goa	14	0.068	82	0.006	bol	6	0.313	16	0.006
		bol	15	0.068	82	0.007	riv	7	0.375	20	0.007
		tai	14	0.084	81	0.008	kaa	7	0.553	10	0.008
bak	14	0.173	75	0.010	pes	6	0.563	14	0.010		
voo	15	0.188	84	0.013	rok	6	0.563	14	0.013		
pes	14	0.229	82	0.017	tai	7	0.578	18	0.017		
rok	15	0.330	78	0.025	bak	7	0.688	17	0.025		
vir	14	0.391	67	0.050	voo	6	1.000	10	0.050		
LTM	4	<u>sta</u>	<u>16</u>	<u>0.0002*</u>	<u>133</u>	<u>0.002</u>	ban	5	0.063	15	0.002
		sto	15	0.0002*	118	0.003	bez	5	0.063	15	0.003
		ban	15	0.005	107	0.003	eri	5	0.063	15	0.003
		chi	15	0.005	107	0.003	eur	5	0.063	15	0.003
		eur	15	0.006	115	0.003	gen	5	0.063	15	0.003
		cro	15	0.007	106	0.003	inc	5	0.063	15	0.003
		poc	16	0.008	118	0.003	lav	5	0.063	15	0.003
		eri	15	0.009	114	0.004	pac	5	0.063	15	0.004
		gen	15	0.035	97	0.004	rab	5	0.063	15	0.004
		var	15	0.036	97.5	0.004	sin	5	0.063	15	0.004
		ama	16	0.044	107	0.005	ama	4	0.125	10	0.005
		sin	15	0.061	93.5	0.005	poc	4	0.125	10	0.005
		inc	15	0.073	92	0.003	<u>sta</u>	<u>4</u>	<u>0.125</u>	<u>10</u>	<u>0.003</u>
		pac	15	0.073	92	0.006	chi	5	0.125	14	0.006
		lav	15	0.135	87	0.007	nua	5	0.125	14	0.007
		clo	15	0.252	81	0.008	var	5	0.125	14	0.008
		nua	15	0.421	75	0.010	stoa	5	0.188	13	0.010
		cur	16	0.433	84	0.013	cur	4	0.250	9	0.013
		moj	16	0.706	60	0.017	moj	4	0.250	1	0.017
		rab	15	0.720	67	0.025	cro	5	0.313	12	0.025
bez	15	0.978	59	0.050	clo	5	1.000	7	0.050		

Macaques copulate at distant locations

Table 2: Audience effects of all adult individuals in long-tailed macaque groups, comparing sexual scans with matched control scans. Statistics of the Wilcoxon signed rank test (*N,P,V*) are provided in column 3-5 for female subjects and 8-10 for male subjects. *P*-values smaller than the Bonferroni corrected alpha value (column 6 and 11) are marked (*). Results for alpha males are underlined

group	Female subjects					Male subjects				
	bystander	N	P	V	Bonferroni corrected α	bystander	N	P	V	Bonferroni corrected α
3	sil	14	0.001*	100	0.0023	bak	7	0.375	20	0.0023
	tre	14	0.007	94	0.0024	bam	6	1.000	10	0.0024
	pot	14	0.020	89	0.0025	bol	6	0.844	12	0.0025
	yuk	14	0.020	89	0.0026	foe	7	0.578	18	0.0026
	fos	14	0.030	87	0.0028	fos	7	0.813	16	0.0028
	voi	14	0.035	86	0.0029	goa	7	0.938	13	0.0029
	foe	14	0.035	86.5	0.0031	kaa	7	0.297	7	0.0031
	riv	14	0.103	79	0.0033	kar	7	0.813	12	0.0033
	mok	14	0.135	77	0.0036	mok	7	0.938	13	0.0036
	<u>nac</u>	<u>15</u>	<u>0.169</u>	<u>85</u>	<u>0.0038</u>	<u>nac</u>	<u>6</u>	<u>0.313</u>	<u>16</u>	<u>0.0038</u>
	kaa	14	0.194	74	0.0042	pes	6	0.156	18	0.0042
	pes	15	0.307	78.5	0.0045	pot	6	0.313	16	0.0045
	bak	14	0.326	69	0.0050	riv	7	0.156	23	0.0050
	kar	14	0.326	69	0.0026	rok	6	0.844	12	0.0026
	tai	14	0.326	69	0.0063	sep	7	0.813	16	0.0063
	voo	15	0.454	74	0.0071	sil	7	0.219	22	0.0071
	bol	14	0.485	56	0.0083	tai	7	0.469	19	0.0083
	sep	14	0.542	63	0.0100	tre	7	1.000	14	0.0100
	bam	15	0.600	70	0.0125	vir	7	0.297	7	0.0125
	vir	14	0.626	61	0.0167	voi	7	0.688	17	0.0167
rok	15	0.639	51	0.0250	voo	6	1.000	10	0.0250	
goa	14	0.670	60	0.0500	yuk	6	0.844	12	0.0500	
4	<u>sta</u>	<u>14</u>	<u>0.003*</u>	<u>110</u>	<u>0.0024</u>	eri	5	0.0625	15	0.0024
	eri	14	0.007	58	0.0025	eur	5	0.0625	15	0.0025
	var	14	0.012	93	0.0026	sto	5	0.0625	15	0.0026
	eur	15	0.032	100	0.0028	inc	5	0.0625	15	0.0028
	sto	14	0.038	86	0.0029	pac	5	0.0625	15	0.0029
	poc	15	0.058	83	0.0031	<u>sta</u>	<u>4</u>	<u>0.125</u>	<u>10</u>	<u>0.0031</u>
	inc	14	0.058	83	0.0033	lav	5	0.125	14	0.0033
	ama	15	0.064	93	0.0036	gen	5	0.125	14	0.0036
	lav	14	0.068	82	0.0038	sin	5	0.125	14	0.0038
	gen	14	0.091	80	0.0042	nua	5	0.125	14	0.0042
	chi	14	0.135	77	0.0045	var	5	0.1875	13	0.0045
	bez	14	0.326	69	0.0050	poc	4	0.25	9	0.0050
	pac	14	0.426	66	0.0026	ama	4	0.25	10	0.0026
	sin	14	0.583	62	0.0063	moj	4	0.25	1	0.0063
	moj	15	0.600	50	0.0071	cur	4	0.25	9	0.0071
	cur	15	0.706	59	0.0083	bez	5	0.3125	12	0.0083
	cro	14	0.761	58	0.0100	rab	5	0.4375	11	0.0100
	nua	14	0.875	49.5	0.0125	cro	5	0.625	10	0.0125
	ban	14	0.950	54	0.0167	clo	5	0.625	5	0.0167
	rab	14	0.975	51.5	0.0250	ban	5	0.7656	9	0.0250
clo	14	38.000	0.6247	0.0500	chi	5	0.812	9	0.0500	

-Comparing sexual scans and matched control scans

During matched control scans, male long-tailed macaques were positioned at larger distances from the alpha male (mean: $12.12 \pm \text{SD } 3.2$) than females (mean: $10.12 \pm \text{SD } 3.59$). (Kolmogorov-Smirnov test: $D = 0.7$, $N_1 = 6$, $N_2 = 15$, $p = 0.03$). There was no difference in the distance of females towards the alpha male between sexual scans (mean: $11.36 \pm \text{SD } 3.49$) and matched control scans (Wilcoxon signed rank test: $V = 85$, $N = 15$, $p = 0.17$). However, during sexual scans, females were at larger distances (mean: $10.6 \pm \text{SD } 2.5$) from the third ranking bystander female than during matched control scans (mean $8.3 \pm \text{SD } 3.3$) (Wilcoxon signed rank test: $V = 100$, $N = 14$, $p = 0.001$).

There was no difference in the distance of males towards the alpha male between sexual scans (mean: $12.13 \pm \text{SD } 3.16$) and matched control scans (Wilcoxon signed rank test: $V = 16$, $N = 6$, $p = 0.31$). None of the other (male or female) bystanders had a significant effect on the position of sexual behaviour of (male or female) group members.

Group 4

-Comparing sexual scans and general scans

During general scans, male long-tailed macaques were positioned at larger distances from the alpha male (mean = $13.76 \pm \text{SD } 2.01$) than females (mean = $10.6 \pm \text{SD } 1.70$) (Kolmogorov-Smirnov test: $D = 0.75$, $N_1 = 18$, $N_2 = 4$, $p = 0.034$). During sexual scans, females were at significantly larger distances from the alpha male (mean: $15.91 \pm \text{SD } 3.93\text{m}$) than during general scans (Wilcoxon signed rank test: $V = 133$, $N = 16$, $p = 0.0002$). For males results were in the same direction of larger distances during sexual scans (mean = $17.40 \pm \text{SD } 2.69$) compared to general scans, however, this difference was not significant (Wilcoxon signed rank test: $V = 10$, $N = 4$, $p = 0.13$).

Other individuals than the alpha male also influenced the position of group members during sexual behaviour. The distance to bystander females during sexual scans was larger than during general scans when distances were calculated from the 19th ranking bystander female (Wilcoxon signed rank test: ($V = 118$, $N = 15$, $p = 0.0002$). None of the other (male or female) bystanders significantly influenced the positions of (male or female) group members during sexual behaviour. The audience effect strength of a (female or non-alpha male) bystander on the positions of females during sexual behaviour (MOD) was significantly dependent on the rank of the bystander (GLM: coefficient = $-0.13 \pm \text{SD } 0.05$, $t = -2.55$, $p = 0.02$), but not on the bystander's general proximity to the alpha male (GLM: coefficient = $-0.08 \pm \text{SD } 0.13$, $t = -0.58$, $p = 0.57$).

-Comparing sexual scans and matched control scans

During matched control scans, the distance from the alpha male for non-alpha males (mean = $14.26 \pm \text{SD } 1.54$) did not differ significantly from that for females (mean = $12.47 \pm \text{SD } 2.58$) (Kolmogorov Smirnov test: $D = 0.56$, $N_1 = 4$, $N_2 = 16$, $p = 0.26$). Females tended to be further away from the alpha male during sexual scans (mean = $15.72 \pm \text{SD } 6.57$) than during matched control scans, but after Bonferroni correction this was not significant (Wilcoxon signed rank test: $V = 110$, $N = 14$, $p = 0.003$). Likewise, each of the males was positioned further away from the alpha male during sexual scans (mean = $16.90 \pm \text{SD } 2.73$) than during matched control scans, but this difference was not

significant (Wilcoxon signed rank test: $V = 0$, $N = 4$, $p = 0.13$). None of the other individuals had a significant effect on the position of sexual behaviour of group members.

DISCUSSION

Sneaky mating has been documented in both rhesus (Ruiz de Elvira and Herndon 1986, Overduin-de Vries et al. 2012) and long-tailed (Overduin - de Vries et al. 2012) macaques. However, it remains unclear which (cognitive) mechanisms are underlying these behaviours. We systematically analysed whether sneaky mating results from (1) exploiting peripheral positions, (2) creating peripheral positions, (3) sexual behaviour near opaque objects, (4) sexual behaviour behind opaque objects or (5) true hiding. Additionally, we investigated for which bystanders sexual behaviour is concealed, and what characteristics of bystanders determine their effect on the concealment of sexual behaviour of group members.

Surprisingly, none of the four observed groups systematically used opaque objects to hide sexual behaviour. They even did not use the screens when these were fully opaque, relatively large and individuals were given the opportunity to learn their concealing properties, by keeping large opaque screens in the same location of the cage for a longer time period (group 2: 31 days). Sexual behaviour near opaque objects was seldom observed, and when observed, it equally often occurred on the side visible and invisible for the alpha male. These negative results may be due to the limited space in captivity. If hiding places are not distant enough from bystanders, individuals may be too afraid that a bystander might pop up from behind the screen. Alternatively, certain characteristics of our screens may not have been optimal for the monkeys. However, our results did not change when we considerably increased the available space (group 4 relative to group 1-3), or when we changed the properties of the screens (group 3,4 relative to group 1,2: larger screens, half opaque, full opaque, opaque with peek-holes). Therefore, the most plausible explanation of our results is that macaques do not make use of opaque objects to hide their sexual behaviour, eliminating strategies 3 to 5.

Actually, we have clear evidence for the use of the other strategy to hide sexual behaviour, namely both partners involved in a sexual interaction are actively distancing themselves from bystanders (strategy 2). Males of both macaque species (rhesus and long-tailed macaques) occupied more distant positions from the alpha male compared to females. This is consistent with a peripheral positioning of non-alpha males (Kaufmann 1965, Drickamer 1974, Berard et al. 1994, Inoue and Takenaka 2008, Dubuc et al. 2011). A peripheral position of non-alpha males may intrinsically result in sneaky mating when females willing to copulate approach these males (strategy 1) (Berard et al. 1994). That way, no active separation from bystanders is necessary for sneak copulations. Indeed, female macaques occupy more distant locations from the alpha male during sexual behaviour than during non-sexual behaviour. This was found for two different species in four different groups and in one of the groups (group 3) it was even found when comparing positions during sexual behaviour with non-sexual behaviour only five minutes later. However, also male rhesus macaques increase their distance from the alpha male during sexual behaviour compared to non-sexual events. Therefore, sneaky mating in rhesus macaques is more than a consequence of the peripheral position of

non-alpha males and more consistent with strategy 2: creating distant positions. Although similar to rhesus macaque males, long-tailed macaques males were on average further away during sexual than non-sexual events, this effect was not significant. This lack of result may be due to limited sample size and statistical power, rather than a difference between species. Namely, results of long-tailed macaque males were in the same direction as rhesus males; nine out of ten observed long-tailed macaque males occupied positions further away from the alpha male during sexual scans than during general scans, but the sample sizes per group (six and four males) were too small to reach significance. Moreover, when comparing sexual scans with the scans made five minutes after a sexual behaviour (matched control scans), controlling for differences in activity level, it was found that all but one of the ten long-tailed macaque males had longer distances from the alpha male during sexual scans. Presumably, both females and males distance themselves from the alpha male during sexual behaviour, implying that if females seek non-alpha males at the periphery of the group, the female and non-alpha male move away even further from the alpha male before they start copulating. Therefore, sneaky mating in both macaque species is more than a result from the peripheral positioning of non-alpha males and comprises active distancing from the alpha male (strategy 2).

Within the long-tailed macaque groups, the effects of bystander individuals other than the alpha male were studied. In addition to the effect of alpha males, also some females influenced the positioning of sexual behaviour of female group members. One of the females in group 3 also had a significant bystander effect when comparing sexual scans with matched control scans. Therefore (at least for this female), larger inter-individual distances during sexual behaviour compared to non-sexual behaviour were not just a consequence of lower activity levels during non-sexual behaviour.

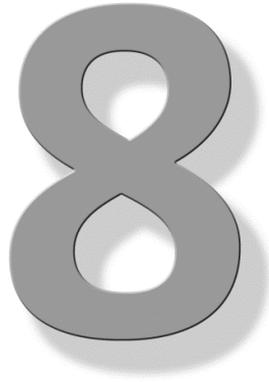
We could not find evidence for males distancing themselves from other bystanders than the alpha male. Therefore, the effects of female bystanders on other females may be due to the peripheral positioning of non-alpha males. However, if only male peripherality would be responsible for the effects of female bystanders on other females, it is expected that all female bystanders would have had an effect on other females, which was not the case. Alternatively, the sample size of males was too low to statistically proof the weaker audience effects of non-alpha individuals. Therefore, high-ranking individuals other than the alpha male possibly have an effect on the positioning of males and females during sexual behaviour. This is consistent with audience effects from non alpha individuals found in rhesus macaques (Overduin-de Vries et al. 2012) and long-tailed macaques (Overduin - de Vries et al. 2012).

The effect of other individuals than the alpha male maybe a side effect of the alpha male's effect in combination with the proximity of some individuals to the alpha male. However, in group 3 we found a trend of rank dependent audience effect strengths, that existed in the statistical model despite the significant effect of proximity of the alpha male. Moreover, in group 4 the strength of the effect of an individual was not predicted by this individual's proximity to the alpha male, and the dominance rank of the bystander significantly influenced its audience effect strength. This indicates that specifically high-ranking non-alpha individuals can affect sexual behaviour of group members independently of the alpha male.

From our results it can be concluded that sneaky mating most probably results from tactical deception level 1. Individuals actively create distance between themselves and the audience when involved in sexual behaviour. We have shown that these enlarged distances were specifically linked to sexual behaviour and more than the result from the peripheral positioning of non-alpha males. In order to fulfil the definition of tactical deception level 1 (Byrne and Whiten 1990), the actor must benefit from the action. Individuals may hypothetically benefit from increased distances during sexual behaviour by experiencing less disruptive or punishment behaviours from certain bystanders. However, due to the low frequency of observed disruptions it was impossible to quantify the rate of disruptions at different distances from certain bystanders. Since disruptions are infrequent, long-term observations of a large number of individuals is necessary to confirm this suggestion for tactical deception level 1. No indication for tactical deception level 1.5 or higher is found, because individuals do not show an understanding of the visual perspectives of others, despite the opportunity we gave them to perfectly hide themselves behind one of the provided opaque structures.

In summary, our results indicate that sneaky mating by macaques is not accomplished by searching positions near or behind opaque objects (strategy 3-5). Instead, the peripheral positions of non-alpha males are exploited during sneaky mating (strategy 1: exploiting peripheral positions). However, significant results with rhesus macaque and similar trends of long-tailed macaque males show that non-alpha males further increase their distance from the alpha male during sexual events compared to their positions during non-sexual behaviour. Therefore, both sexes actively increase their distance from the alpha male before engaging in sexual behaviour (strategy 2: seeking peripheral positions). The inhibiting effect on sexual behaviour was not unique for the alpha male. Some females also had comparable effects, and the audience effect strength depended on the dominance rank of male and female bystanders. Therefore, dominance-dependent sexual competition appears to be an important factor in the sexual dynamics of macaques. The mechanism used to conceal sexual behaviour most probably involves tactical deception level 1. However, in order to fulfil the definition of tactical deception level 1, additional evidence is necessary on the actual benefits obtained from increasing distances from potential disruptive bystanders. Reducing sexual competition is not necessarily accomplished by high cognitive mechanisms such as visual perspective taking. In contrast, our results show that the concealment of sexual behaviour in macaques most probably results from operant conditioning to enlarge the distance from bystanders during sexual interactions.





Summary and Discussion

Cognitive complexity is one of the main characteristics that make humans unique animals. One of the complex elements of human cognition is Theory of Mind (ToM). ToM is made up of different underlying cognitive capacities differing in cognitive complexity. Since separate elements of ToM may be useful without having a full blown ToM, several elements of ToM may be present in other animals, and especially their presence and distribution in non-human primates may provide their evolutionary history and may reveal their function. Visual Perspective Taking (VPT), the capacity to understand what other individuals can see, is one of the elements of ToM that is thought to be present in non-human primates.

The aim of this thesis is to study the presence of VPT and its prerequisites in monkeys, and subsequently investigate whether these cognitive capacities are used in their social life.

VPT in non-human primates

Low level gaze following is present in many animals, including all studied primate species. A next step to VPT requires that an individual cannot only discern the gaze direction, but also the target of attention. This is a prerequisite for VPT. So far studies measured the presence of this capacity by studying whether monkeys can follow gaze geometrically i.e. around a barrier (Burkart and Heschl 2006, Amici et al. 2009, Goossens et al. 2012). However alternative explanations involving cognitively simpler mechanisms such as move in the gazed direction are possible. Moreover, positive results in another paradigm may be explained by a conditionally learned expectancy (Scerif et al. 2004). We

developed a new paradigm that tests the existence of this prerequisite of VPT (chapter 2 & 3).

Although the presence of VPT is evident in apes (Hare et al. 2000, Melis et al. 2006), in monkeys results are controversial (Hare et al. 2003, Flombaum and Santos 2005, Burkart and Heschl 2006, Burkart and Heschl 2007). One feasible option for the lack of unequivocal evidence for VPT in monkeys is that the paradigms used in earlier research were not optimal and positive results may be explained by cognitively simpler rules than VPT. Therefore, we adjusted an existing paradigm to study VPT (Hare et al. 2000, Hare et al. 2003) that tests whether monkeys prefer to approach a food item that cannot be seen by their opponent (Chapter 4). Our adjustments of the original experiment excluded cognitively simpler rules, namely behavioural reading and choosing less accessible food.

In *Chapter 2*, we confronted long-tailed macaque subjects with pictured social scenes involving their group members that were either congruent or incongruent with the dominance hierarchy of the group. The pictured scenes only differed in the facial expression and target of attention of one of the pictured individuals, and results indicated that subjects were able to understand the target of attention of this pictured individual. In contrast, in *Chapter 3* by using a similar design, we find no evidence that common marmosets, a New World monkey species, understand the target of attention. Although, this confirms the proposed increase in complexity of cognitive capacities from New World to Old World monkeys, some critical notes have to be made. First, the results in long-tailed macaques were exclusively found for males, and it is not clear why females did not respond to our stimuli the way the males did. Second, the methods in *Chapter 3* were not optimal for common marmosets, since they were not able to recognize familiar conspecifics from pictures, and the pictures involving the target of attention were qualitatively less well constructed than in *Chapter 2*. Therefore, we may have failed to establish the capacity to understand the target of attention in common marmosets and additional research is warranted. Nevertheless, we can conclude that a prerequisite of VPT, understanding the target of another's attention is present in Old World monkeys (Figure 1). This supports the view that primitive forms of complex human cognitive capacities are found in monkey species.

In *Chapter 4* we find evidence that long-tailed macaques understand what their competitor sees. They were able to use two different strategies in order to maximise their food intake. The most often used strategy was applied in cases where subordinate subject monkeys were not quick enough to obtain both pieces, they preferably approached a food item that was invisible for their opponent. This strategy is similar to the strategy used by subordinate chimpanzees (Hare et al. 2000), and it limits the risk of being punished by the opponent, because the opponent was not aware of the invisible food object. When our subjects obtained both food items before the dominant could, they adopted an alternative strategy and preferred to approach the visible food item first. This way they secured the possession of the most at risk food item, before they approached the other food item that the opponent was not aware of. This strategy is similar to the strategy used by dominant chimpanzees (Hare et al. 2000). Like dominant chimpanzees, long-tailed macaques in some trials may have been secure enough about their speed of obtaining the food relative to their opponent and, therefore, adopted the alternative strategy.

The fact that we found positive results for VPT, whereas former experiments with monkeys solely produced negative results may be caused by several differences in methods and species. (1) In previous studies no results are provided about the number of food items obtained per trial. If the proportion of trials in which the alternative strategy is used was near 50 %, no overall preference may be found. (2) While our subjects continuously saw their competitor, for capuchins and marmosets the competitive situation may not be obvious once the dominant competitor was no longer visible during the choice of the subject. (3) Second, marmosets and capuchins are monkeys with a relatively egalitarian social structure compared to long-tailed macaques, and may, therefore, be less sensitive to competitive situations. (4) Differences in cognitive flexibility between Old World monkeys and New World monkeys may underlie the difference. In order to investigate whether the reported difference between species is due to a difference in methods, social or cognitive abilities, several species differing in cognitive flexibility and social tolerance should be tested with the current method.

It can be concluded that our study expanded the capacity of VPT from humans and apes to Old World monkeys. Therefore, VPT may be a feature that was present in the common ancestor of Old World monkeys and humans (Figure 1) and future studies with other species and similar methods may reveal whether VPT is present in more monkey species. This opens the possibility that cognitive advanced capacities such as geometric gaze following, may have evolved earlier than what is now evident from experimental studies.

VPT in a social context

Several hypotheses exist on the selective pressure behind the evolution of complex cognitive capacities (Parker and Gibson 1977, Byrne and Whiten 1988, Dunbar 1995, Herrmann et al. 2007) such as VPT. The best known hypothesis is the social brain hypothesis (Byrne and Whiten 1988, Dunbar 1995), which predicts that primates evolved relatively large and complex brain structures because they have complicated social systems. Living in large social groups with complex social relationships requires extensive processing of social interactions.

Moreover, an individual may learn crucial information about its environment when observing and processing interactions of group members with their (social) environment. Additionally, living in large social groups is associated with intergroup competition for resources, and cognitive capacities may aid an individual to outwit its group members. Therefore, it is hypothesized that in large groups of animals, individuals with complex cognitive capacities, profit in several ways. First, an individual may learn tactics to obtain individuals may learn about dominance relationships between group members by observing resources such as food or copulation partners before their group members do. Second, interactions among others. This may prevent individuals from making social mistakes such as threatening an individual which occupies a relatively high dominance rank. Third, individuals may learn about the quality of potential mates. By observing sexual interactions or attention of same sexed individuals towards certain individuals of the opposite sex, an

individual may strategically apply mate copying (Yorzinski and Platt 2010). Fourth, individuals may locate food and predators more easily if they follow the gaze of their group members. Fifth, individuals may learn characteristics of objects in their

environment such as whether they are tasty or not by observing emotions of group members directed at certain objects. However, these benefits are all hypothetically and few studies have empirically shown the benefits of ToM and specifically VPT within a social context.

One of the social contexts where VPT might be beneficial is sexual behaviour. Sexual behaviour in male macaques is often skewed, and most sexual interactions are performed by the alpha-male (Altmann 1962). However, females and subordinate males do not necessarily benefit from this monopolisation, and may hide their copulations in order to avoid punishment by the alpha male. Although several studies have investigated whether sexual behaviour is inhibited by the presence of certain individuals (Ruiz de Elvira and Herndon 1986) or concealed (Gygax 1995), the inhibition or concealment of sexual behaviour was not assigned to the presence of a particular audience (Ruiz de Elvira and Herndon 1986, Gygax 1995). Moreover, it was not clear whether a preference for opaque structures was actually linked to sexual behaviour or based on a general preference to reside near these structures (Gygax 1995). Therefore, we studied in captive social macaque groups if sexual behaviour is concealed for specific individuals. Moreover, we investigated whether they use (prerequisites of) VPT in a sexual context. Because hiding may be based on different cognitive mechanisms with or without Visual Perspective Taking, we investigated which cognitive method was used by the monkeys. We tested this in rhesus and long-tailed macaques.

In *chapter 5* we found that if rhesus macaques have access to two visually separated compartments, they perform sexual behaviour almost exclusively in absence of the alpha male, consistent with an audience effect of the alpha male on the sexual behaviour of group members. Based on the literature, we expected that the concealment of copulations most likely results from female initiatives since females benefit from reduced interruptions (Ruiz de Elvira and Herndon 1986, Manson 1996), while male benefits are controversial. Males do not experience fitness loss from disruptions (Berard et al. 1994), but may benefit from reduced aggression (Wilson 1981, Bruce and Estep 1992). Indeed, we found evidence that females contribute to the concealment of sexual behaviour by soliciting copulations less often in presence than in absence of the alpha male. However, a trend in male behaviours indicates that also males contribute to the concealment of sexual behaviour. This suggests that either both sexes benefit from hiding their sexual interactions, or that only one partner has direct benefits, while the other indirectly benefits if its partner is more willing to copulate.

Additionally, the audience effect was not unique for the alpha male. An upcoming non-alpha male also inhibited copulations of its group members, and three other non-alpha males inhibited female copulation solicitations. Therefore, sexual behaviour is not only concealed for the alpha male, but also for other males. Although the results suggest an audience specific effect, it is not clear whether the audience effects found are due to a specific avoidance of certain individuals rather than avoiding (almost) all individuals. Therefore, in the next chapter on long-tailed macaques, we investigated not only the effect of males, but also the effect of females, and we statistically measured each individual's audience effect strength, which enabled us to link the audience effect strength to certain bystanders and their characteristics. Moreover, we investigated whether the separation from the group of a dyad involved in sexual behaviour is a

coordinated behaviour by both partners or the result of one partner that approaches the other partner which just happens to be separated from the group.

In *Chapter 6* we found that an audience effect on sexual behaviour was also found in long-tailed macaques. Similar to rhesus macaques, we found that besides the alpha male, also other males had audience effects. Additionally, we found audience effects of several females. The audience effect was strongest in the alpha male, and audience effects by males significantly depended on the bystander male's rank. In contrast, the audience effects of females were independent of rank. The effects of non-alpha bystanders were independent of the bystanders proximity to the alpha male. Therefore, the reported audience effects resulted from avoidance of specific individuals rather than the avoidance of the alpha male and some individuals that just happen to be in his proximity. Similar to rhesus macaques, long-tailed macaque females were actively involved in the concealment of sexual behaviour by soliciting copulations more often in the absence than in the presence of the alpha male. Moreover, the active involvement of males that was only a trend in rhesus macaques was significant in long-tailed macaques. Presumably both males and females benefit from concealing sexual behaviour from the alpha male, in line with the costs associated with the disruption of sexual behaviour for both males (Wilson 1981, Bruce and Estep 1992) and females (Ruiz de Elvira and Herndon 1986, Manson 1996). Alternatively, one sex benefits, while the other sex indirectly benefits if the partner is more willing to copulate in occluded conditions.

Since both sexes contribute to the concealment of sexual behaviour, the audience effect may be the result of a coordinated behaviour. Females and subordinate males may tactically deceive the alpha male, by separating themselves in a coordinated way, indicating tactical deception, from the group (Byrne and Whiten 1990). If the separation of one individual from the group quickly follows after the separation of its copulation partner, we would have some evidence that at least one of the partners intentionally separates itself. However, we found no evidence that the separation from the group of both partners involved in a sexual interaction is a coordinated action, since the time between both partners' separation from the group was not significantly different between sexual and non sexual contexts. However, the results were in the expected direction, and additional sampling may reveal a significant coordination of separation from the group. Altogether, concealed copulations are most likely the result of an exploitation of the peripheral positioning of non-alpha males. Males spent more time in the group periphery than females, they spent more time in absence of the alpha male than females, and males were often the first of a dyad to be separated from the group before a sexual event. With sexual behaviour predominantly taking place in the periphery of the group, concealment of sexual behaviour may simply result from females approaching subordinate males which just happen to be in the group periphery. However, since in both studies (chapter 5 and 6) our data were corrected for the time each dyad spent together in presence and absence of the bystander, the audience effects cannot be attributed to the periphery of non-alpha males only and both females and subordinate males adjust their sexual behaviour to the absence of an audience. Concluding, audience effects most likely result from females approaching non-alpha males in the periphery of the group and subsequently paying attention to whether specific individuals are present.

In chapter 7 we further investigated the mechanisms behind concealed sexual behaviour. We systematically recorded inter-individual distances during sexual and nonsexual behaviour. Additionally, we provided rhesus and long-tailed macaques with several opaque barriers that allowed them to hide their sexual behaviour. In line with the effect of the peripheral positions of non-alpha males in Chapter 6, we found that female rhesus and long-tailed macaques significantly increased their distance from the alpha male during sexual events, compared to non-sexual events. Moreover, rhesus macaque males significantly increased and long-tailed macaque males tended to increase their distance from the alpha male during sexual interactions, rendering the increase in distance from the alpha male more than the result of a peripheral positioning of non-alpha males. To our surprise, and in contrast with previous research (Gygax 1995), individuals of both species only sporadically copulated near opaque objects and these copulations were not consistently hidden from the alpha male. In the study by Gygax the monkeys were provided a high number of screens and no elevated sitting beams without barriers, enhancing the frequency of any behaviour near the barrier. In addition, half of the screens were located at a peripheral position. Indeed, the peripheral screens were used most (Gygax 1995). Therefore, the results of Gygax probably do not reflect a choice of the animals to copulate near barriers. Concluding, concealment of sexual behaviour in macaques is not based on a strategy to copulate near or behind opaque objects. Nor is it the result of the peripheral positions of non-alpha males. We found no evidence that males and females tactically separate themselves from the group (Chapter 6). Therefore, the concealment of sexual behaviour is not based on the highest level of tactical deception (level 2) where individuals understand that they deceive someone. Instead, both females and males actively increase their distance from the alpha male before they initiate sexual behaviour. This suggests evidence for the lowest level of tactical deception (level 1): “acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the benefit of the agent”. The observed behaviour may be explained as tactical deception level 1 because individuals actively avoided particular competitors (Byrne and Whiten 1992) and it is clear that distancing is specifically linked to sexual behaviour suggesting a benefit of the agent by concealed sexual behaviours. However, due to low numbers of disturbances we were not able to link distancing to benefits of reduced disturbance. Therefore, additional research is necessary with longitudinal data on disturbances related to spatial positioning.

Comparison of ToM in different non-human primate species

Current evidence indicates that primate species possess cognitive capacities underlying ToM, but that species from different clades differ in the cognitive capacities they exhibit (Figure 1). An increase in complexity of cognitive capacities is found within the primate lineage in line with their relatedness to humans (Deaner et al. 2006). In order to comprehend the chronological steps of primate cognitive evolution it would be best to do comparative analysis of cognitive capacities in many primate species and reconstruct the evolution of each cognitive capacity along the phylogenetic tree. The problem is that not all species have been tested experimentally for all cognitive capacities. Therefore, it may be better to look at the presence of separate cognitive capacities in separate clades

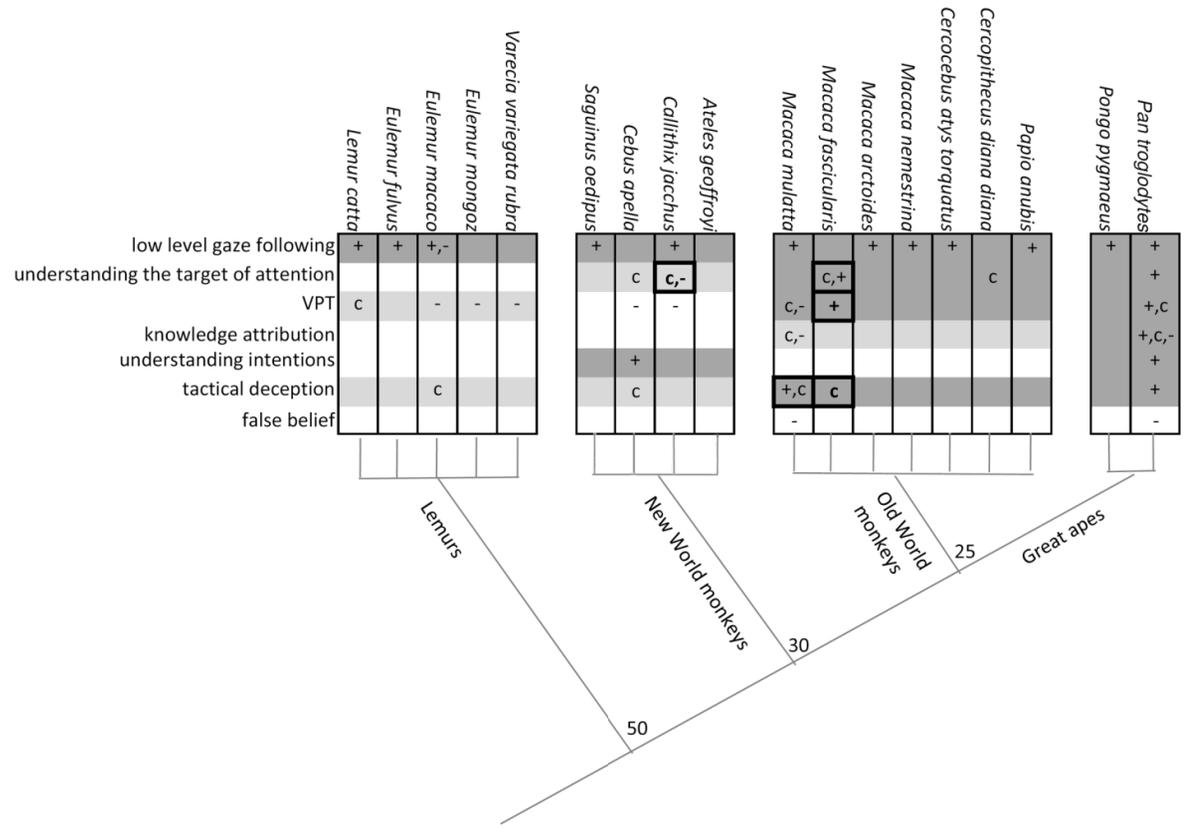


Figure 1: reconstruction of the evolution of cognitive capacities (on the left column) in non-human primate species (top row). Signs below species names indicate the results for that species concerning a specific cognitive capacities: (-) negative results; (c) controversial evidence; (+) unequivocal evidence. Bold circumferenced signs indicate findings within this thesis. Shadings indicate the presence of cognitive capacities on the clade level: *dark* grey: at least one specie within the clade has unequivocal evidence; light grey: no unequivocal evidence, but at least one species has controversial evidence; no shading: only negative results or non tested species. Numbers between separate branches in the phylogenetic tree indicate the number of million years ago each divergence occurred (Byrne 2000).

of primates: (1) great apes, (2) Old World monkeys, (3) New World monkeys, and (4) lemurs (Figure 1). Indeed, simple cognitive capacities such as reflexive gaze following are present in many primate species ranging from the most distantly related non-human primate species, the lemurs (Anderson and Mitchell 1999, Shepherd and Platt 2008, Ruiz et al. 2009), to New World monkeys (Neiworth et al. 2002, Burkart and Heschl 2006), Old World monkeys (Tomasello et al. 1998, Vick and Anderson 2003) and our closest relatives the apes (Itakura and Tanaka 1998, Tomasello et al. 1998). Whereas some, more complex capacities: geometric gaze following and knowledge attribution, are exclusively unequivocally evidenced in apes (Tomasello et al. 1999, Hare et al. 2000, Hare et al. 2001, Melis et al. 2006, Okamoto-Barth et al. 2007). Moreover, understanding false belief, one of the most complex cognitive capacities is probably a uniquely human capacity (Call and Tomasello 1999, Hare et al. 2001, Kaminski et al. 2008). Up to here the presence of cognitive capacities is consistent with a proposed general increase in cognitive complexity during primate evolution. However, there are three relatively complex capacities that deviate from this pattern and that are found both in apes and in monkey species despite the absence of cognitively simpler capacities in these species. Tactical deception is found in Old World monkeys (Santos et al. 2006, This thesis, Chapter 7); understanding intentions is found in New World monkeys (Phillips et al. 2009) and we found evidence for VPT in an Old World monkey (This thesis, Chapter 4). There are two ways to interpret these patterns. On the one hand VPT, deception and understanding intentions may constitute another domain of cognition than the other cognitive capacities and may have evolved independently. On the other hand cognitively simpler capacities which are currently only evidenced in apes; understanding intentions and Geometric gaze following, may have evolved earlier in the primate lineage than what is now evident from comparative studies. Therefore, additional studies on understanding intentions and geometric gaze following are necessary in order to investigate the presence of these capacities in other primates than apes and humans.

An alternative approach to study the evolution of primate intelligence is to combine several cognitive capacities into one single component reflecting a general level of intelligence. This approach was used to combine reported incidents of innovation, tool use, extractive foraging, tactical deception and social learning within a general intelligence “g”. It was found that high levels of general intelligence evolved independently at least four times: in capuchins, baboons, macaques and apes. This contrasts with the view of an increase of intelligence from prosimians to New World monkeys to Old World monkeys to apes, but it is in concordance with the presence of relatively complex cognitive capacities in the visual domain. Although no data was found for baboons (besides reflexive gaze following), capuchins were found to understand intentions (Phillips et al. 2009), macaques possess VPT (Chapter 4) and tactical deception (Santos et al. 2006), and apes possess high level gaze following, VPT, knowledge attribution, understanding intentions and tactical deception. None of these capacities was found in other primate species than capuchins, macaques and apes.

The social brain hypothesis

The social brain hypothesis predicts that cognitive capacities such as VPT give individuals benefits in the social context. Although we find evidence that monkeys *can* use VPT

(Chapter 4), we found no evidence that Visual Perspective Taking is actually used in naturally occurring social behaviour of monkeys (Chapter 7). Hiding oneself involves manipulating what another individual sees, this may be more cognitively demanding than understanding what another individual sees. Possibly monkeys are not able to make this higher cognitive step while they are capable of understanding what another individual sees. Although the capacity of a subordinate primate to obtain food items in the vicinity of dominants by preferably approaching items invisible for their opponent (Hare et al. 2000, This thesis, Chapter 4) most probably gives them benefits in their natural social context, the setting in these studies is experimentally manipulated, and it remains necessary to proof the use of VPT in natural settings concerning food competition or sexual behaviour.

Previous research on other capacities related to ToM in a social context are sparse. Although gaze following is used by monkeys in their natural behaviour (Shepherd and Platt 2008), it is not known whether they actually benefit from this behaviour. It is known that within an experimental setting, target objects are more easily detected if the target is cued by the gaze of a conspecific (Deaner and Platt 2003). However, whether this also holds in natural settings is unknown. Similarly, tactical deception is reported in several primate species' natural behaviour (Byrne and Whiten 1990). In the reported events, the actors benefitted from misleading other individuals. However, because these reports are all anecdotal, it is difficult to ascertain the use of tactical deception. Apart from finding benefits of ToM capacities in social contexts, evidence for the social brain hypothesis has been found by comparing the group structure of different primate species and correlate that with the level of cognitive complexity associated with those species. The social brain hypothesis predicts that species with more complicated social group structures have evolved more complex brain structures. Some of the measurements of social complexity have been found to correlate with measures of brain structure: Social living mammals (monkeys, wolves, dolphins) have relatively larger brains than solitary living mammals of the same size; (Byrne 1997); Neocortex ratio is correlated with group size in primates and bats (Byrne 1997). However, both the complexity of social groups and the complexity of brains are difficult to measure. One measure of group complexity is group size, but also the number of matriline within one group, the stability of dominance hierarchies, the presence of alliances etc. may complicate group structures (Whiten and Byrne 1997). On the other hand, brain complexity may be measured by absolute brain size, brain size relative to body size, absolute neocortex size, the ratio between the size of the neocortex and the size the rest of the brain and executive brain ratio etc (Byrne 1997, Reader et al. 2011). For most of these brain size measurements it is unknown how much they relate to a species cognitive capacities. Nevertheless, some of these measures correlated with g_s , a general level of intelligence measured by the number of reported incidences of behavioural flexibility (Reader et al. 2011). However, comparative analysis of 62 primate species revealed no correlation between the species' g_s score and group size (Reader et al. 2011). Although, group size may not be the best measure of social complexity, there were additional results questioning the social brain hypothesis. Cognitive capacities in different domains: social, technical and ecological, most probably have coevolved suggesting an increase in general intelligence rather than specialisations in specific domains (Reader et al. 2011). This supports the hypothesis of a general increase in cognitive capacities in primate evolution

(Deaner et al. 2006) rather than a socially driven increase (Byrne and Whiten 1988, Dunbar 1995).

Another way of comparing social structure with cognitive capacities is to look at species with evidenced cognitive capacities, and compare their social structures with those of species for which negative results exist. Therefore, it is necessary that many more primate species are studied for their cognitive abilities by using experimental paradigms that can be used in many species. For example, several species have been studied for VPT by using the food competition paradigm, originally designed by Hare (2000). Although several difference in the methods may account for differences found between species (Chapter 4), let's for reasons of simplicity assume that if all species would be tested in the same way the results for the different species would remain as is. Then, positive results exist for chimpanzees and long-tailed macaques, while negative results exist for capuchins and common marmosets (Figure 1). The social organisation of these species may indicate what social factors may enhance this particular cognitive capacity. Chimpanzees live in large fission fusion groups containing up to more than a hundred individuals that regularly interact with each other (Watts 1998). These large groups are subdivided into smaller parties of 1 to 47 individuals that only exist a few days and are dependent on habitat characteristics and temporal changes such as female oestrus (Matsumoto-Oda et al. 1998). Males form linear dominance hierarchies (Goldberg and Wrangham 1997). Females also form dominance hierarchies and strong social bonds (Goodall 1986). Similarly, long tailed macaques live in large groups of 6 to 58 individuals (van Schaik and van Noordwijk 1985) that may temporarily split in smaller parties in times of food scarcity (van Schaik and Van Noordwijk 1988). In long-tailed macaques, both males and females form linear dominance hierarchies and form social bonds (Massen et al. 2012). In contrast, capuchins and marmosets live in smaller groups of respectively 10 to 25 (Izawa 1980) and 3 to 15 (Stevenson and Rylands 1988, Ferrari and Lopes Ferrari 1989) individuals. Capuchin males and females have dominance hierarchies that are correlated with age. Apart from definite fissions when group sizes approach 20 and the migration of young males, capuchin groups remain stable over a number of years (Janson 1990). Capuchin males form strong social bonds (Izawa 1980). Marmoset groups are stable unless one of the adults dies resulting in the group falling apart (Lazaro-Perea 2001). Apart from kin relations they do not form social bonds. The few breeding individuals are dominant over non-breeders in the group, and among non-breeders the dominance hierarchy is related to age (Digby 1995). Therefore, if the different results of VPT experiments with different species reflect true differences in this cognitive capacity between species, the evolution of VPT can be linked to large group size, regular fission fusion dynamics and dominance hierarchies which are independent of age, since these social factors are characteristic for primate species that possess VPT. Future studies with additional non-human primate species may reveal whether this link between social factors and VPT is consistent over the primate lineage. The difference found between the social structures of species with and without VPT (Hare et al. 2000, this thesis, Chapter 4, Hare et al. 2003, Burkart and Heschl 2007) is suggestive for a socially driven evolution of VPT.

Concluding remarks

Simple cognitive capacities underlying ToM such as gaze following are present in all primate species. A slightly more advanced cognitive capacity: understanding the target of attention is present in an Old World monkey (Chapter 2), but could not be evidenced in a New World monkey (Chapter 3). One step higher on the scale of cognitive complexity; VPT, being able to understand what other individuals can see, is present in Old World monkeys (Chapter 4). The results of VPT in the Old World monkey were similar to the results with apes (Hare et al. 2000). Therefore, monkeys share complex cognitive capacities with apes, and primitive forms of complex human cognitive capacities are not only present in apes, but also in monkey species. Although sneaky mating is often used as an example of the use of complex cognitive capacities such as VPT and tactical deception in a social context, at least two species of Old World monkeys (rhesus and long-tailed macaques) probably do not use VPT when concealing sexual behaviour, because monkeys did not make use of consistently provided opaque objects (Chapter 7). Moreover, we found no evidence that high level tactical deception (>level 1.5) (Byrne and Whiten 1990) was used, because two partners involved in a sexual interaction did not coordinate their separation from the group (Chapter 6). Instead, these monkeys use simpler cognitive mechanisms, namely creating distance between themselves and the audience while involved in sexual behaviour (Chapter 7). This strategy may involve low level tactical deception (level 1) (Byrne and Whiten 1990), since individuals specifically search peripheral positions during sexual behaviour, and not during non-sexual behaviour. In order to confirm this proposition, more evidence is needed on the benefits obtained by peripheral sexual behaviour.



Nederlandse samenvatting

De intelligentie van primaten

Omdat intelligentie één van de belangrijkste eigenschappen is die waarschijnlijk substantieel verschilt tussen mensen en andere dieren, is kennis van de evolutie van menselijke intelligentie zeer belangrijk voor het reconstrueren van de evolutie van de mens. Een belangrijk element van de humane intelligentie, dat een groot deel van het menselijke gedrag beïnvloedt, is "Theory of Mind" (ToM): het vermogen om mentale toestanden toe te schrijven aan jezelf en anderen, en te begrijpen dat anderen gedachten, verlangens en intenties hebben die kunnen verschillen van die van jezelf (Premack and Woodruff 1978). ToM bestaat uit verschillende onderliggende capaciteiten die variëren in cognitieve complexiteit. Om meer te weten te komen over de evolutie van menselijke intelligentie is het belangrijk om te weten welke onderdelen aanwezig zijn in de huidige primatensoorten en dit in verband te brengen met hun verwantschap aan de mens. Cognitieve capaciteiten die ten grondslag liggen aan ToM die in dit proefschrift besproken worden zijn: *het begrijpen van het object van aandacht* en *Visueel Perspectief Nemen*. Deze cognitieve capaciteiten kunnen in sociaal gedrag toegepast worden voor *tactische misleiding*.

Hoewel het volgen van iemand anders zijn blikrichting soms een reflexmatig gedrag is of een aangeleerde truc om bepaalde objecten te traceren, kan het ook gebaseerd zijn op een ingewikkelder mechanisme, waarbij individuen begrijpen dat een andere individu naar een interessant object (*het object van aandacht*) kijkt. Voor zowel mensapen (Tomasello et al. 1999, Okamoto-Barth et al. 2007) als voor andere apensoorten (Burkart and Heschl 2006, Amici et al. 2009, Goossens et al. 2012) is er bewijs dat het volgen van blikrichting meer dan een reflexmatig gedrag is, omdat ze een blikrichting geometrisch kunnen volgen, d.w.z. naar een verborgen locatie. Hoewel er overtuigend bewijs is dat mensapen weten dat een ander naar iets kijkt, kunnen de resultaten voor andere apen worden verklaard door simpelere verklaringen dan het begrijpen van het object van aandacht.

Visueel Perspectief Nemen (VPN) stelt iemand in staat om te begrijpen welke objecten zichtbaar zijn vanuit een ander standpunt en dat voor hem zichtbare objecten onzichtbaar kunnen zijn voor anderen, en vice versa (Salatas and Flavell 1976, Flavell 1981). VPN is onbetwistbaar aangetoond in mensapen (Hare et al. 2000, Hare et al. 2006, Melis et al. 2006), maar de resultaten met Oude Wereld apen (Flombaum and Santos 2005) en lemuren (Sandel et al. 2011) kunnen verklaard worden door simpelere mechanismes. Subjecten zouden namelijk eenvoudigweg de ogen van hun concurrent kunnen vermijden terwijl ze het betwiste voedsel benaderen.

Deze cognitieve capaciteiten kunnen worden toegepast in misleidend gedrag. *Tactische misleiding* is het actief achterhouden of veranderen van informatie voor omstanders met als doel hen te misleiden. Tactische misleiding omvat het verstoppen van objecten of gedrag voor anderen of het misleiden van anderen door expres bepaalde signalen te

geven in de verkeerde context. Tactische misleiding wordt beschreven op verschillende niveaus. Niveau 1 bestaat uit "Handelingen uit het normale repertoire van de actor, die zo worden gebruikt dat een ander individu waarschijnlijk een verkeerde conclusie trekt, in het voordeel van de actor" (Byrne and Whiten 1990). Dit type misleiding kan het gevolg zijn van operante conditionering. Dit is aangetoond in lemuren (Genty et al. 2008), Nieuwe Wereld apen (Fujita et al. 2002, Amici et al. 2009, Wheeler 2009), Oude Wereld apen (Santos et al. 2006, Amici et al. 2009) en mensapen (Melis et al. 2006). Tactische misleiding op niveau 2 vereist een bewuste misleiding van anderen en is geen simpele, door operante conditionering, aangeleerde truc. Tactische misleiding op niveau 2 is aangetoond in mensapen (Melis et al. 2006) en Oude Wereld apen (Fujita et al. 2002), maar niet voor Nieuwe Wereld apen en lemuren.

Cognitieve capaciteiten zoals het begrijpen van het object van aandacht en VPN zijn mogelijk geëvolueerd in een gezamenlijke voorouder van Nieuwe Wereld apen en mensen. Echter, de aanwezigheid van deze capaciteiten in Nieuwe en Oude Wereld apen is niet onomstotelijk bewezen, omdat de paradigma's die tot dusverre zijn gebruikt geen uitsluitsel geven. Ook simpeler verklaringen voor het gedrag werden niet uitgesloten. Nieuwe paradigma's zijn nodig, naast het testen van de vele soorten die nog niet getest zijn. Daarom onderzoeken we in dit proefschrift met nieuwe of aangepaste testen de aanwezigheid en het gebruik van VPN gerelateerde cognitieve capaciteiten in makaken: Java-ape en rhesusape (Oude Wereld apen) en trekken we parallellen met penseelaapjes (een Nieuwe Wereld aap).

Een van de belangrijkste hypothesen voor de evolutie van menselijke intelligentie is de "Machiavellian intelligence hypothesis" (Byrne and Whiten 1988, Dunbar 1998). Deze hypothese veronderstelt dat diersoorten met complexere sociale structuren geavanceerder hersenstructuren ontwikkelden om te kunnen omgaan met alle interacties tussen groepsgenoten. Deze soorten ontwikkelden daarom complexe cognitieve capaciteiten die vooral belangrijk waren in een sociale context. Echter, als sociale complexiteit de evolutionaire drijfveer achter de ontwikkeling van cognitieve capaciteit is geweest, is het van belang om aan te tonen dat cognitief complexe capaciteiten voordelen opleveren in een sociale context. Daarom onderzoeken we tevens in dit proefschrift of apen gebruik maken van aan VPN gerelateerde cognitieve capaciteiten in hun sociale gedrag, met name ten bate van tactische misleiding.

Visuele cognitieve capaciteiten in Oude en Nieuwe Wereld apen

In *Hoofdstuk 2* confronteerden we Java-ape met afgebeelde sociale situaties tussen hun groepsgenoten die wel of niet congruent waren met de dominantie hiërarchie binnen de groep. De afgebeelde situaties verschilden alleen van elkaar in de faciale expressie van één van de afgebeelde apen en in hetgeen dat bekeken werd door deze aap, i.e. het object van aandacht. Mannelijke Java-ape keken langer naar de incongruente plaatjes dan naar de congruente plaatjes. Deze resultaten impliceren dat Java-ape in staat waren om te begrijpen waar deze afgebeelde aap naar keek. Bij penseelaapjes (Nieuwe Wereld apen) daarentegen, vinden we in *Hoofdstuk 3* geen indicatie dat ze begrijpen

waar een ander naar kijkt. Hoewel dit zou kloppen met de voorgestelde toename in cognitieve complexiteit van Nieuwe Wereld apen naar Oude Wereld apen, moeten er een aantal kritische kanttekeningen gemaakt worden. Ten eerste waren de resultaten met de Java-aperen alleen gevonden bij mannetjes en is het onduidelijk waarom vrouwtjes niet op dezelfde manier op de stimuli reageerden als de mannetjes. Ten tweede faalden de penseelaapjes mogelijk omdat de methodes in hoofdstuk 3 niet optimaal waren voor de penseelaapjes, daar de plaatjes van de sociale situaties minder goed geconstrueerd waren dan in *Hoofdstuk 2*. Bovendien bleken de penseelaperen niet in staat bekende individuen van plaatjes te herkennen. Desondanks kunnen we wél concluderen dat een basisvoorwaarde voor VPN, *het begrijpen van het object van aandacht*, bestaat in oude wereld apen. Dit ondersteunt de hypothese dat capaciteiten, die de basis vormen voor de complexe menselijke cognitieve capaciteit ToM, aanwezig zijn bij apen.

In *Hoofdstuk 4* tonen we aan dat Java-aperen begrijpen wat hun concurrent kan zien. Twee individuen, een subordinaat en een dominant, werden tegenover elkaar gezet met midden tussen hen in twee voedsel-items. Eén van de voedsel-items was zichtbaar voor beide individuen, terwijl het andere item zichtbaar was voor de subordinaat, maar verborgen voor de dominant. De subordinaat werd eerder losgelaten in het midden dan de dominant. De subordinaten pasten twee verschillende strategieën toe, waarmee ze hun aandeel van het voedsel maximaliseerden. De meest gebruikte strategie was om alleen het voedsel-item te pakken dat niet zichtbaar was voor hun concurrent. Deze strategie is gelijk aan de strategie die gebruikt werd door ondergeschikte chimpansees (Hare et al. 2000). Deze strategie limiteert het risico om gestraft te worden door de concurrent, omdat die zich niet bewust is van het verstopte voedsel. Net als dominante chimpansees (Hare et al. 2000) waren Java-aperen soms in staat om beide voedselitems te bemachtigen en hadden in die gevallen een voorkeur om het niet verstopte voedsel-item eerst te pakken en daarna pas het verstopte item. Op deze manier brengen ze eerst het voedsel dat het meest risico loopt afgepakt te worden in veiligheid en hebben ze vervolgens de gelegenheid om ook het tweede voedsel-item te bemachtigen. Uit dit experiment blijkt dat Java-aperen weten wat een ander kan zien, oftewel, ze kunnen *Visueel Perspectief Nemen* (VPN).

De toepassing van visuele cognitieve capaciteiten door apen in een sociale context

Makaken (o.a. resusaperen en Java-aperen) leven in grote groepen waarin meerdere mannetjes en meerdere vrouwtjes samen leven. Beide seksen paren met meerdere partners. En hoewel de alfaman alle vrouwtjes voor zichzelf opeist en probeert te voorkomen dat andere mannetjes ook paren is het voor de niet-alfamannetjes van belang dat zij ook paren. Bovendien hebben vrouwtjes er ook belang bij om met meerdere mannetjes te kunnen paren. Vrouwtjes en lager rangende mannetjes kunnen aan de monopolistische alfaman ontsnappen door te paren zonder dat de alfaman dit merkt. Deze situatie leent zich daarom uitstekend voor het bestuderen van tactische misleiding in het natuurlijke gedrag van apen.

In *Hoofdstuk 5* tonen we aan dat wanneer resusaperen toegang hebben tot twee visueel gescheiden compartimenten, ze seksueel gedrag bijna uitsluitend in afwezigheid van de

alfaman vertonen. Dit is consistent met een “omstander-effect” van de alfaman op seksueel gedrag van groepsgenoten, waarbij louter de aanwezigheid van een individu een remmend effect heeft op het gedrag van anderen. Gebaseerd op de literatuur verwachtten we dat het verbergen van paringen hoogst waarschijnlijk het resultaat is van de initiatieven van vrouwtjes, omdat vrouwtjes voordeel hebben van verminderde verstoringen (Ruiz de Elvira and Herndon 1986, Manson 1996), terwijl de voordelen voor mannetjes niet duidelijk zijn. Ook mannetjes zouden baat kunnen hebben bij het verminderen van agressie tijdens verstoringen (Wilson 1981, Bruce and Estep 1992), maar verstoringen leiden niet tot minder nakomelingen bij mannetjes (Berard et al. 1994). Inderdaad vinden we dat vrouwtjes bijdragen aan het verbergen van seksueel gedrag door minder vaak de mannetjes uit te nodigen voor een paring in aanwezigheid dan in afwezigheid van de alfaman. Echter, een trend in de gedragingen van de mannetjes wijst erop dat ook mannetjes bijdragen aan het verbergen van seksueel gedrag. Dit suggereert dat beide seksen profiteren van het verstoppen van hun seksueel gedrag, of dat alleen een van de twee seksen een voordeel heeft en de ander indirect profiteert omdat de partner meer bereid is om te paren. Het “omstander-effect” was niet uniek voor de alfaman. Ook andere mannetjes remden het seksuele gedrag van hun groepsgenoten. Hoewel de resultaten suggereren dat de effecten individu specifiek zijn, is het niet helemaal duidelijk of de gevonden “omstander-effecten” niet zijn toe te wijten aan het vermeden van (bijna) alle individuen.

In *Hoofdstuk 6* hebben we bij Java-apen daarom niet alleen naar de effecten van mannetjes, maar ook naar de effecten van vrouwtjes op het seksueel gedrag van hun groepsgenoten gekeken. Daarnaast hebben we voor elk individu de sterkte van het “omstander-effect” bepaald, wat ons in staat stelde om het “omstander-effect” te correleren aan verschillende eigenschappen van de omstanders. Ook hebben we onderzocht of een koppel dat gaat paren onderling coördineert wanneer het zich afzondert van de rest van de groep, of dat een paring in afzondering het resultaat is van een van de partners die de ander benadert op het moment dat deze zich toevallig heeft afgezonderd.

De Java-apen bleken niet alleen “omstander-effecten” te hebben van mannetjes, maar ook van een aantal vrouwtjes. Het “omstander-effect” was het sterkst voor de alfaman, en onder de mannetjes was de sterkte van het “omstander-effect” afhankelijk van de dominantie rang. Daarentegen was de sterkte van het “omstander-effect” van de vrouwtjes rangsonafhankelijk. De effecten van niet-alfadieren waren onafhankelijk van hun nabijheid tot de alfaman. Daarom zijn de beschreven “omstander-effecten” het resultaat van het vermijden van specifieke individuen en niet van het vermijden van de alfaman en een aantal individuen die toevallig veel in zijn nabijheid zijn. Net als bij de resusapen, waren ook de Java-aap vrouwtjes actief betrokken bij het vermijden van de alfaman. Daarnaast bleken Java-aap mannetjes ook minder vaak in aanwezigheid dan in afwezigheid van de alfaman vrouwtjes uit te nodigen voor een paring en ook bij resusaap mannetjes lijkt het erop dat ze de alfaman mijden tijdens seksueel gedrag. Klaarblijkelijk profiteren bij makaken beide seksen direct of indirect van het verstoppen van hun seksuele gedrag.

Omdat beide seksen actief bijdragen aan het verbergen van seksueel gedrag, zou het een gecoördineerd gedrag kunnen zijn tussen beide partners. Vrouwtjes en subordinate mannetjes zouden de alfaman tactisch kunnen misleiden door gezamenlijk of vlak na elkaar de groep te verlaten voordat ze gaan paren (Byrne and Whiten 1990). Wanneer voorafgaand aan een paring de afzondering van het ene individu snel volgt op de afzondering van de seksuele partner, zouden we een indicatie hebben dat tenminste een van de partners zich afsplitst van de groep met een bepaalde intentie. Echter, wij vonden hiervoor geen bewijs, omdat de tijden tussen de afsplitsingen van beide partners voorafgaand aan seksuele interacties niet significant verschilden van deze tijden bij niet-seksuele interacties. Desondanks waren de resultaten in de verwachte richting en zouden extra waarnemingen een significante coördinatie van gedrag kunnen onthullen.

Verborgene copulaties zouden het resultaat kunnen zijn van de positionering van niet-alfamannetjes aan de buitenrand van de groep. Vanwege deze positionering, brachten niet-alfamannetjes meer tijd in afwezigheid van de alfaman door dan de vrouwtjes. Vrouwtjes die mannetjes benaderen om te gaan paren komen automatisch uit bij de rand van de groep en dus vaak in afwezigheid van de alfaman. Inderdaad vond seksueel gedrag voornamelijk aan de buitenrand van de groep plaats. Echter, in beide studies (*Hoofdstuk 5 en 6*) waren de data gecorrigeerd voor de tijd dat elk koppel doorbrengt in aan- en afwezigheid van de alfaman, oftewel, deze dieren gedroegen zich anders in aan- dan afwezigheid van de alfaman. Daarnaast passen niet alleen vrouwtjes, maar ook mannetjes hun gedrag aan in aanwezigheid van de alfaman. Concluderend, “omstandereffecten” in het seksuele gedrag zijn hoogst waarschijnlijk het resultaat van vrouwtjes die toenadering zoeken tot mannetjes aan de rand van de groep en vervolgens houden beide partners de aanwezigheid van de alfaman in de gaten voordat ze een paring beginnen.

In *Hoofdstuk 7* gaan we verder in op de mechanismen achter het verbergen van seksueel gedrag. We registreerden systematisch interindividuele afstanden gedurende seksuele en niet-seksuele interacties. Daarnaast hebben we de verblijven van resus- en Java-ape voorzien van verschillende transparante en ondoorzichtige schermen, die de ape in staat stelden om hun seksuele gedrag erachter te verstoppen. Conform de paringen aan de rand van de groep in hoofdstuk 6, vonden we dat vrouwtjes resus- en Java-ape hun afstand tot de alfaman significant vergrootten tijdens seksuele interacties vergeleken met niet-seksuele interacties. Echter, resusaapmannetjes vergrootten ook hun afstand tot de alfaman tijdens seksuele interacties en Java-aapmannetjes leken hetzelfde te doen. Dat maakt de grote afstand die de dieren nemen tot de alfaman tijdens seksueel gedrag meer dan het resultaat van de positionering van de niet-alpha mannetjes.

Tot onze verbazing, en in tegenstelling met eerder onderzoek (Gygax 1995), bleken individuen van beide soorten slechts sporadisch te paren in de nabijheid van de schotten en werden deze copulaties niet consequent verborgen voor de alfaman. Echter, vanwege de methodes van Gygax weerspiegelen zijn resultaten waarschijnlijk niet zozeer een voorkeur voor seksueel gedrag in de nabijheid van schotten, maar eerder een algemene voorkeur van de ape om zich in de nabijheid van schotten op te houden.

Concluderend, het verbergen van seksueel gedrag door makaken is niet gebaseerd op een strategie om in de buurt van ondoorzichtige objecten te paren. Ook vonden wij geen sluitend bewijs dat een mannetje en vrouwtje zich tactisch afzonderen van de groep om in afzondering te gaan paren (*Hoofdstuk 6*). Daarom is het verbergen van seksueel gedrag geen voorbeeld van niveau 2 "tactische misleiding", waarbij individuen begrijpen dat ze een ander kunnen misleiden door zich te verstoppen. Hoewel de positionering van niet-alfamannetjes aan de rand van de groep bijdraagt aan het verbergen van seksueel gedrag voor de alfaman, gebeurt er meer dan dat. Zowel mannetjes als vrouwtjes vergrootten hun afstand ten opzichte van de alfaman alvorens ze gaan paren. Dit suggereert "tactische misleiding niveau 1: "Handelingen uit het normale repertoire van de actor, die zo worden gebruikt dat een ander individu waarschijnlijk een verkeerde conclusie trekt, in het voordeel van de actor" (Byrne and Whiten 1990). Het geobserveerde gedrag kan worden geïnterpreteerd als "tactische misleiding" niveau 1 omdat individuen actief bepaalde concurrenten vermijden (Byrne and Whiten 1992) en het is duidelijk dat het vergroten van de afstand tot deze concurrenten specifiek gekoppeld is aan seksueel gedrag, wat een voordeel voor de actor suggereert in het verbergen van seksueel gedrag. Echter, vanwege de lage aantallen geobserveerde verstoringen was het niet mogelijk om het afzonderingsgedrag te koppelen aan voordelen in de vorm van verminderde verstoringen. Daarvoor is een grootschalig longitudinaal onderzoek nodig van meerdere apen groepen met gegevens van verstoringen gerelateerd aan de ruimtelijke positionering binnen de groep.

Conclusie

De cognitieve capaciteit: het begrijpen van het object van aandacht, is aanwezig in een Oude Wereld aap (*Hoofdstuk 2*), maar kon niet worden aangetoond in een Nieuwe Wereld aap (*Hoofdstuk 3*). Een stap hoger op de ladder van cognitieve complexiteit: VPN, het begrijpen van wat een ander individu kan zien, is aanwezig in een Oude Wereld aap (*Hoofdstuk 4*). De resultaten van VPN met de Oude wereld apen waren vergelijkbaar met de resultaten van mensapen (Hare et al. 2000). Daarom delen Oude Wereld apen complexe cognitieve capaciteiten met mensapen en komen voorlopers van complexe menselijke cognitieve capaciteiten dus ook voor in Oude Wereld apen.

Hoewel stiekem paren vaak wordt aangedragen als een voorbeeld van het gebruik van cognitief complexe gedragingen, zoals VPN en tactische misleiding in een sociale context, gebruiken ten minste twee verschillende soorten Oude Wereld apen geen VPN bij het verbergen van hun paargedrag, omdat ze geen gebruik maakten van aanwezige schotten (*hoofdstuk 7*). Daarnaast vinden we geen bewijs dat een hoger niveau (niveau 2) (Byrne and Whiten 1990) van tactische misleiding wordt gebruikt, omdat twee partners betrokken bij een copulatie hun separatie van de groep niet coördineerden (*Hoofdstuk 6*). In plaats daarvan gebruiken de apen cognitief simpeler mechanismes, namelijk door afstand te creëren tussen zichzelf en de alfaman gedurende seksueel gedrag (*Hoofdstuk 7*). Deze strategie betreft waarschijnlijk niveau 1 tactische misleiding, omdat de dieren hun seksueel gedrag aanpassen aan de situatie en het met name vertonen als anderen er niet zijn. Dit zou hen directe voordelen, niet verstoorte paringen, en indirecte voordelen, een grotere kans op nakomelingen, kunnen opleveren. Teneinde dit voorstel te

bevestigen is uitgebreider onderzoek nodig naar de voordelen van seksueel gedrag op grote afstand van de alfaman.

Alles bij elkaar zien we dat makaken weten waar een ander naar kijkt en wat hij kan zien, complexe cognitieve capaciteiten die ze delen met mensapen en mensen. Ook vertonen makaken vaker seksueel gedrag in afwezigheid van dieren die hen kunnen storen, dan in hun aanwezigheid. Echter, de complexe cognitieve capaciteiten lijken ze hier niet voor in te zetten. Deze resultaten spreken de veronderstelling dat sociale complexiteit aanleiding heeft gegeven voor de evolutie van complexe cognitieve capaciteiten tegen.

References

- Alberts, S. C., J. C. Buchan and J. Altmann** 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour* **72**: 1177-1196.
- Alfaro, J. W. L.** 2005. Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology* **67**: 313-328.
- Alfaro, J. W. L.** 2005. Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology* **67**: 313-328.
- Altmann, S. A.** 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Sciences* **102**: 338-435.
- Altmann, S. A.** 1967. The structure of primate social communication. In: *Social communication among primates*. (S. A. Altmann ed.). Chicago, University of Chicago Press: pp. 325-336.
- Amici, F., F. Aureli and J. Call** 2008. Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology* **18**: 1415-1419.
- Amici, F., F. Aureli and J. Call** 2010. Monkeys and apes: are their cognitive skills really so different? *American Journal of Physical Anthropology* **143**: 188-197.
- Amici, F., J. Call and F. Aureli** 2009. Variation in withholding of information in three monkey species. *Proceedings of the Royal Society B-Biological Sciences* **276**: 3311-3318.
- Amici, F., E. Visalberghi, F. Aureli and J. Call** 2009. Spider Monkeys (*Ateles geoffroyi*) and Capuchin Monkeys (*Cebus apella*) Follow Gaze Around Barriers: Evidence for Perspective Taking? *Journal of Comparative Psychology* **123**: 368-374.
- Anderson, J. R. and R. W. Mitchell** 1999. Macaques but not lemurs co-orient visually with humans. *Folia Primatologica* **70**: 17-22.
- Angst, W.** 1974. *Das ausdrucksverhalten des javaneraffen Macaca fascicularis Raffles 1821*. Berlin, Parey. 1-90 p.
- Baron-Cohen, S., A. M. Leslie and U. Frith** 1985. Does the autistic child have a "theory of mind"? *Cognition* **21**: 37-46.
- Barrett, L., P. Henzi and R. Dunbar** 2003. Primate cognition: From 'what now?' to 'what if?' *Trends in cognitive sciences* **7**: 494-497.
- Baumgartner, G.** 1983. Organization and function of the neocortex. *Neuro-Ophthalmology* **3**: 1-14.
- Berard, J.** 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates* **40**: 159-175.
- Berard, J. D., P. Nurnberg, J. T. Epplen and J. Schmidtke** 1993. Male rank, reproductive-behavior, and reproductive success in free-ranging rhesus macaques. *Primates* **34**: 481-489.
- Berard, J. D., P. Nurnberg, J. T. Epplen and J. Schmidtke** 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* **129**: 177-201.
- Bercovitch, F. B., A. Widdig, A. Trefilov, M. J. Kessler, J. D. Berard, J. Schmidtke, P. Nurnberg and M. Krawczak** 2003. A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. *Naturwissenschaften* **90**: 309-312.
- Bergman, T. J., J. C. Beehner, D. L. Cheney and R. M. Seyfarth** 2003. Hierarchical Classification by Rank and Kinship in Baboons. *Science* **302**: 1234-1236.
- Bergstrom, M. L. and L. M. Fedigan** 2009. Strength and stability of dominance hierarchies in female white-faced capuchins (*Cebus capucinus*) at Santa Rosa National Park, Costa Rica. *American Journal of Primatology* **71**: 103-103.
- Birkhead, T.** 2000. *Promiscuity: An evolutionary history of sperm competition and sexual conflict*. London, Faber & Faber. 272 p.
- Boesch, C., G. Kohou, H. Nene and L. Vigilant** 2006. Male competition and paternity in wild chimpanzees of the Tai forest. *American Journal of Physical Anthropology* **130**: 103-115.
- Bovet, D. and B. L. Deputte** 2009. Matching vocalizations to faces of familiar conspecifics in grey-cheeked mangabeys (*Lophocebus albigena*). *Folia Primatol* **80**: 220-232.
- Brauer, J., J. Call and M. Tomasello** 2005. All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology* **119**: 145-154.

- Bruce, K. E. and D. Q. Estep** 1992. Interruption of and harassment during copulation by stump-tail macaques, *Macaca arctoides*. *Animal Behaviour* **44**: 1029-1044.
- Buchan, J. C., S. C. Alberts, J. B. Silk and J. Altmann** 2003. True paternal care in a multi-male primate society. *Nature* **425**: 179-181.
- Bugnyar, T., M. Stowe and B. Heinrich** 2004. Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**: 1331-1336.
- Bulger, J. B.** 1993. Dominance rank and access to estrous females in male savanna baboons. *Behaviour* **127**: 67-103.
- Burkart, J. and A. Heschl** 2006. Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology* **120**: 120-130.
- Burkart, J. M. and A. Heschl** 2007. Understanding visual access in common marmosets, *Callithrix jacchus*: perspective taking or behaviour reading? *Animal Behaviour* **73**: 457-469.
- Byrne, R. W.** 1995. *The thinking ape. Evolutionary origins of intelligence*. Oxford, Oxford University Press. 266 p.
- Byrne, R. W.** 1997. Machiavellian intelligence. *Evolutionary Anthropology* **5**: 172-180.
- Byrne, R. W.** 2000. Evolution of primate cognition. *Cognitive Science* **24**: 543-570.
- Byrne, R. W. and A. Whiten** 1988. *Machiavellian intelligence: social complexity and the evolution of intellect in monkeys, apes and humans*. Oxford, Oxford University Press. 432 p.
- Byrne, R. W. and A. Whiten** 1988. Towards the next generation in data quality - a new survey of primate tactical deception. *Behavioral and Brain Sciences* **11**: 267-271.
- Byrne, R. W. and A. Whiten** 1990. Tactical deception in primates: The 1990 database. *Primate Report* **27**: 1-101.
- Byrne, R. W. and A. Whiten** 1992. Cognitive evolution in primates - evidence from tactical deception. *Man* **27**: 609-627.
- Call, J., B. Agnetta and M. Tomasello** 2000. Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition* **3**: 23-34.
- Call, J., B. Hare, M. Carpenter and M. Tomasello** 2004. 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Developmental Science* **7**: 488-498.
- Call, J., B. A. Hare and M. Tomasello** 1998. Chimpanzee gaze following in an object-choice task. *Animal cognition* **1**: 89-99.
- Call, J. and M. Tomasello** 1999. A nonverbal false belief task: the performance of children and great apes. *Child Development* **70**: 381-395.
- Call, J. and M. Tomasello** 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences* **12**: 187-192.
- Carne, C., S. Wiper and S. Semple** 2011. Reciprocation and Interchange of Grooming, Agonistic Support, Feeding Tolerance, and Aggression in Semi-Free-Ranging Barbary Macaques. *American Journal of Primatology* **73**: 1127-1133.
- Chapais** 1983. Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. *Behavioral Ecology and Sociobiology* **12**: 215-228.
- Cheney, D. L. and R. M. Seyfarth** 1990. Attending to behaviour versus attending to knowledge: examining monkeys' attribution of mental states. *Animal Behaviour* **40**: 742-753.
- Cheney, D. L. and R. M. Seyfarth** 1990. The representation of social relations by monkeys. *Cognition* **37**: 167-196.
- Cheney, D. L. and R. M. Seyfarth** 1999. Recognition of other individuals' social relationships by female baboons. *Animal Behaviour* **58**: 67-75.
- Cheney, D. L., R. M. Seyfarth and J. B. Silk** 1995. The response of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *Journal of comparative psychology* **109**: 134-141.
- Cicirello, D. M. and J. O. Wolff** 1990. The effects of mating on infanticide and pup discrimination in white-footed mice. *Behavioral Ecology and Sociobiology* **26**: 275-279.
- Clay, Z., S. Pilka, T. Gruber and K. Zuberbühler** 2011. Female bonobos use copulation calls as social signals. *Biological Letters* **7**: 513-516.
- Coltman, D. W., W. D. Bowen and J. M. Wright** 1999. A multivariate analysis of phenotype and paternity in male harbor seals, *Phoca vitulina*, at Sable Island, Nova Scotia. *Behavioral Ecology* **10**: 169-177.
- Cowlshaw, G. and R. I. M. Dunbar** 1991. Dominance rank and mating success in male primates. *Animal Behaviour* **41**: 1045-1056.

References

- Davies, N. B.** 2000. Multi-male breeding groups in birds: ecological causes and social conflicts. In: *Primate males: causes and consequences of variation in group composition*. (P. M. Kappeler ed.). Cambridge, Cambridge University Press: pp. 11-20.
- de Bruyn, P. J. N., C. A. Tosh, M. N. Bester, E. Z. Cameron, T. McIntyre and I. S. Wilkinson** 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. *Animal Behaviour* **82**: 445-451.
- de Ruiter, J. R., W. Scheffrahn, G. J. M. Trommelen, A. G. Uiterlinden, R. D. Martin and J. A. R. A. M. van Hooff** 1992. Male social rank and reproductive success in wild long-tailed macaques. In: *Paternity in primates: genetic tests and theories*. (R. D. Martin, A. F. Dixon and E. J. Wickings ed.). Basel, Karger: pp. 175-191.
- de Ruiter, J. R. and J. A. R. A. M. van Hooff** 1993. Male-dominance rank and reproductive success in primate groups. *Primates* **34**: 513-523.
- de Vries, H.** 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour* **50**: 1375-1389.
- de Vries, H.** 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour* **55**: 827-843.
- de Vries, H., W. J. Netto and P. L. H. Hanegraaf** 1993. Matman - a program for the analysis of sociometric matrices and behavioral transition matrices. *Behaviour* **125**: 157-175.
- de Waal, F. B. M.** 1977. The organization of agonistic relations within two captive groups of Java-monkeys (*Macaca fascicularis*). *Zeitschrift fur Tierpsychologie* **44**: 225-282.
- de Waal, F. B. M.** 1997. Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology* **111**: 370-378.
- de Waal, F. B. M. and L. M. Luttrell** 1985. The formal hierarchy of rhesus macaques: An investigation of the bared-teeth display. *American Journal of Primatology* **9**: 73-85.
- Deaner, R. O. and M. L. Platt** 2003. Reflexive social attention in monkeys and humans. *Current Biology* **13**: 1609-1613.
- Deaner, R. O., S. V. Shepherd and M. L. Platt** 2007. Familiarity accentuates gaze cuing in women but not men. *Biology Letters* **3**: 64-67.
- Deaner, R. O., C. P. van Schaik and V. Johnson** 2006. Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology* **4**: 149-196.
- Dekleva, M.** 2011. *Tools Treats Toys: What human and non-human primates recall about their past and plan for their future* PhD thesis, Utrecht University.
- Dennett, D.** 1987. *The intentional stance*. Cambridge, MIT Press. 388 p.
- Digby, L. J.** 1995. Social organization in a wild population of *Callithrix jacchus*: II. Intragroup social behavior. *Primates* **36**: 361-365.
- Dixon, A. F.** 1998. *Primate sexuality: comparative studie of the prosimians, monkeys, apes, and human beings*. Oxford, Oxford University Press. 546 p.
- Dixon, A. F. and M. J. Anderson** 2002. Sexual selection, seminal coagulation and copulatory plug formation in primates. *Folia Primatologica* **73**: 63-69.
- Drickamer, L. C.** 1974. Social rank, observability, and sexual behavior of rhesus-monkeys (*Macaca mulatta*). *Journal of Reproduction and Fertility* **37**: 117-120.
- Dubuc, C., L. Muniz, M. Heistermann, A. Engelhardt and A. Widdig** 2011. Testing the priority-of-access model in a seasonally breeding primate species. *Behavioral Ecology and Sociobiology* **65**: 1615-1627.
- Dunbar, R. I. M.** 1995. Neocortex size and group-size in primates - a test of the hypothesis. *Journal of Human Evolution* **28**: 287-296.
- Dunbar, R. I. M.** 1998. The social brain hypothesis. *Evolutionary Anthropology* **6**: 178-190.
- Duvall, S. W., I. S. Bernstein and T. P. Gordon** 1976. Paternity and status in a rhesus monkey group. *Journal of Reproduction and Fertility* **47**: 25-31.
- Ebensperger, L. A.** 1998. Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* **73**: 321-346.
- Emery, N. J.** 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews* **24**: 581-604.
- Emery, N. J., E. N. Lorincz, D. I. Perrett, M. W. Oram and C. I. Baker** 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology* **111**: 286-293.
- Emlen, S. T. and L. W. Oring** 1977. Ecology, sexual selection and evolution of mating systems. *Science* **197**: 215-223.

- Engelhardt, A. 2004. *The significance of male and female reproductive success in wild longtailed macaques (Macaca fascicularis)*. Göttingen, Cuvillier verlag. 109 p.
- Engelhardt, A., J. K. Hodges and M. Heistermann 2007. Post-conception mating in wild long-tailed macaques (*Macaca fascicularis*): Characterization, endocrine correlates and functional significance. *Hormones and Behavior* **51**: 3-10.
- Engh, A. L., S. M. Funk, R. C. Van Horn, K. T. Scribner, M. W. Bruford, S. Libants, M. Szykman, L. Smale and K. E. Holekamp 2002. Reproductive skew among males in a female-dominated mammalian society. *Behavioral Ecology* **13**: 193-200.
- Evers, E., H. de Vries, B. M. Spruijt and E. H. M. Sterck 2011 Better Safe than Sorry - Socio-Spatial Group Structure Emerges from Individual Variation in Fleeing, Avoidance or Velocity in an Agent-Based Model. *Plos One* **6** DOI: 10.1371/journal.pone.0026189.
- Evers, E., H. de Vries, B. M. Spruijt and E. H. M. Sterck 2012. Look before you leap - individual variation in social vigilance shapes socio-spatial group properties in an agent-based model. *Behavioral Ecology and Sociobiology* **66**: 931-945.
- Fagot, J. and C. Deruelle 2002. Perception of pictorial eye gaze by baboons (*Papio papio*). *Journal of Experimental Psychology-Animal Behavior Processes* **28**: 298-308.
- Ferrari, S. and M. Lopes Ferrari 1989. A re-evaluation of the social organization of the Callitrichidae, with reference to the ecological differences between genera. *Folia Primatologica* **52**: 132-147.
- Fisher-Thompson, D. and J. A. Peterson 2004. Infant side biases and familiarity-novelty preferences during a serial paired-comparison task. *Infancy* **5**: 309-340.
- Flavell, J. H. 1981. Cognitive monitoring. In: *Children's oral communication skills*. (W. P. Dickson ed.).
- Flombaum, J. I. and L. R. Santos 2005. Rhesus monkeys attribute perceptions to others. *Current Biology* **15**: 447-452.
- French, J. A., C. M. Schaffner, R. E. Shepherd and M. E. Miller 1995. Familiarity with intruders modulates agonism towards outgroup conspecifics in wild black-tufted-ear marmoset (*Callithrix kuhli*, Primates, callitrichidae) *Ethology* **99**: 24-38.
- Fujita, K., H. Kuroshima and T. Masuda 2002. Do tufted capuchin monkeys (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys. *Animal cognition* **5**: 19-25.
- Garcia, C., K. Shimizu and M. Huffman 2009. Relationship Between Sexual Interactions and the Timing of the Fertile Phase in Captive Female Japanese Macaques (*Macaca fuscata*). *American Journal of Primatology* **71**: 868-879.
- Genty, E., J. Foltz and J. J. Roeder 2008. Can brown lemurs (*Eulemur fulvus*) learn to deceive a human competitor? *Animal cognition* **11**: 255-266.
- Goldberg, T. L. and R. W. Wrangham 1997. Genetic correlates of social behavior in wild chimpanzees: evidence from mitochondrial DNA. *Animal behaviour* **54**: 559-570.
- Goodall, J. 1986. *The chimpanzees of Gombe*. Cambridge, Belknap. 673 p.
- Goossens, B. M. A., M. Dekleva, S. M. Reader, E. H. M. Sterck and J. J. Bolhuis 2008. Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour* **75**: 1673-1681.
- Goossens, B. M. A., L. M. van den Berg, S. M. Reader and E. H. Sterck 2012. An analysis of gaze following to a hidden location in long-tailed macaques (*Macaca fascicularis*). *Behaviour* **149**: 1319-1337.
- Gouzoules, H. 1974. Harassment of sexual behavior in the stumptailed macaque (*Macaca arctoides*). *Folia Primatologica* **22**: 208-217.
- Gygax, L. 1995. Hiding behaviour of long-tailed macaques (*Macaca fascicularis*): I. Theoretical background and data on mating. *Ethology* **101**: 10-24.
- Hanby, J. P. and C. E. Brown 1974. The development of sociosexual behaviours in Japanese Macaques *Macaca Fuscata*. *Behaviour* **49**: 152-195.
- Hare, B., E. Addessi, J. Call, M. Tomasello and E. Visalberghi 2003. Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour* **65**: 131-142.
- Hare, B., J. Call, B. Agnetta and M. Tomasello 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* **59**: 771-785.
- Hare, B., J. Call and M. Tomasello 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour* **61**: 139-151.
- Hare, B., J. Call and M. Tomasello 2006. Chimpanzees deceive a human competitor by hiding. *Cognition* **101**: 495-514.
- Hare, B. and M. Tomasello 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour* **68**: 571-581.

References

- Harrison, M. L. and S. D. Tardif** 1988. Kin preference in marmosets and tamarins: *Saguinus oedipus* and *Callithrix jacchus* (Callitrichidae, primates). *American Journal of Physical Anthropology* **77**: 377-384.
- Hasegawa, T. and M. Hiraiwa-Hasegawa** 1990. Sperm competition and mating behavior. In: *The chimpanzees of the Mahala-mountains*. (T. Nishida ed.). Tokyo, University of Tokyo press: pp. 115-132.
- Hausfater, G. and S. B. Hrdy** 1984. *Infanticide. Comparative and evolutionary perspectives*. New York, Aldine 598 p.
- Hayakawa, S.** 2007. Female Defensibility in Small Troops of Japanese Macaques vis-a-vis Nontroop Males and Copulation on the Periphery of the Troop. *International Journal of Primatology* **28**: 73-96.
- Heistermann, M., T. Ziegler, C. P. Van Schaik, K. Launhardt, P. Winkler and J. K. Hodges** 2001. Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**: 2445-2451.
- Herrmann, E., J. Call, M. V. Hernandez-Lloreda, B. Hare and M. Tomasello** 2007. Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science* **317**: 1360-1366.
- Hill, R. A. and R. I. M. Dunbar** 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour* **135**: 411-430.
- Hochberg, Y.** 1988. A sharper Bonferroni procedure for multiple tests of significance *Biometrika* **75**: 800-802.
- Hogg, J. T.** 1987. Intrasexual competition and mate choice in Rocky-Mountain bighorn sheep. *Ethology* **75**: 119-144.
- Honjo, S., F. Cho, T. Fujinara, Y. Yoshioka, K. Masuko, K. Kurihara, M. Yabe and Y. Noguchi** 1978. Breeding of cynomolgous monkeys through successive generations by indoor cage system. *Japanese Journal of Medical Science and Biology* **31**: 301-310.
- Horton, K. E. and C. A. Caldwell** 2006. Visual co-orientation and expectations about attentional orientation in pileated gibbons (*Hylobates pileatus*). *Behavioural Processes* **72**: 65-73.
- Hrdy, S. B.** 1979. Infanticide among animals - Review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* **1**: 13-40.
- Huang, B., T. W. Wey and D. T. Blumstein** 2011. Correlates and Consequences of Dominance in a Social Rodent. *Ethology* **117**: 573-585.
- Ihaka, R. and R. Gentleman** 1996. R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics* **5**: 299-314.
- Inoue, E. and O. Takenaka** 2008. The effect of male tenure and female mate choice on paternity in free-ranging Japanese macaques. *American Journal of Primatology* **70**: 62-68.
- Itakura, S.** 2004. Gaze-following and joint visual attention in nonhuman animals. *Japanese Psychological Research* **46**: 216-226.
- Itakura, S. and M. Tanaka** 1998. Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology* **112**: 119-126.
- Izawa, K.** 1980. Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates* **21**: 443-467.
- Janson, C. H.** 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour* **40**: 910-921.
- Janson, C. H.** 2000. Primate socio-ecology: The end of a golden age. *Evolutionary Anthropology* **9**: 73-86.
- Janson, C. H. and C. P. Schaik, van** 2000. The behavioral ecology of infanticide by males. In: *Infanticide by Males and Its Implications*. (C. P. Schaik, van and C. H. Janson ed.). Cambridge, Cambridge University Press: pp. 469-494.
- Jensen, K., J. Call and M. Tomasello** 2007. Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 13046-13050.
- Jerison, H. J.** 1976. Paleoneurology and the evolution of mind. *Scientific American* **234**: 90-101.
- Jerison, H. J.** 1979. Brain, body and encephalization in early primates. *Journal of Human Evolution* **8**: 615-635.
- Kaminski, J., J. Call and M. Tomasello** 2008. Chimpanzees know what others know, but not what they believe. *Cognition* **109**: 224-234.
- Kaminski, J., J. Riedel, J. Call and M. Tomasello** 2005. Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour* **69**: 11-18.
- Kaufmann, J. H.** 1965. A 3-year study of mating-behavior in a freeranging band of rhesus-monkeys. *Ecology* **46**: 500-512.

- Kavanagh, M. and E. Laursen** 1984. Breeding seasonality among long-tailed macaques, *Macaca fascicularis*, in Peninsular Malaysia. *International Journal of Primatology* **5**: 17-29.
- Kehmeier, S., C. Schloegl, I. B. R. Scheiber and B. M. Weiss** 2011. Early development of gaze following into distant space in juvenile Greylag geese (*Anser anser*). *Animal cognition* **14**: 477-485.
- Kim, I. K. and E. S. Spelke** 1992. Infants' sensitivity to effects of gravity on visible object motion. *Journal of experimental psychology* **18**: 385-393.
- Klinkova, E., J. K. Hodges, K. Fuhrmann, T. de Jong and M. Heistermann** 2005. Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *International Journal of Primatology* **26**: 357-384.
- Koenig, A. and R. Hartmut** 1994. Effects of familiarity on the behaviour towards intruders in captive common marmosets (*Callithrix jacchus*). *Primates* **35**: 89-93.
- Krachun, C., M. Carpenter, J. Call and M. Tomasello** 2009. A competitive nonverbal false belief task for children and apes. *Developmental Science* **12**: 521-535.
- Kummer, H.** 1968. *Social organization of Hamadryas baboons: a field study*. Chicago, University of Chicago Press. 189 p.
- Kummer, H., G. Anzenberger and C. K. Hemelrijk** 1996. Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology* **110**: 97-102.
- Kummer, H. and M. Cords** 1991. Cues of ownership in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour* **42**: 529-549.
- Lambert, D. M., C. D. Millar, K. Jack, S. Anderson and J. L. Craig** 1994. Single-locus and multilocus DNA-fingerprinting of communally breeding pukeko - Do copulations or dominance ensure reproductive success. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 9641-9645.
- Laporte, M. N. C. and K. Zuberbuhler** 2010. Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour* **80**: 467-473.
- Lazaro-Perea, C.** 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defense and assessment of neighbours. *Animal Behaviour* **62**: 11-21.
- Lindburg, D. G.** 1971. The rhesus monkey in north India: an ecological and behavioural study. In: *Primate behaviour: developments in field and laboratory research*. ed.). New York, Academic Pr. **2**: pp. 1-106.
- Maestripieri, D. and K. Wallen** 1997. Affiliative and submissive communication in rhesus macaques. *Primates* **38**: 127-138.
- Manson, J. H.** 1996. Male dominance and mount series duration in Cayo Santiago rhesus macaques. *Animal Behaviour* **51**: 1219-1231.
- Martcorena, D. C. W., A. M. Ruiz, C. Mukerji, A. Goddu and L. R. Santos** 2011. Monkeys represent other's knowledge but not their beliefs. *Developmental Science* **14**: 1406-1416.
- Massen, J. J. M., A. M. Overduin - de Vries, A. J. M. de Vos - Rouweler, B. M. Spruijt, G. G. M. Doxiadis and E. H. M. Sterck** 2012. Male mating tactics in captive rhesus macaques, *Macaca mulatta*: the influence of dominance, markets and relationship quality. *International Journal of Primatology* **33**: 73-92.
- Matsumoto-Oda, A., K. Hosaka, M. A. Huffman and K. Kawanaka** 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *International Journal of Primatology* **19**: 999-1011.
- McMillan, C. A.** 1989. Male age, dominance, and mating success among rhesus macaques. *American Journal of Physical Anthropology* **80**: 83-89.
- Melis, A. P., J. Call and M. Tomasello** 2006. Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology* **120**: 154-162.
- Miklosi, A., R. Polgardi, J. Topa and V. Csanyi** 1998. Use of experimenter-given cues in dogs. *Animal cognition* **1**: 113-121.
- Miller, C. T. and A. W. Thomas** 2012. Individual recognition during bouts of antiphonal calling in common marmosets. *Journal of Comparative Physiology, A* **198**: 337-346.
- Miller, R. E. and J. V. Murphy** 1956. Social interactions of rhesus-monkeys. 1. Food-getting dominance as a dependent variable. *Journal of Social Psychology* **44**: 249-255.
- Neiworth, J. J., M. A. Burman, B. M. Basile and M. T. Lickteig** 2002. Use of experimenter-given cues in a visual co-orienting and in an object-choice task by a New World monkey species, cotton top tamarins (*Saguinus oedipus*). *Journal of comparative Psychology* **116**: 3-11.
- Newton, P. N.** 1988. The variable social-organization of hanuman langurs (*presbytis-entellus*), infanticide, and the monopolization of females. *International Journal of Primatology* **9**: 59-77.

References

- Niemeyer, C. L. and J. R. Anderson** 1983. Primate harassment of matings. *Ethology and Sociobiology* **4**: 205-220.
- Niemeyer, C. L. and A. S. Chamove** 1983. Motivation of harassment of matings in stumptailed macaques. *Behaviour* **87**: 298-323.
- Nikitopoulos, E., M. Heistermann, H. De Vries, J. Van Hooff and E. H. M. Sterck** 2005. A pair choice test to identify female mating pattern relative to ovulation in longtailed macaques, *Macaca fascicularis*. *Animal Behaviour* **70**: 1283-1296.
- Noldus, L. P. J. J.** 1991. The Observer: a software system for collection and analysis of observational data. *Behavior Research Methods, Instruments and Computers* **23**: 415-429.
- Nunn, C. L.** 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour* **58**: 229-246.
- Nunn, C. L., J. L. Gittleman and J. Antonovics** 2000. Promiscuity and the primate immune system. *Science* **290**: 1168-1170.
- Okamoto-Barth, S., J. Call and M. Tomasello** 2007. Great apes' understanding of other individuals' line of sight. *Psychological Science* **18**: 462-468.
- Ostner, J., C. L. Nunn and O. Schulke** 2008. Female reproductive synchrony predicts skewed paternity across primates. *Behavioral Ecology* **19**: 1150-1158.
- Overduin-de Vries, A. M., J. J. M. Massen, B. M. Spruijt and E. H. M. Sterck** 2012. Sneaky Monkeys: An Audience Effect of Male Rhesus Macaques (*Macaca mulatta*) on Sexual Behavior. *American Journal of Primatology* **74**: 217-228.
- Overduin - de Vries, A. M., C. U. Uhrenholt Olesen, H. De Vries, B. M. Spruijt and E. H. M. Sterck** 2013 Sneak copulations in long-tailed macaques (*Macaca fascicularis*): no evidence for tactical deception *Behavioral Ecology and Sociobiology* **67**: 101-111.
- Parker, S. T. and K. R. Gibson** 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *Journal of Human Evolution* **6**: 623-641.
- Parr, L. A., J. T. Winslow, W. D. Hopkins and F. B. M. de Waal** 2000. Recognizing facial cues: Individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology* **114**: 47-60.
- Paul, A., J. Kuester, A. Timme and J. Arnemann** 1993. The association between rank, mating effort, and reproductive success in male barbary macaques (*Macaca sylvanus*). *Primates* **34**: 491-502.
- Phillips, W., J. L. Barnes, N. Mahajan, M. Yamaguchi and L. R. Santos** 2009. 'Unwilling' versus 'unable': capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science* **12**: 938-945.
- Piaget, J.** 1970. *Genetic epistemology (trans)*. New York: Vicking. p.
- Pokorny, J. J. and F. B. M. De Waal** 2009. Monkeys recognize the faces of group mates in photographs. *Proc Natl Acad Sci U S A* **106**: 21539-21543.
- Povinelli, D. J., S. T. Boysen and K. E. Nelson** 1990. Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **104**: 203-210.
- Povinelli, D. J., K. A. Parks and M. A. Novak** 1991. Do rhesus-monkeys (*Macaca mulatta*) attribute knowledge and ignorance to others. *Journal of Comparative Psychology* **105**: 318-325.
- Powell, G. V. N.** 1974. Experimental analysis of social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour* **22**: 501-505.
- Premack, D. and G. Woodruff** 1978. Does the chimpanzee have a Theory of Mind. *Behavioral and Brain Sciences* **1**: 515-526.
- Preuschoft, S.** 1995. 'Laughter' and 'smiling' in macaques, Utrecht University.
- Pulliam, H. R.** 1973. Advantages of flocking. *Journal of Theoretical Biology* **38**: 419-422.
- R Development Core Team** 2009. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.
- R Development Core Team** 2009. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.
- Reader, S. M., Y. Hager and K. N. Laland** 2011. The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B-Biological Sciences* **366**: 1017-1027.
- Reader, S. M. and K. N. Laland** 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 4436-4441.
- Reinhardt, V.** 1987. Are Male Rhesus Monkeys More Aggressive Than Females? *Primates* **28**: 123-125.
- Robbins, M. M.** 1999. Male mating patterns in wild multimale mountain gorilla groups. *Animal Behaviour* **57**: 1013-1020.

- Rowell, T. E. 1977. Variation in age at puberty in monkeys. *Folia Primatologica* **27**: 284-296.
- Ruiz, A., J. C. Gomez, J. J. Roeder and R. W. Byrne 2009. Gaze following and gaze priming in lemurs. *Animal cognition* **12**: 427-434.
- Ruiz de Elvira, M. and J. G. Herndon 1986. Disruption of sexual behaviour by high ranking rhesus monkeys (*Macaca mulatta*). *Behaviour* **96**: 227-239.
- Salatas, H. and J. H. Flavell 1976. Perspective taking: the development of two components of knowledge. *Child Development* **47**: 103-109.
- Sandel, A. A., E. L. MacLean and B. Hare 2011. Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. *Animal Behaviour* **81**: 925-931.
- Santos, L. R. and M. D. Hauser 1999. How monkeys see the eyes: cotton-top tamarins' reaction to changes in visual attention and action. *Animal cognition* **2**: 131-139.
- Santos, L. R., A. G. Nissen and J. A. Ferrugia 2006. Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour* **71**: 1175-1181.
- Scerif, G., J. Gomez and R. W. Byrne 2004. What do Diana monkeys know about the focus of attention of a conspecific? *Animal Behaviour* **68**: 1239-1247.
- Schaffner, C. M. and N. G. Caine 2000. The peacefulness of cooperatively breeding primates. In: *Conflict resolution*. (F. Aureli and F. B. M. De Waal ed.). California, University of California press: pp. 155-169.
- Schel, A. M. and K. Zuberbuhler 2012. Predator and non-predator long-distance calls in *Guereza colobus* monkeys. *Behavioural Processes* **91**: 41-49.
- Schell, A., K. Rieck, K. Schell, K. Hammerschmidt and J. Fischer 2011. Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. *Animal cognition* **14**: 503-509.
- Simple, S., M. S. Gerald and D. N. Suggs 2009. Bystanders affect the outcome of mother-infant interactions in rhesus macaques. *Proceedings of the Royal Society B-Biological Sciences* **276**: 2257-2262.
- Seyfarth, R. M. 1987. Vocal communication and its relation to language. In: *Primate societies*. (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker ed.). Chicago, University of Chicago press: pp. 440-451.
- Shepherd, S. V., R. O. Deaner and M. L. Platt 2006. Social status gates social attention in monkeys. *Current Biology* **16**: R119-R120.
- Shepherd, S. V. and M. L. Platt 2008. Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*). *Animal Cognition* **11**: 13-20.
- Shillito, D. J., R. W. Shumaker, G. G. Gallup and B. B. Beck 2005. Understanding visual barriers: evidence for Level 1 perspective taking in an orang-utan, *Pongo pygmaeus*. *Animal Behaviour* **69**: 679-687.
- Silwa, J., J. R. Duhamel, O. Pascalis and S. Wirth 2011. Spontaneous voice-face identity matching by rhesus monkeys for familiar conspecifics and humans. *Proc Natl Acad Sci U S A* **108**: 1735-1740.
- Small, M. F. 1990. Consortships and conceptions in captive rhesus macaques (*Macaca mulatta*). *Primates* **31**: 339-350.
- Smith, D. G. 1993. A 15-year study of the association between dominance rank and reproductive success of male rhesus macaques. *Primates* **34**: 471-480.
- Smith, D. G. 1994. Male dominance and reproductive success in a captive group of rhesus macaques (*macaca mulatta*). *Behaviour* **129**: 225-242.
- Smith, T. 2006. Individual Olfactory Signatures in Common Marmosets (*Callithrix jacchus*). *American Journal of Primatology* **68**: 585-604.
- Smuts, B. B. 1985. *Sex and friendship in baboons*. New York, Aldine de Gruyter. 303 p.
- Smuts, B. B., D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker 1987. *Primate societies*. London, the University of Chicago Press. p.
- Smuts, B. B. and R. W. Smuts 1993. Male-aggression and sexual coercion of females in nonhuman-primates and other mammals - evidence and theoretical implications. *Advances in the Study of Behavior* **22**: 1-63.
- Soltis, J. 2002. Do primate females gain nonprocreative benefits by mating with multiple males? Theoretical and empirical considerations. *Evolutionary Anthropology* **11**: 187-197.
- Soltis, J., F. Mitsunaga, K. Shimizu, M. Nozaki, Y. Yanagihara, X. DomingoRoura and O. Takenaka 1997. Sexual selection in Japanese macaques .2. female mate choice and male-male competition. *Animal Behaviour* **54**: 737-746.
- Soltis, J., R. Thomsen and O. Takenaka 2001. The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Animal Behaviour* **62**: 485-494.

References

- Steckenfinger, S. A. and A. A. Ghazanfar** 2009. Monkey visual behavior falls into the uncanny valley. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 18362-18366.
- Stephenson, G. R.** 1975. Social structure of mating activity in Japanese macaques. In: *Proceedings of the Fifth Congress of the International Primatological Society*. (S. Kondo, M. Kawai, A. Ehara and S. Kawamura ed.). Tokyo, Japan Science Press: pp. 63-115.
- Sterck, E. H. M. and S. Begeer** 2010. Theory of Mind: Specialized capacity or emergent property? *European Journal of Developmental Psychology* **7**: 1-16.
- Sterck, E. H. M. and R. Steenbeek** 1997. Female dominance relationships and food competition in the sympatric thomas langur and long-tailed macaque. *Behaviour* **134**: 749-774.
- Stevenson, M. F. and T. B. Poole** 1976. An ethogram of the common marmoset (*Calithrix jacchus jacchus*): general behavioural repertoire. *Animal Behaviour* **24**: 428-451.
- Stevenson, M. F. and A. B. Rylands** 1988. The marmosets, genus *Callithrix*. In: *Ecology and behavior of neotropical primates*. (R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca ed.). Washington DC, World Wildlife Fund: pp. 131-222.
- Sueur, C., O. Petit, A. De Marco, A. T. Jacobs, K. Watanabe and B. Thierry** 2011. A comparative network analysis of social style in macaques. *Animal Behaviour* **82**: 845-852.
- Takahata, Y., M. A. Huffman, S. Suzuki, N. Koyama and J. Yamagiwa** 1999. Why dominants do not consistently attain high mating and reproductive success: A review of longitudinal Japanese macaque studies. *Primates* **40**: 143-158.
- Taylor Parker, S. and M. L. McKinney** 1999. *Origins of Intelligence: The Evolution of Cognitive Development in Monkeys, Apes, and Humans*. Baltimore, The Johns Hopkins University Press. 404 p.
- Teufel, C., A. Gutmann, R. Pirow and J. Fischer** 2010. Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. *Developmental Science* **13**: 913-922.
- Thierry, B.** 2004. Social epigenesis. In: *Macaque societies: A model for the study of social organization*. (B. Thierry, M. Singh and W. Kaumanns ed.). Cambridge, Cambridge University Press: pp. 267-289.
- Thrall, P. H., J. Antonovics and A. P. Dobson** 2000. Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**: 1555-1563.
- Tomasello, M. and J. Call** 1997. *Primate cognition*. Oxford, Oxford university Press. 517 p.
- Tomasello, M., J. Call and B. Hare** 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour* **55**: 1063-1069.
- Tomasello, M., B. Hare and B. Agnetta** 1999. Chimpanzees, Pan troglodytes, follow gaze direction geometrically. *Animal Behaviour* **58**: 769-777.
- Torigoe, T.** 1985. Comparison of Object Manipulation Among 74 Species of Non-human Primates. *Primates* **26**: 182-194.
- Townsend, S. W., T. Deschner and K. Zuberbühler** 2008. Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS ONE* **3**: 1-7.
- Townsend, S. W. and K. Zuberbühler** 2009 Audience effects in chimpanzee copulation calls. *Communicative & Integrative Biology* **2** DOI: 10.1371/journal.pone.0002431.
- Triesch, J., C. Teuscher, G. O. Deak and E. Carlson** 2006. Gaze following: why (not) learn it? *Developmental Science* **9**: 125-147.
- Tutin, C. E. G.** 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes-schweinfurthii*). *Behavioral Ecology and Sociobiology* **6**: 29-38.
- van Hooff, A. R. A. M.** 1962. Facial expressions in primates. *Symp. Zool. Soc. Lond.* **8**: 97-125.
- van Noordwijk, M. A. and C. P. van Schaik** 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates* **40**: 105-130.
- van Noordwijk, M. A. and C. P. van Schaik** 2000. Reproductive patterns in eutherian mammals: adaptations against infanticide? In: *Infanticide by males and its implications*. (C. P. van Schaik and C. H. Janson ed.). Cambridge, Cambridge University Press: pp. 322-360.
- van Noordwijk, M. A. and C. P. van Schaik** 2004. Sexual selection and the careers of primate males: paternity concentration, dominance acquisition tactics and transfer decisions. In: *Sexual selection in primates: new and comparative perspectives*. (P. M. Kappeler and C. P. van Schaik ed.). Cambridge, Cambridge university press: pp. 208-229.
- van Schaik, C. P., S. A. Pandit and E. R. Vogel** 2004. A model for within-group coalitionary aggression among males. *Behavioral Ecology and Sociobiology* **57**: 101-109.

- van Schaik, C. P. and M. A. van Noordwijk** 1985. Evolutionary effect of the absence of felids on the social organization of the macaques on the island of Simeulue (*Macaca fascicularis*, Miller 1903). *Folia Primatologica* **44**: 138-147.
- van Schaik, C. P. and M. A. Van Noordwijk** 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* **105**: 77-98.
- Vernes, M. K. and A. L. Louwerse** 2010. *BPRC's enrichment manual for macaques & marmosets*. Rijswijk, Biomedical Primate Research Centre. 79 p.
- Vick, S. J. and J. R. Anderson** 2003. Use of human visual attention cues by olive baboons (*Papio anubis*) in a competitive task. *Journal of Comparative Psychology* **117**: 209-216.
- Warneken, F., B. Hare, A. P. Melis, D. Hanus and M. Tomasello** 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology* **5**: 1414-1420.
- Warneken, F. and M. Tomasello** 2006. Altruistic helping in human infants and young chimpanzees. *Science* **311**: 1301-1303.
- Watts, D. P.** 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* **44**: 43-55.
- Wellman, H. M. and S. A. Gelman** 1992. Cognitive-development - foundational theories of core domains. *Annual Review of Psychology* **43**: 337-375.
- Wheeler, B. C.** 2009. Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B-Biological Sciences* **276**: 3013-3018.
- Whiten, A. and R. W. Byrne** 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge, Cambridge University Press. 416 p.
- Wich, S. A. and E. H. M. Sterck** 2003. Possible audience effect in Thomas Langurs (Primates; *Presbytis thomasi*): An experimental study on male loud calls in response to a tiger model. *American Journal of Primatology* **60**: 155-159.
- Wickings, E. J., T. Bossi and A. F. Dixson** 1993. Reproductive success in the mandrill, *Mandrillus sphinx* - correlations of male-dominance and mating success with paternity, as determined by DNA-fingerprinting. *Journal of Zoology* **231**: 563-574.
- Widdig, A., F. B. Bercovitch, W. J. Streich, U. Sauermaun, P. Nurnberg and M. Krawczak** 2004. A longitudinal analysis of reproductive skew in male rhesus macaques. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**: 819-826.
- Williams, M. F.** 2002. Primate encephalization and intelligence. *Medical Hypotheses* **58**: 284-290.
- Willisch, C. S., I. Biebach, U. Koller, T. Bucher, N. Marreros, M. P. Ryser-Degiorgis, L. F. Keller and P. Neuhaus** 2012. Male reproductive pattern in a polygynous ungulate with a slow life-history: the role of age, social status and alternative mating tactics. *Evolutionary Ecology* **26**: 187-206.
- Willisch, C. S. and P. Neuhaus** 2009. Alternative mating tactics and their impact on survival in adult male alpine ibex (*Capra ibex ibex*). *Journal of Mammalogy* **90**: 1421-1430.
- Wilson, M. E.** 1981. Social dominance and female reproductive behaviour in rhesus monkeys (*macaca mulatta*). *Animal Behaviour* **29**: 472-482.
- Wilson, M. E., M. L. Walker, N. S. Pope and T. P. Gordon** 1988. Prolonged lactation infertility in adolescent rhesus monkeys. *Biology of reproduction* **38**: 163-174.
- Wittig, R. M. and C. Boesch** 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology* **24**: 847-867.
- Wolff, J. O. and D. W. Macdonald** 2004. Promiscuous females protect their offspring. *Trends in Ecology & Evolution* **19**: 127-134.
- Yorzinski, J. L. and M. L. Platt** 2010 Same-Sex Gaze Attraction Influences Mate-Choice Copying in Humans. *Plos One* **5** DOI: 10.1371/journal.pone.0009115.
- Zeh, J. A. and D. W. Zeh** 2003. Toward a new sexual selection paradigm: Polyandry, conflict and incompatibility (Invited article). *Ethology* **109**: 929-950.

Dankwoord

Dit werk kon slechts tot stand komen dankzij de steun en hulp van vele mensen. Bijzondere dank gaat uit naar mijn promotors, Liesbeth Sterck en Berry Spruijt, voor het aanreiken van het onderwerp, de interactieve manier waarop zij mij hielpen bij het bedenken van nieuwe experimenten en het kritisch evalueren van de teksten.

Daarnaast wil ik de vele studenten bedanken die mij hebben geholpen met het verzamelen van de data voor de verschillende experimenten in dit proefschrift. Anne-Marie Arnolds, Matthijs Graner, Caroline Oleson, Nick Stolk, Raissa de Boer, Marlous Ouwendijk, Marie-lyne Despres-Einspenner, Frederique Bakker, Barbara Winkelman en Maaïke Berdowski ontzettend bedankt voor jullie hulp, enthousiasme en inzet. De experimenten vereisten vaak fysiek zwaar werk zoals het sjouwen van loodzware schotten en het bouwen van hoge stellages, ik ben blij dat ik daar zoveel helpende handen bij heb gehad. Vele studenten hebben de kou moeten doorstaan bij het observeren van de java-apen en het paargedrag van de resusapen dat alleen in de winter plaatsvindt. Veel van mijn experimenten zouden niet mogelijk zijn geweest zonder dat de apen maanden voor het begin van een experiment getraind waren door verschillende studenten en medewerkers (in het bijzonder Coby de Wit en Esther den Heijer). Voor het trainen van de java-apen was veel geduld en discipline nodig, mijn respect hiervoor.

Niet alleen studenten hebben mij geholpen met het praktische werk, maar ook de medewerkers van het BPRC waren zeer behulpzaam bij fysieke en technische uitdagingen die mij alleen niet gelukt waren. Willem Ritters, Ron Kluivers, Rob Hollman en Tjeerd Fluïtsma enorm bedankt voor al jullie fysieke inspanningen en technische hulp. Tjeerd, zonder jouw fantastische U-profielen waren mijn schotten nooit zo goed blijven hangen en hadden we nooit geweten of apen sex willen hebben achter schotten. Saskia van Soest en Willem van der Spek bedankt voor jullie hulp tijdens de laatste experimenten met de Java-apen. En dan wil ik natuurlijk alle andere dierverzorgers bedanken voor hun dagelijkse zorg voor de apen en hun medewerking tijdens mijn onderzoeken. Omdat bij het BPRC mensen werken die veel ervaring hebben met apen heb ik veel goede adviezen mogen ontvangen over het werken met deze dieren. Annet Louwerse en Marit Verness bedankt voor jullie input bij het uitdenken van experimenten en het opzetten van trainings protocollen voor de apen.

Mijn baan als AIO heb ik voornamelijk te danken aan het BPRC. Ik ben het BPRC enorm dankbaar voor het aanbieden van deze positie en voor de financiering. In het bijzonder wil ik Jan Langermans en zijn voorganger Peter Heidt bedanken voor hun leiding van de Animal Science Department en hun betrokkenheid met dit project.

Last but not least zou ik niet in staat zijn geweest deze promotie tot een goed einde te brengen zonder de steun van mijn familie en vrienden. Ten eerste Marco, je hebt veel geduld getoond en mij vrijgelaten om (vooral tijdens de laatste fase van mijn proefschrift) regelmatig 's avonds en in het weekend te werken, terwijl ik weet dat je eigenlijk liever samen iets leuks was gaan doen. Het was niet altijd even makkelijk met het inplannen van onze gezamenlijke vakanties vanwege onverwacht uitlopen van experimenten etc., maar samen wisten we er altijd wel een mouw aan te passen. Je hebt altijd veel interesse in mijn onderzoek getoond en ik vond het fijn dat ik altijd al mijn frustraties met je kon delen wanneer er iets niet lukte of wanneer ik erg op zag tegen het geven van een mondelinge presentatie. Je bood altijd een luisterend oor wanneer ik een

praatje wilde oefenen ook al had je het al 10 keer gehoord en was het in het Engels voor jou best moeilijk te volgen.

Mijn familie heeft mij veel steun gegeven tijdens mijn promotie. Weekendjes weg met de hele familie waren een welkome afwisseling op de doordeweekse werkzaamheden. Pap, bedankt voor het doorlezen van teksten en het altijd klaar staan voor het geven van goede adviezen. Mam, bedankt voor het oppassen als ik weer eens naar mijn werk moest op maandag. Ik wil jullie beiden ook bedanken voor de motivatie die jullie me hebben gegeven om te gaan studeren en om door te zetten wat ik wil bereiken. Jullie hebben mij nooit gepushed om hard te studeren, maar ik ben blij dat jullie altijd achter mijn keuzes hebben gestaan en mij vertrouwen hebben gegeven in wat ik kan.

Tijdens mijn opleiding biologie waren Leo, Harry en Wim altijd in voor lol en gezelligheid. Nu houden we daar nog steeds van alleen wonen we wat ver uitelkaar, waardoor we elkaar veel minder zien, maar als we dan weer bijelkaar zijn is het weer net alsof we weer in de collegebanken zitten. We zijn alle vier de uitdaging van een promotie aangegaan en daardoor motiveren en inspireren we elkaar goed. Leonie, Anne, Jolanda, en Marleen, jullie zorgen continu voor gezellige uitjes en weekendjes weg. We hebben allemaal een druk schema, maar maken zo nu en dan tijd voor een super gezellig avondje stappen. Heerlijk waren de weekends in Italië en Zweden, het is dan zo gezellig met elkaar dat je de rest van de wereld (en de proefschrift stres) even vergeet.

De dames van de zumba wil ik bedanken voor de welkome afleiding elke donderdagavond. Ik kan zumba echt aanraden voor iedereen die energie wil opdoen!

Curriculum Vitae

De schrijfster van dit proefschrift werd geboren op 7 oktober 1980 in Emmeloord (Noordoostpolder). Het grootste deel van haar basisonderwijs heeft ze hier gevolgd tot ze verhuisde naar het westen van het land. Haar middelbaar onderwijs genoot ze voornamelijk aan de Vrije School in Leiden. Nadat ze haar propedeuse had afgerond in de milieukunde aan de hogeschool Delft, begon ze aan haar opleiding Biologie aan de Universiteit van Leiden. Ze specialiseerde zich voornamelijk op het gebied van ecologie, milieu biologie en gedragsbiologie. In het derde jaar van de opleiding liep ze haar eerste stage bij de afdeling gedragsbiologie, waar ze werd begeleid door Marie-Jeane Holveck en Katarina Riebel. Ze onderzocht tijdens deze stage bij



zebravinken de relatie tussen morfologische eigenschappen die gerelateerd zijn aan de fysieke conditie en de zangkwaliteit. In het vierde jaar volgde ze een stage bij dezelfde onderzoeksgroep, maar deze keer werd ze begeleid door Erwin Ripmeester en Hans Slabbekoorn en deed ze onderzoek naar de communicatieve functie van zang karakteristieken van Merels. Voor haar laatste stage reisde Anne samen met haar studiegenote, Leonie Doorduyn, af naar Kameroen, om daar onderzoek te doen naar de faciliterende werking van het grazen van nijlpaarden voor andere herbivoren. Dit onderzoek werd begeleid door Ralph Buij, Hans de long en Paul Loth, verbonden aan het Centrum voor Milieukunde in Leiden. In 2006 behaalde Anne haar diploma en in 2007 begon ze als promovendus bij de Universiteit van Utrecht in dienst van het Biomedical Primate Research Centre (BPRC) in Rijswijk. Hier deed ze gedurende vijf jaar onderzoek aan de verschillende apen kolonies, wat resulteerde in dit proefschrift.

Publicaties

- Ripmeester, EAP, de Vries, AM, Slabbekoorn, H.** 2007. Do blackbirds signal motivation to fight with their song? *Ethology* **113**: 1021-1028 DOI: 10.1111/j.1439-0310.2007.01398.x
- Massen, JJM, Overduin-de Vries, AM, de Vos-Rouweler, AJM, Spruijt, BM, Doxiadis, GGM, Sterck, EHM.** 2012. Male Mating Tactics in Captive Rhesus Macaques (*Macaca mulatta*): The Influence of Dominance, Markets, and Relationship Quality. *International journal of primatology*. **33**: 73-92 DOI: 10.1007/s10764-011-9552-5
- Overduin-De Vries, AM, Massen, JJM, Spruijt, BM, Sterck, EHM.** 2012. Sneaky Monkeys: An Audience Effect of Male Rhesus Macaques (*Macaca mulatta*) on Sexual Behavior. *American journal of primatology*. **74**: 217-228 DOI: 10.1002/ajp.21988
- Overduin-De Vries, AM, de Vries, H, Spruijt, BM, Sterck, EHM.** 2013. Sneak copulations in long-tailed macaques (*Macaca fascicularis*): no evidence for tactical deception *Behavioral Ecology and Sociobiology*. **67**: 101-111 DOI: 10.1007/s00265-012-1430-4