The Structure and Function of Male Thomas Langur Loud Calls

The Structure and Function of Male Thomas Langur Loud Calls

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Chapter 10

Chapter 1

Introduction

Introduction

Early socioecological models have emphasized the role of ecological factors in determining the social organization of primates (Wrangham 1980; van Schaik 1989). The ecological factors determine tempero-spatial patterns of distribution of individuals and determine the competition regimes between animals which, subsequently, shape their relationships (van Schaik 1989). Recent studies, however, indicate that ecological factors are not sufficient to explain primate social organization (van Schaik 1996; Sterck et al. 1997). In addition, sexual selection processes are thought to be of importance for further understanding primate social organisations (van Schaik 1996; Treves and Chapman 1996; Sterck et al. 1997; van Schaik and Kappeler 1997; van Schaik and Janson 2000). Three aspects of sexual selection are supposed to be of importance, namely: male mate competition; female mate choice; and male coercion (cf. Smuts & Smuts 1993). Primate females are influenced by the sexual strategies of males, especially by male coercion in the form of infanticide (Hrdy 1979; Sterck et al. 1997; Steenbeek 1999a; van Schaik and Janson 2000). For a male that takes over the dominant position from a predecessor, infanticide on young infants (offspring of his predecessor) may speed up the return of lactating females to a fertile condition (Struhsaker & Leland 1985; Sommer 1994). Thereby, he may increase the number of offspring he can generate during the limited period that he has access to fertile females (Hrdy 1974). In addition, it has been suggested that extra-group males commit infanticide to lure females to him (Sterck 1997, Steenbeek 1999a). In either way, females are affected by infanticidal strategies of males. It is expected that an important female counter-stratgey is mate choice in the form of female selective dispersal and association with males (e.g. Marsh 1979; Sterck 1997; van Schaik and Kappeler 1997; Steenbeek 1999a; Sterck and Korstjens 2000).

Thomas langurs are an appropriate primate species to study the role of sexual selection processes on male and female sexual strategies. These medium sized arboreal foli-frugivores (Sterck 1995) are found in three social constellations: mixed-sex groups, all-male bands and as solitary males (Sterck 1997; Steenbeek 1999a). Mixed-sex groups typically consist of one resident male and several females (1-7) with usually a number of immatures. Individuals of both sexes disperse (Sterck 1997; Steenbeek 1999a). Females have two ways to associate with a new male: usually females transfer to a new male (either in an existing mixed-sex group or to a solitary male, Steenbeek et al. 2000), but male take-overs of groups also occur (Steenbeek 1999). Females also show secondary transfer (Sterck 1997; Sterck and Korstjens 2000). Therefore, females may reside in a number of groups during their lifetime. A mixed-sex group is defined to cease existing when all reproductive females have left the male. This results in a fluid social organization in which bisexual groups have a limited life span and go through a few distinct phases. The early phase of a male's tenure starts when females associate with a new breeding male and thus form a new groups. This can be the result of an (aggressive) group take-over or by the gradual association of females. The middle phase of a male tenure starts when females begin to reproduce and the first offspring is born. During the late phase of a male's tenure, females leave the male to associate with a new breeding male. This often results in leaving behind an all-male band consisting of the former breeding male and his male offspring (Steenbeek et al. 2000).

It has been suggested that female transfer in Thomas langurs is an effective anti-infanticidal strategy, being the expression of female mate choice (Sterck 1997; Steenbeek 1999a; Sterck and Korstjens 2000). It is important, however, to separate two different choice females have to make. First, the females need to decide when to leave their current male and second, they need to decide to which male to transfer. There is support for the suggestion that females indeed time their transfer. Steenbeek (1999a) has shown that female transfer is most likely to occur when a resident male loses competitive strength and is no longer able to effectively to defend his females against harassment by extra-group males (Steenbeek 1999b). Thus, the dispersal is timed so as to minimize the risk that dependent offspring are harmed. The alternative explanations for female transfer such as inbreeding avoidance or food competition are not supported for Thomas langurs (Sterck 1997, Steenbeek 1999a, this thesis chapter 9).

It is likely, therefore, that the newly chosen male is "better" than the deserted male. Previous research on Thomas langurs suggests that the most important quality of a male may be his ability to prevent infanticide by extra-group males (Steenbeek 1999a; b), but as yet we lack data about whether females indeed transfer to such better protector males.

The quality of a male may depend on a number of factors, but the studies just mentioned indicate that fighting ability (i.e. protection of females and their offspring) is an important, if not the most important feature. Fighting abilities, however, are not easy to assess, because encounters between adult males are not very common. Even when these are witnessed, these are often calm and without overt aggression. In addition, the conditions in a tropical forest often hinder detailed observations of aggressive interactions. Nevertheless, Steenbeek (1999b) has shown that females could potentially use male behaviour during between-group encounters to assess the relative strength of males. She has shown that males in their late tenure are less successful in keeping intruders away, provoked other groups less often ands joined morning call bouts less often than during the middle tenure phase. This is an important results; it suggests that there are physiological and/or other behavioural correlates of this reduction in male strength at the end of his tenure. For instance, high-quality males may have higher levels of testosterone (e.g. Birkhead et al. 1998, Duckworth et al. 2001, Gonzales et al. 2001), lower levels of stress hormones, carry fewer parasites than low-quality males, have higher loud call rates (e.g. McComb 1991) or certain loud call characteristics (e.g. Ryan 1985).

Among the several potential factors important in primate male quality, loud calls have often been suggested to be important in relation to mate attraction and mate choice (Waser 1977; Mitani 1985; Cowlishaw 1992; Mitani and Nishida 1993). For several bird species song characteristics, such as song length, frequency, and variation, are related to male quality and reproductive success (Lambrechts 1992; Genevois and Bretagnolle 1994; Lambrechts and Dhondt 1996). In addition, female choice is based on male call characteristics (Ryan 1988; Ryan and Keddy-Hector 1992; Searcy 1992; Andersson 1994; Searcy and Yasukawa 1996).

The aim of this thesis is, therefore, to evaluate the structure and function of one of the likely indicators of male quality, the loud call in male Thomas langurs. To provide a solid basis for the understanding of the function of loud calls in the Thomas langurs, the first part of the thesis consists of acoustical analyses of male loud calls on three levels: individual, context, and age. The second part of the thesis is concentrated on the function of the loud call in the social organization of the Thomas langur. The latter is important since there are several hypothesised functions for loud calls other then mate-attraction, such as inter-group spacing, territorial defence, predator alarm and within-group spacing (Waser 1977).

One important prerequisite for loud calls to be used in female mate choice is that there is individual variation. The second chapter deals with acoustic variation in identity and context. Since Thomas langur males give loud calls in four different behavioural contexts: morning calls, vocal responses to other groups, between-group encounter calls and alarm calls, it is important to correct for such variation when examining individual variation.

Once individual identity is established it is important to determine whether loud calls of individuals change during their tenure. This is the aim of the third chapter. In addition this chapter shows results on the total number of loud calls during given by males during their various life-stages and also on the percentage of mornings that morning calls are produced. Since morning are thought to be especially costly to produce (Whitten 1980, Cowlishaw 1996) it expected that males at the end of their tenure would show a reduction in the days that they will make loud calls, a reduction in the number of calls per day or certain changes in the acoustical properties of a loud call. Alternatively, males in their end tenure could attempt to give loud calls that sound like males in a good condition. This would, however, not be possible when loud calls are honest signals (Zahavi 1975). In this chapter we will also present testosterone levels for the four life-stages. A possible link between loud call development and testosterone levels is suggested.

Whereas the previous chapters investigated individual and developmental differences in male loud calls, the following chapters deal with the function of Thomas langur loud calls, and with whether in the Thomas langur react differently to differences in male loud calls.

The fourth chapter addresses the multiple functions of loud calls in a large variety of primates by conducting a comparative analyses. The major functions that have been proposed for the function of loud calls in intergroup communication are examined in this chapter, such as mate-defence, mate attraction and resource-defence.

Chapter five addresses the role of loud calls in intergroup communication and the role of the location in a groups;s range from where the loud call is given. By playing back loud calls from the neighbouring males from the centre and edge of a test group's own home range the importance of the mate- and resource-defence functions of loud calls are evaluated.

The aim of chapter six is to test experimentally whether Thomas langurs react differently to loud call playbacks from different males. The experimental set-up used here has its roots in ornithological research where a number of studies have shown that individuals respond differently to neighbour and stranger call playbacks. This response is generally thought to be adaptive because differentiating calls from neighbours and strangers can prevent the costs of unnecessary contests. We furthermore hypothesise that in Thomas langurs discriminating between neighbouring and strange males can be of importance for infanticide risk reduction.

In chapter seven the infanticide hypothesis is evaluated in more detail by experiments in which langur groups are exposed to playbacks of young and old adult male loud calls. Since most of the infanticidal attempts are committed by young adult males (Sterck 1997; Steenbeek1999a; Wich unpublished data), we expect that distinguishing between these two call types would be functional for both Thomas langur males and females (cf. McComb et al. 1993).

The alarm function of loud calls is examined experimentally in chapter eight. Primate loud calls have been suggested to function both in warning conspecifics that a predator is around and to warn the predator that it has already been spotted by the prey (Zuberbühler et al. 1997). By observing the reaction of langur groups and solitary individuals to a fake tiger skin and a white striped blanket the alarm function of the male Thomas langur loud call is evaluated.

In chapter nine a review is provided of the possible factors influencing female transfer. In this chapter several proximate (e.g. number of loud calls per day, percentage of days on which morning calls are given etc) and ultimate (e.g. food competition, predator avoidance, infanticide) factors are examined for 13 years of data on wild Thomas langurs.

Chapter ten provides a summary of the previous chapters and suggestions for future research.

Chapter 2

Individual and Contextual Variation in Thomas Langur Male Loud Calls

With S. Koski, C. P. van Schaik

(Ethology, in press)

Abstract

Individual and contextual differences in male loud calls of wild Thomas langurs (*Presbytis thomasi*) were studied in northern Sumatra, Indonesia. Loud calls were given in the following contexts: morning calls, vocal responses to other groups, between-group encounter calls and alarm calls. Loud call spectrograms were analyzed for a large number of variables. With discriminant analyses, 16 variables were found to be important in distinguishing individuals and contexts. Loud calls were assigned to the correct individual in 97.2 % of the cases (94.4 % with 'leave-one-out' validation) and to the correct context in 50.3 % of the cases (34.6 % with 'leave-one-out' validation). A multivariate general linear model showed significant differences in both temporal and frequency variables between individuals and contexts. Although differences were small, loud calls seemed to differ between the contexts in functionally meaningful ways, relating to the distance of the intended receivers and to the urgency of the message. Observation showed that females in the caller's group collected infants more often in the between-group encounter context and in the alarm call context than in the vocal exchange context. These differential responses could suggest that the monkeys also perceived the measurable differences in loud call characteristics between the various contexts.

Introduction

In several primate species, there is evidence for individual variation in long distance vocalizations or loud calls (e.g. Marler & Hobbett 1975; Waser 1977; Snowdon & Cleveland 1980; Chapman & Weary 1990; Steenbeek & Assink 1998). Individual variation in loud calls may be adaptive for several reasons. First, it may serve individual recognition. In fission-fusion species this facilitates re-establishing contact or selection of particular associates (Chapman & Lefebre 1990). In general, individual recognition may be used to discriminate between the loud calls of neighbors and strangers (Ydenberg et al. 1988; Wich et al. chapter five). This can be especially important in species where infanticidal attempts are more likely to come from either stranger or neighboring males, such as in Thomas langurs where stranger males are more likely to be infanticidal than neighbors (Sterck 1995; Wich et al. in press). Second, loud call variation could also be indicative of male quality and thus may influence female choice in cases where females transfer to other males (Steenbeek & Assink 1998) or be of importance in male-male competition (Steenbeek et al. 1999).

Vocalizations of the same individual are also known to differ between social contexts (e.g. Clark & Wrangham 1993; Vercauteren-Drubbel & Gautier 1993; Nocross & Newman 1993). Contextual variation in call features can produce acoustically distinct categories with no intermediate call types or be graded, with continuous variation between the call types (Hammerschmidt & Fischer 1998). Different call types for predators have also been found for several primates (Seyfarth et al. 1980; Seyfarth & Cheney 1990; Zuberbühler et al. 1997) and also for different social interactions (e.g. Elowson et al. 1991; Aich et al. 1990).

In this study we investigated both individual and contextual variation in loud calls of wild Thomas langurs, a medium sized (7-8 kg, Sterck 1995) arboreal endemic colobine species living in Northern Sumatra, Indonesia. These primates are characterized as folivore-frugivores with limited food competition (Sterck 1995, 1997; Sterck & Steenbeek 1997). Populations consist of one-male, multi-female groups, as well as a smaller number of all-male bands and solitary males (Sterck 1995). Males always leave their natal group, whereas females show a preference for staying in a familiar habitat, but sometimes leave both the familiar home range and familiar conspecifics. To describe this system, Steenbeek (1999a) coined the term "flexible philopatry". During between-group encounters males of opposing groups often behave aggressively towards one another, whereas females do not (van Schaik et al. 1992; Steenbeek 1999b). Infanticide by extra-group males occurs and is considered to have a major influence on the Thomas langur's social organization (Sterck 1995; Steenbeek 1999a) and is mainly due to unfamiliar or strange males (Wich et al. in press).

The aim of this paper is to re-examine the individual differences between male loud calls using a larger and more balanced sample than the study that first demonstrated this (Steenbeek & Assink 1998), and in addition to examine possible differences in male loud calls during different contexts. Variation in loud calls is expected since loud calls are given in a variety of contexts (morning calls, vocal responses, between-group encounters, and predation threat), in which calls may serve different functions and thus potentially convey varying information. To assess whether possible contextual differences in loud calls had any biological significance the reaction of females was assessed after loud calls of their resident male in different contexts. A difference was expected since the different contexts presumably entailed different risks to females and their offspring.

Methods

Study site

This study was conducted at Ketambe Research Station (3° 41' N, 97° 39' E), Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia. The study area consists of primary lowland rain forest and was described by Rijksen (1978) and van Schaik and Mirmanto (1985).

Loud call recordings and categories

Loud calls were recorded from seven adult males of mixed-sex study groups. The history of each of these groups and the individuals therein is well known since Thomas langurs have been studied in this area since 1988 (Sterck 1995; Steenbeek 1999). Tape recordings of loud calls were made from March 1998 to July 1999 with a Sony WM-D6C-recorder and Sony ECM-T140 microphone.

Loud calls were recorded opportunistically while following the monkeys from dawn till dusk, i.e. from the sleeping tree in the morning to the sleeping tree in the evening. When a loud call occurred, the identity of the caller and the time of the day were noted as well as the behavioral context associated with the call. The following behavioral contexts were distinguished: 1) Morning call (MC): male gives out a loud call in early morning before 6:30 from a sleeping tree; 2) Vocal response calls (VR): vocal communication of two or more groups at any time of the day, (excluding the morning calls), without visual contact between groups; 3) Between-group encounter calls (GE): male loud calls during a between-group encounter with a neighboring group or an all-male band; a between-group encounter was defined to occur when groups were within 50 meters (Steenbeek 1999b); 4) Alarm calls (AL): calls given when a predator has been seen or heard, always preceded by a large number of hiccups by the male. Likely predators for Thomas langurs are tigers (*Panthera tigris*); clouded leopards (*Neofelis nebulosa*); and pythons (*Python recticulatus*). In practice it was easy to assign a call to the right context since several groups were followed simultaneously and therefore the distances to other groups were known.

We also recorded female responses to the calls in all but the MC context, in particular whether they collected their offspring after loud calls of their own male in the different loud call contexts. Data from 17 females from 9 different groups were analyzed for this purpose. These data were collected on 444 full follow days from dawn to dusk.

Acoustic analyses

Thomas langur loud calls last approximately 4 seconds (Fig. 1; for details: Steenbeek & Assink 1998; Steenbeek 1999a).

Loud calls were analyzed following the methods described in Steenbeek and Assink (1998). A total of 229 calls were analyzed from seven males with the Macintosh application Canary 1.2 (Cornell Laboratory of Ornithology, Ithaca). For each male several calls were analyzed for each context. A call was only analyzed after visual inspection of the spectrogram showed that all parts of the call were recorded well and could be analyzed.

Calls were converted into spectrograms (temporal measurements: filter bandwidth 353 Hz, time resolution 1.4 ms, frequency resolution 10.9 Hz; frequency measurements: filter bandwidth 176 Hz, time resolution 2.9 ms, frequency resolution 5.4 Hz.). The same variables were measured as those described in Steenbeek and Assink (1998).

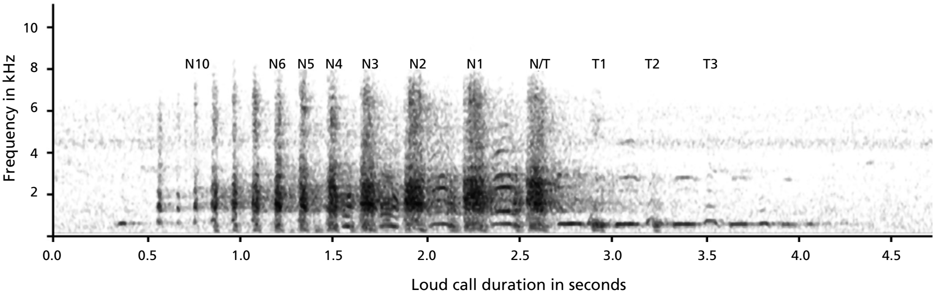

Figure 1. Spectrograph of a male Thomas langur loud call

Statistical testing

Discriminant analyses were used to examine differences between individuals and contexts (cf. Fischer et al. 2001). All variables were entered with the direct method (cf. Teixidor and Byrne 1999; Fischer et al. 2001). For validation of the group assignments made by the discriminant analysis we used the 'leave-one out' procedure in SPSS 9.0. Variables that passed the tolerance level were used in a multivariate general linear model (GLM) to assess whether differences between individuals and contexts were significant. In this model individual and context were entered simultaneously as factors. Univariate F-tests determined how loud call elements contributed to the results (cf. Randall 1989). For female behaviour following a loud call we tabulated for each female the number of times they collected their infant and the number of times they did not, for three contexts: Vocal response (VR); group-encounter (GE); and alarm (AL). For each female for each context we then calculated the proportion in which they collected their infant.

All tests were performed with SPSS 9.0 and considered significant when $\alpha < 0.05$. Significance levels were corrected for with the sharper Bonferroni procedure (Hochberg 1988) to reduce the chance of type I errors. When data were not distributed normally we used non-parametric tests (Siegel and

Castellan 1988). In the Tables, the following conventions are used: $p<0.01$ = ★★, $p<0.05$ = ★, $p<0.1$ = ~.

Results

Discriminant analyses

The discriminant analyses showed that calls could be well classified on the basis of individuals. The first discriminant function accounted for 69.8% of the variance, the second for 14.6% and the remaining four functions for a combined variance of 15.6%. With these functions it was possible to assign a call to the correct individual in 97.2% of the cases (94.4% with 'leave-one-out' validation). At the level of the individuals predicted group memberships varied between 88.9-100.0%.

For contextual differences three discriminant functions were calculated. The first and second discriminant functions accounted for, respectively, 58.5% and 32.2% of the variance. The percentage of calls that were assigned to the correct group was 50.3 % (34.6 % with 'leave-one-out' validation). Especially loud calls in the VR context were difficult to assign to the proper group (23.5). For the other context this was higher (MC=65.0%, GE=65.1%, and AL=53.3%).

Table 1. **Overview of variables**

Variables	Description of variables
N-units	Total number of N-units
T-units	Total number of T-units
Duration	Duration from the first element to the last element (ms)
N2ex	Fundamental frequency in the middle of the element (Hz)
N2in	Fundamental frequency in the middle of the element (Hz)
N1ex	Fundamental frequency in the middle of the element (Hz)
N1in	Fundamental frequency in the middle of the element (Hz)
T2ex	Fundamental frequency in the middle of the element (Hz)
N10-N8	Interval from N10-unit to N8-unit (ms)
N10-N2	Interval from N10-unit to N8-unit (ms)
N10-N1	Interval from N10-unit to N1-unit (ms)
N8-N7	Interval from N8-unit to N7-unit (ms)
N8-N5	Interval from N8-unit to N5-unit (ms)
N8-N4	Interval from N8-unit to N4-unit (ms)
N8-N3	Interval from N8-unit to N3-unit (ms)
N2-T2	Interval from N2-unit to T2-unit (ms)

Variables that passed the tolerance level in the discriminant analyses

Table 2. Individual differences in loud call characteristics

Variable	Qb	Aj	Si	Ek	Gf	He	Ti	F-values
	(n=18)	(n=21)	(n=29)	(n=22)	(n=37)	(n=20)	(n=32)	
N-units	11.6	11.8	11.7	10.3	15.3	11.8	13.9	F= 34.5 **
(number of)	(1.4; 20)	(1.1; 32)	(1.7; 37)	(1.4; 36)	(2.0; 40)	(1.6; 24)	(1.6; 40)	
T-units	6.8	7.1	12.4	7.2	11.1	11.3	13.7	F= 80.4 **
(number of)	(1.2; 20)	(1.7; 32)	(1.9; 37)	(2.0; 36)	(1.5; 40)	(1.5; 24)	(1.5; 40)	
Duration	3356.4	3628.5	3899.0	3300.3	3980.5	3734.2	4296.0	F= 37.7 **
(ms)	(351.8; 20)	(348.5; 32)	(299.3; 37)	(329.3; 36)	(244.4; 40)	(247.9; 24)	(262,2; 40)	
N2ex	433.3	403.7	386.3	399.4	395.5	408.7	423.9	F= 12.5 **
(Hz)	(15.2; 20)	(12.5; 30)	(27.7; 35)	(18.1; 34)	(17.8; 38)	(23.2; 23)	(32.0; 36)	
N2in	636.0	590.9	530.6	666.4	662.3	559.1	511.5	F= 206.9 **
(Hz)	(33.5; 20)	(22.1; 32)	(18.8; 36)	(22.1; 36)	(29.1; 40)	(23.5; 22)	(11.9; 40)	
N1ex	424.0	403.6	385.1	404.9	394.0	401.3	420.6	F= 15.8 **
(Hz)	(12.3; 20)	(351.8; 20)	(24.9; 37)	(20.0; 33)	(21.3; 38)	(17.8; 24)	(33.6; 34)	
N1in	636.3	589.4	534.1	693.3	664.0	558.3	512.0	F= 183.6 **
(Hz)	(34.5; 20)	(16.1; 32)	(22.4; 37)	(27.0; 36)	(31.2; 40)	(20.8; 23)	(11.8; 40)	
T2ex	572.0	570.7	507.6	655.4	602.3	590.0	540.0	F= 193.2 **
(Hz)	(11.5; 20)	(20.0; 28)	(16.7; 37)	(16.9; 35)	(15.8; 40)	(25.0; 24)	(14.3; 40)	

Table 2. Individual differences in loud call characteristics (continued)

Variable	Qb (n=18)	Aj (n=21)	Si (n=29)	Ek (n=22)	Gf (n=37)	He (n=20)	Ti (n=32)	F-values
N10-N8	179.8	192.9	185.3	173.3	179.9	172.0	181.4	F= 9.1 **
(ms)	(9.1; 19)	(13.3; 31)	(12.8; 32)	(8.8; 27)	(10.5; 40)	(12.1; 22)	(7.6; 39)	
N10-N2	1179.0	1342.0	1188.2	1149.2	1238.2	1172.7	1375.2	F= 19.5 **
(ms)	(73.6; 19)	(92.8; 31)	(94.1; 33)	(137.5; 27)	(103.7; 40)	(95.2; 23)	(85.0; 40)	
N10-N1	1519.2	1674.2	1486.9	1514.1	1563.2	1482.3	1654.5	F= 12.7 **
(ms)	(78.3; 19)	(348.5; 32)	(97.6; 33)	(155.2; 27)	(109.1; 40)	(108.6; 23)	(91.4; 39)	
N8-N7	92.2	108.7	101.0	94.8	99.4	91.8	109.3	F= 25.6 **
(ms)	(6.0; 19)	(7.4; 31)	(9.2; 33)	(7.0; 33)	(7.0; 40)	(8.5; 23)	(7.2; 39)	
N8-N5	300.0	364.8	336.0	311.9	332.9	318.2	413.2	F= 45.1 **
(ms)	(14.9; 19)	(23.3; 31)	(30.6; 34)	(15.8; 33)	(25.8; 40)	(41.2; 23)	(43.9; 40)	
N8-N4	440.6	550.8	496.4	445.6	501.0	470.6	648.7	F= 58.9 **
(ms)	(28.8; 19)	(49.0; 31)	(52.1; 34)	(23.2; 33)	(54.2; 40)	(41.8; 23)	(68.3; 40)	
N8-N3	679.1	822.9	722.6	637.8	730.0	708.0	912.4	F= 23.1 **
(ms)	(57.1; 18)	(80.2; 31)	(79.3; 34)	(67.9; 33)	(155.0; 40)	(71.8; 23)	(77.8; 39)	
N2-T2	1466.9	1411.7	1357.3	1517.2	1271.9	1304.2	1224.9	F= 5.1 **
(ms)	(37.0; 18)	(154.7; 23)	(525.6; 33)	(94.2; 26)	(35.4; 40)	(43.6; 23)	(49.7; 40)	

Mean values are presented here (standard deviation; sample size). F-values from the univariate tests. Significance levels were corrected for using a sharper Bonferroni (see methods)

General linear model

To assess whether the loud call variables differed significantly between individuals and contexts a multivariate general linear model was used. The variables used in this model were those that passed the tolerance level in the discriminant analyses (minimum level set at 0.001, Table 1). Significant differences between individuals were found for all temporal and frequency variables (Table 2). Between contexts the only significant differences were of a temporal nature (Table 3). Only one of the frequency measures showed a trend to differ between contexts and the other frequency measures did not differ significantly between calls (Table 3).

Table 3. Contextual differences in loud call characteristics

Variable	VR (n=51)	MC (n=40)	GE (n=43)	AL (n=45)	F-values
N-units	12.4	11.9	13.1	12.6	F= 3.6 ~
(number of)	(2.0; 57)	(2.2; 58)	(1.9; 57)	(2.9; 57)	
T-units	10.5	11.1	9.4	9.9	F= 5.6 *
(number of)	(3.0; 57)	(3.0; 58)	(3.4; 57)	(2.9; 57)	
Duration	3775.2	3931.8	3624.8	3809.7	F= 9.5 **
(ms)	(414.2; 57)	(364.7; 58)	(494.7; 57)	(450.6; 57)	
N2ex	411.6	403.6	408.0	398.6	F= 2.8 ns
(Hz)	(28.7; 55)	(23.8; 56)	(27.7; 50)	(24.7; 55)	
N2in	595.3	593.8	598.8	583.2	F= 4.3 ~
(Hz)	(62.1; 57)	(69.0; 56)	(67.5; 57)	(64.7; 56)	
N1ex	407.4	400.6	404.0	401.3	F= 1.0 ns
(Hz)	(22.9; 53)	(24.5; 55)	(30.3; 53)	(24.1; 56)	
N1in	598.1	599.1	600.9	591.1	F= 1.1 ns
(Hz)	(67.0; 57)	(71.7; 5)	(76.3; 57)	(70.0; 57)	
T2ex	580.4	578.4	573.2	571.4	F= 2.3 ns
(Hz)	(49.4; 57)	(53.3; 56)	(45.1; 54)	(50.1)	
N10-N8	177.9	182.8	177.0	188.2	F= 8.4 **
(ms)	(10.6; 54)	(10.8; 50)	(12.6; 57)	(12.2; 49)	

N10-N2	1277.9	1276.3	1213.2	1299.8	F= 4.4 ~
(ms)	(137.2; 55)	(112.0; 51)	(125.4; 57)	(124.3; 50)	
N10-N1	1541.4	1603.2	1529.7	1593.4	F= 4.6 *
(ms)	(137.1; 54)	(111.1; 51)	(122.7; 57)	(136.2; 50)	
N8-N7	98.7	101.6	98.8	103.5	F= 4.5 ~
(ms)	(9.9; 54)	(9.9; 54)	(10.4; 57)	(8.7; 53)	
N8-N5	341.7	349.9	332.6	356.5	F= 4.5 ~
(ms)	(44.2; 56)	(50.1; 54)	(43.6; 57)	(50.2; 53)	
N8-N4	509.6	527.5	499.3	535.0	F= 4.1 ~
(ms)	(79.3; 56)	(90.0; 54)	(79.5; 57)	(91.6; 53)	
N8-N3	728.4	776.1	737.3	777.3	F= 2.6 ns
(ms)	(156.2; 55)	(116.8; 53)	(112.5; 57)	(125.4; 53)	
N2-T2	1398.1	1361.5	1295.0	1321.1	F= 1.1 ns
(ms)	(410.1; 55)	(144.1; 47)	(93.5; 51)	(139.3; 50)	

Mean values are presented here (standard deviation; sample size). F-values from the univariate tests. Significance levels were corrected for using a sharper Bonferroni (see methods)

Female reaction to the calls

There was a significant difference between the AL, GE, and VR context for the proportion that females collected their infant (Friedman two-way anova: $\chi^2=23.6$, df=2, $p<0.0001$, n=17 females). To asses between which of these contexts the differences where significant we used the multiple comparison procedure from Siegel and Castallan (1988, § 7.2.3). This procedure indicated that contexts would differ significantly from each other when the difference between the sum of mean ranks is larger than 0.821. The difference between AL and GE was 0.36 and thus not significant. The differences between AL and VR, and GE and VR were 1.59 and 1.23 and thus significant at the p=0.05 level. This indicates that females collect their infants more after the AL and GE contexts that after the VR context.

Discussion

The study presented here corroborates results found for individuality in Thomas langur loud calls by Steenbeek and Assink (1998), while correcting for context differences. In the present study, however, more variables were found to be significantly different between individuals. The loud calls of the seven males differed clearly from each other in both temporal and frequency characteristics, so that each male has his own, typical combination of call characteristics. Therefore, as in other primates the loud calls seem to convey information that allows for individual recognition (e.g. Marler & Hobbett 1975; Tenaza 1976; Hohmann & Vogl 1991; Fischer et al. 2001).

Individual recognition of Thomas langur loud calls could be adaptive for the males because it has been suggested that they have differentiated relationships with their various neighbors (Steenbeek 1999a) and the number of aggressive encounters differs between neighbors (Wich, unpublished ms). In addition, the ability to distinguish between individuals' loud calls is also likely to be adaptive to the females as well as the males, because some males are more likely to direct infanticidal attacks to a group than others (Steenbeek 1999). McComb et al. (1993) also suggested such benefits for lions (Panthera leo). This idea is supported by playback studies conducted on the same langur groups as used in this study, which indicate that Thomas langurs discriminate between individuals with different loud calls, and react more cautiously towards possibly infanticidal males (chapter five, six).

In addition to the individual variation there also was variation between loud calls given in different behavioral contexts (cf. Norcross et al. 1999; Fischer et al. 2001). Four temporal variables were significant and several other showed a trend to differ. Only one of the frequency variables (N2in) showed a trend to differ. However, the loud call differences between the various contexts were not completely distinct. Rather, the calls of the different contexts overlapped in their characteristics. This indicates a graded vocal system of loud call types (e.g. Byrne 1982; Hammerschmidt & Fischer 1998). It might be that to classify a call into a certain context, the receiver must know the individual, such as was found in spider monkey (*Ateles geoffroyi*) whinnies, where contextual variation exists within an individually typical call (Teixidor & Byrne 1999). In this case the contextual information is secondary to the individual information in a call.

However, in spite of the gradual nature of differences in call characteristics and small differences therein, it is possible to distinguish between the four types of loud call based on the temporal features: the number of T-units; the duration of the call; and the temporal intervals in the first part of the call N10-N8 and N10-N1. Thus the major difference between the contexts seems to be in duration of the call, which is due to both the time interval between the N-units and the number of T-units.

The high number of T-units in MC and VR calls is expected. These calls should be heard over longer distances than GE and AL calls, and the tonal sounds in the T-units have better propagation than non-tonal ones (Waser & Brown 1986). Loud calls given in the AL and GE context are likely to be directed to either the group of the caller (AL, Wich unpublished data) or both the group of the caller and the other group that is in close proximity (GE). Therefore these calls do not need to be propagated over long distance, which makes it unnecessary to give many T-units. To test the hypothesis that the distance of the recipient is related to the number of T-units, correlations were performed on the number of T-units and the distance of the neighboring group (only for the VR context). For each of the seven males , the correlation between distance and the number of T-units was highly significant (r-values for the males separately ranging from: 0.58-0.80; p-values: 0.005-0.004). This indicates that males are able to manipulate certain parts of their calls in direct relation to the distance of a neighbor, even within the same context. This variation in T-units could be responsible for the lower predicted group membership value for the VR context in relation to the other contexts, because distance between groups may vary considerably in this context.

In addition, we hypothesize that, although only showing a trend, the number of N-units is an indication of the "urgency" of the call. In non-dangerous situations (MC and VR) a smaller number of N-units is given than in potentially dangerous situation (GE and AL), in which females need to react swiftly with collecting their infants and grouping together. Therefore the first part of the call could logically be more important when a swift reaction is needed.

The possible biological significance of the loud call variation between contexts is strengthened by the observations of female responses indicating that females might actually perceive contextual differences in loud calls. Female infant collection occurred significantly more often in threatening situations such as possible predation and between-group encounter (possible infanticide) than in a situation in which the neighboring male is far away (vocal response). Although playback experiments are needed to exclude the possibility that females use other (non-vocal) cues to react adaptively, these observational data suggest which experiments to conduct.

In conclusion the results presented here show that there are both individual and contextual differences in male loud call characteristics and that these might be perceived and reacted to appropriately by females. Because females may have independent assessment of the contexts and the differences between the contexts were small, female responses to playbacks of loud calls of different contexts are needed to determine whether females actually use variation in the call characteristics in their responses.

Chapter 3

Tenure related changes in male loud call characteristics and testosterone levels in wild Thomas langurs

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Abstract

Males in a large number of primate species give loud calls. As with primate vocalisations in general, loud calls characteristics show few or no changes during development in the few studies that are available. In this paper we investigated changes in loud call characteristics and production between four life phases of male Thomas langurs (*Presbytis thomasi*). These phases are all-male band (amb), early, middle, and late tenure phase in bisexual groups. A discriminant analyses correctly assigned loud calls to the all-male band phase in 97.8% (95.7 with 'leave-one-out procedure') of the cases. For the other tenure phases the percentage of calls assigned correctly varied between 69.0-76.3% (66.7-73.1 with 'leave-one-out' procedure). Several temporal characteristics of the loud call, such as total duration and number of N- and T-units differed significantly between the amb phase and the three tenure phases. The frequency characteristics of the loud call as well as the number of loud calls per day did not differ between the four phases. However, males in all-male bands were found to produce significantly less morning calls than males in the other tenure phases. Maturation might be an important factor underlying these differences, since fecal testosterone levels increase between the all-male band and early tenure phase, but remain stable thereafter. In support of the possible influence of testosterone on call characteristics and production no differences were found between the middle and late tenure phase for any of the loud call measures. We postulate that females may use loud call characteristics as a cue to choose between young and old males once they decided to leave their current male, but not to decide when to leave their current male.

Introduction

Primates of various species produce loud vocalizations that can be heard over long distances. Such vocalizations are often referred to as 'loud calls' and are usually produced only by adult males (Waser 1977; Wich & Nunn in press, chapter 4). Due to their long distance of detection and acoustic specialization, it has been assumed that loud calls play a predominant role in long-distance communication (Waser 1977; Wich & Nunn, in press, chapter 4). In addition, loud calls have been proposed to function in mate attraction and mate defense (Waser 1977; van Schaik et al. 1992; Cowlishaw 1992, 1996; Steenbeek et al. 1999).

Primate vocalisations in general appear to show few changes during development (reviews in Seyfarth & Cheney 1997, 1999). However, the available data are partly contradictory as some studies report on developmental changes in call duration and frequency (Lieblich et al. 1980; Seyfarth & Cheney 1986; Gouzoules & Gouzoules 1989; Hauser 1989; Elowson et al. 1992; Snowdon et al. 1997; Hammerschmidt et al. 2000), while others, did not find differences in call characteristics between infants and adults (Winter et al. 1973; Herzog & Hopf 1983). One possible explanation for these different findings might be that more recent studies have used more refined techniques for call analysis (Seyfarth & Cheney 1997). Alternatively, however, the different results could indicate real variation of call development amongst primates.

Amongst studies on call development in primates there are only a few that have paid attention to the development of , specifically, loud calls (review in Seyfarth & Cheney 1999). These few studies show that there are no or very few changes in loud call structure during development (Seyfarth & Cheney 1999). Studies addressing (loud) call changes once a male reaches adulthood are even more sparse (Hohmann & Vogl 1991; Butynsksi et al. 1992) and indicate that (loud) call characteristics remain stable once adulthood is reached.

The functions of bird and primate calls have often been compared. This has revealed a remarkable difference. Bird songs change markedly during development whereas such changes in call structure have hardly been found in primates (Snowdon & Elowson 1992; Seyfarth & Cheney 1997). Snowdon (1988) suggests that the lack of parallels between research on bird song and primate vocalisations during development could be due to the focus of primate research on a limited number of call types and species. Loud calls are especially interesting, since these have been suggested to be a possible functional equivalent of bird song (Waser 1977; Hodun et al. 1980).

The aim of this paper is to provide a comparative analysis of male loud call characteristics and production in wild Thomas langurs accross four male life phases. Loud calls in this species have been suggested to be indicative for male quality (Steenbeek & Assink 1998) and are known to be of importance in spatial communication and neighbour-stranger recongnition (Wich et al. 2002a, b, chapter 5, 6). In addition, we investigate possible physiological correlates of loud call characteristics by examining changes in fecal testosterone levels. Testosterone is as well known factor in bird song development (e.g. Groothuis 1993; Ballintijn & ten Cate 1997; Nottebohm 1999) and could influence vocalisations in primates as well.

Methods

Study site and population

This study was conducted at the Ketambe Research Station (3° 41' N, 97° 39' E), Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia. The study area consists of primary lowland rain forest and was described by Rijksen (1978) and van Schaik & Mirmanto (1985). The history of each of these groups and the individuals therein is well known, since Thomas langurs have been studied in this area continuously since 1988 (Sterck 1995; Steenbeek 1999).

Male life phases

We have examined loud call characteristics and fecal testosterone levels in Thomas langur males during four phases in their life (details see below, Steenbeek et al. 2000). Thomas langur groups typically consist of one adult male, one to seven adult females, and immatures. Non-breeding males travel solitary or in all-male bands (Sterck 1997). Young males usually join an all-male band (amb phase) when they are expelled from their natal group (Steenbeek et al. 2000). These all-male bands consist mainly of juvenile/sub-adult/young adult males, but can also contain old males that have been deserted by their females or expelled from their groups by other males. Immature males are obviously inferior in fighting abilities compared to mature males, and they flee from mature bisexual group males during inter-group encounters (Sterck 1997; Steenbeek 1999). However, these immature all-male-band males gradually become more aggressive during such inter-group encounters and may eventually replace a mature male in a bisexual group or acquire females of their own. Once a male associates with adult females a male is defined to be in the early-tenure phase (terminology follows Steenbeek). After the birth of the male's first offspring (after about 8 months), the male is said to enter the middle-tenure phase. This is considered to be a relatively stable period since there are hardly any changes in adult group composition for some time to come. This phase lasts 4-5 years on average, when the male seems to be in his prime (Steenbeek et al., 2000). As the male ages, aggressive provocation by other males intensifies and females may desert him and transfer to other groups (Steenbeek 1999). Groups with old males are known to avoid other groups, indicating the male's inability to defend the group against other males (Steenbeek 1999). This last phase is the late-tenure phase, and is defined in retrospect as the last year before the last female leaves (Steenbeek 1999) or as the last year before the group is taken over by a new male (this study). The group is defined to end when the last female leaves or when a new male replaces the previous one.

Loud call recordings and categories

Thomas langur males produce loud calls in various contexts: at dawn; when encountering other groups; when hearing another group; and when a predator is encountered (Wich et al. unpublished data)

Loud calls (n=462) from a total of 24 different males were recorded (six all-male band [all immature], three early-, eight middle-, and seven late-tenure). These recordings were made opportunistically during 'following days' from dawn to dusk. Tape recordings of loud calls were made from 1993 to 2000 with a Sony WM-D6C-recorder combined with a Sennheiser MKH 416 p48 or a Sony ECM-T140 microphone. When a loud call occurred, the identity of the caller and the time of the day were noted as well as the behavioral context associated with the call.

Acoustic analyses

Loud calls were measured following the methods described in Steenbeek and Assink (1998) and last approximately 4 seconds (Fig. 1; for details: Steenbeek & Assink 1998; Steenbeek 1999). Thomas langur loud calls consist of two main parts. The first part is a sequence of harsh non-tonal (N-units) elements and the second part consists of tonal elements (T-units). A total of 462 calls were analysed with the Macintosh application Canary 1.2 (Cornell

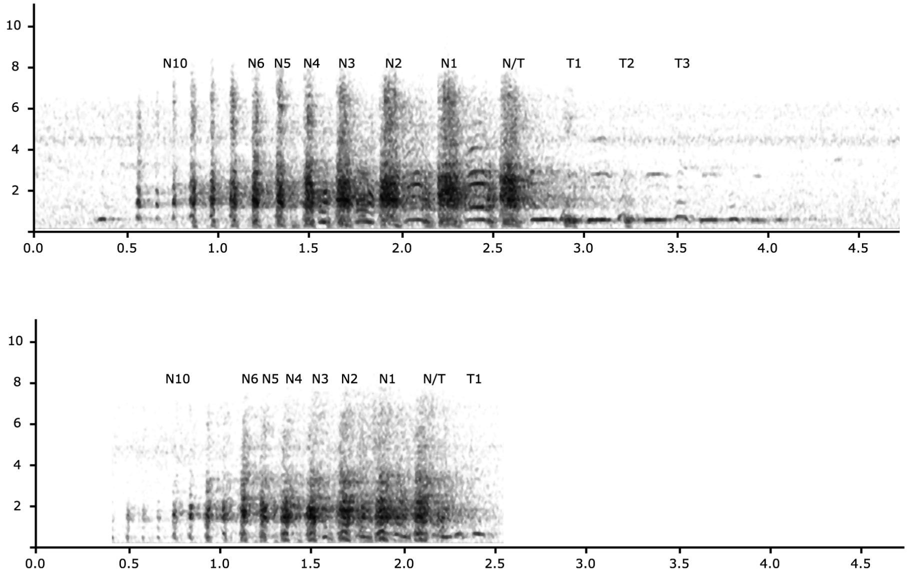

Figure 1. Loud call spectogram from male Thomas langur loud calls. The upper spectogram is from an middle tenure male and the lower spectogram is from an all-male band male. The x-axis represents the call duration in seconds and the y-axis the frequency in kHz.

Laboratory of Ornithology, Ithaca). A call was only analysed after visual inspection of the spectrogram showed that all parts of the call were recorded well and could be analyzed.

Each call was converted into a spectrogram (temporal measurements: filter bandwidth 353 Hz, time resolution 1.4 ms, frequency resolution 10.9 Hz; frequency measurements: filter bandwidth 176 Hz, time resolution 2.9 ms, frequency resolution 5.4 Hz.). The same variables were measured as those described in Steenbeek and Assink (1998) and Wich et al. (in review, chapter 1).

Total number of loud calls and morning calls

To examine loud call rates per day we used the total number of loud calls given by a male per follow day. Data for these analyses were collected under the responsibility of several observers during the period from 1988 until 2000 and a total of 1008 days were sampled for the analysis of loud call (Sterck 1995; Steenbeek 1999; Korstjens & Wich). To calculate call rates per day, only full follow days from dawn to dusk were included. We also calculated the percentage of days that a male gave morning calls; we divided the number of days that males gave morning calls by the total number of mornings observations made on that group . For these analyses we used data from six all-male band males, nine males during early tenure, 15 during middle tenure, and 15 during late tenure. For several males data were available from two or more life phases permitting us to do pairwise comparisons.

Collection of fecal samples and testosterone analysis

A total of 415 fecal samples were collected from 14 males (four AMB (all immature) -, four early tenure -, three middle tenure -, and three late tenure males). The samples were collected immediately after defecation and preserved in 10-15 ml 90% ethanol until analysis (Wasser et al. 1988). For each male, numerous samples were analysed (range: 3-93, mean: 29).

Prior to hormone analysis, fecal samples were homogenized in their original ethanolic solvent and extracted according to the methods described by Ziegler et al. (2000). The remaining fecal pellets were finally dried in a vacuum oven and the dry weight of each sample determined. The efficiency of the extraction procedure, determined by monitoring the recovery of ^{3}H-progesterone (150.000 cpm) added to a subset of samples (n=30) prior to homogenization was 86.4(6.2%).

Fecal extracts were measured for levels of immunoreactive testosterone (iT) by microtiterplate enzyme immunoassay according to the procedures described in detail by Kraus et al. (1999). In brief, fecal extracts were diluted 1:300 in assay buffer (0.04 M PBS, pH 7.2) and duplicate aliquots (50μl) taken to assay along with 50 μl aliquots of reference standard over the range of 0.15-

20 pg/well. The sensitivity of the assay at 90% binding was 0.2 pg. Serial dilutions of fecal extracts from samples of different males gave displacement curves parallel to that obtained with the testosterone standard. Intra- and interassay coefficients of variation of high- and low-value quality controls were 8.7% (n=17) and 13.0% (n=16) (high) and 10.8% (n=17) and 15.2% (n=16) (low), respectively. Fecal concentrations of iT were given as μg/g dry weight (DW).

Statistical testing

Discriminant analyses were used to examine differences in loud call characteristics between tenure phases (cf. Fischer et al. 2001). All variables were entered with the direct method (cf. Teixidor & Byrne 1999; Fischer et al. 2001). For validation of group assignments made by the discriminant analyses we used the 'leave-one-out' procedure in SPSS 9.0. Variables that passed the tolerance level (0.01) were used in a multivariate general linear model (GLM) to assess whether differences between tenure phases were significant. Univariate F-tests determined which loud call characteristics showed significant differences between the tenure phases (cf. Randall 1989).

All tests were performed with SPSS 9.0 and were considered significant when $p<0.05$. Significance levels were corrected for with the sharper Bonferroni procedure (Hochberg 1988) to reduce the chance of type I errors. In the Tables, the following conventions are used: $p<0.01$ = ★★, $p<0.05$ = ★, $p<0.1$ = ~.

Results

Loud call characteristics

The discriminant analyses showed that calls could be assigned correctly with a high percentage to the all-male band phase (97.8% [95.7 with 'leave-one-out procedure']) and with a somewhat lower percentage to the other three tenure phases (69.0-76.3% [66.7-73.1 with 'leave-one-out' procedure], Table 1). The variables that were used for the general linear model are shown

Table 1. Predicted group membership in percentages

Tenure-phase	AMB	Early	Middle	Late
AMB	97.8 (95.7)	2.2 (4.3)	0.0 (0.0)	0.0 (0.0)
Early	0.0 (1.1)	76.3 (73.1)	20.4 (22.6)	3.2 (3.2)
Middle	0.0 (0.0)	10.3 (11.4)	72.3 (71.2)	17.4 (69.0)
Late	0.0 (0.8)	14.3 (15.9)	16.7 (16.7)	69.0 (66.7)

The original predicted group membership is presented in percentages with the 'leave-one-out' values given in brackets

Table 2. Loud call characteristics used in GLM

Variables	Description of variables
N-units	Total number of N-units
T-units	Total number of T-units
Duration	Duration from the first element to the last element of the call (ms)
N2ex	Fundamental frequency in the middle of the N2ex element (Hz)
N2in	Fundamental frequency in the middle of the N2in element (Hz)
N1ex	Fundamental frequency in the middle of the N1ex element (Hz)
N1in	Fundamental frequency in the middle of the N1in element (Hz)
N7-N5	Time interval from N7-unit to N5-unit (ms)
N7-N4	Time interval from N7-unit to N4-unit (ms)
N7-N3	Time interval from N7-unit to N3-unit (ms)
N7-N2	Time interval from N7-unit to N2-unit (ms)
N7-N1	Time interval from N7-unit to N1-unit (ms)
N7-N/T	Time interval from N7-N/T change (ms)
N5-N4	Time interval from N5-unit to N4-unit (ms)
N5-N1	Time interval from N5-unit to N1 unit (ms)
N2-N1	Time interval from N2-unit to N1-unit (ms)

in Table 2 and their average values per tenure phase are presented in Table 3. Several developmental changes in loud call characteristics are apparent from Table 3. Thus the total call duration and other temporal variables significantly increase after the amb phase and continue to slightly do so during the early tenure phase, but do not change much after the early tenure phase. The number of N-units significantly decreases, whereas the number of T-units significantly increases after the amb phase. The frequency measures do not show a strong pattern, although N1in and N2in are slightly but not significantly lower in the middle and late tenure than in the amb phase and early tenure. Post-hoc tests revealed that most of the significant differences were due to differences between the all-male band phase and the other three tenure phases (Table 3). In addition, several loud call characteristics, such as N7-N2 and N5-N4 also showed significant differences between the middle- and late-tenure phase.

Total number of loud calls per day and morning calls

Unfortunately, there were no data available for the amb phase, concerning the number of calls per day. The number of calls per day did not differ between the other life phases. (Table 4). During early and middle tenure the same number of loud calls were given per day (paired t-test: n=8, t=1.7, ns). Between middle tenure and late tenure there was also no significant difference for the total number of calls (paired t-test: n=10, t=0.61, ns). The percentage of days

Table 3. Average loud call characteristics per tenure phase and results of GLM

Variables	Amb phase n=46	Early tenure phase n=94	Middle tenure phase n=184	Late tenure phase n=138	F-values, significance, and post-hoc results
N-units	17.0 (2.5)	12.3 (1.1)	13.6 (2.1)	11.7 (1.8)	F=7.6 ** amb > early, middle, late
T-units	1.2 (0.6)	7.8 (1.9)	10.5 (2.0)	11.2 (2.4)	F=38.1 ** amb < early, middle, late and early < middle, late
Duration	2444.3 (209.6)	3583.8 (190.4)	3754.0 (238.5)	3896.4 (299.5)	F=44.8 ** amb < early, middle, late
N2ex	405.5 (35.5)	420.3 (16.4)	399.9 (17.8)	414.6 (24.4)	F=0.7 ns
N2in	605.9 (40.1)	622.7 (24.6)	555.0 (61.9)	571.0 (39.2)	F=0.6 ns
N1ex	400.9 (27.0)	415.4 (10.9)	405.4 (42.8)	414.8 (24.8)	F=0.3 ns
N1in	655.8 (42.0)	624.4 (29.5)	575.0 (74.4)	578.1 (38.6)	F=3.3 ns
N7-N5	221.1 (17.1)	228.4 (27.9)	230.7 (12.6)	256.9 (33.8)	F=2.9 ns
N7-N4	355.1 (34.2)	391.2 (53.3)	394.6 (30.4)	445.9 (60.2)	F=4.6 ns
N7-N3	525.7 (67.7)	638.7 (74.8)	633.3 (49.8)	708.7 (76.8)	F=15.7 ** amb < early, middle, late
N7-N2	636.8 (111.2)	948.1 (89.6)	933.3 (43.4)	1013.5 (76.6)	F=8.4 ** amb < early, middle, late and middle < late
N7-N1	1036.1 (114.1)	1275.4 (95.7)	1250.1 (40.4)	1333.9 (77.9)	F=10.4 ** amb < early, middle, late
N7-N/T	1343.1 (115.1)	1615.3 (110.8)	1572.5 (55.4)	1703.7 (143.8)	F=12.3 ** amb < early, middle, late and middle < late
N5-N4	132.5 (18.7)	162.0 (26.0)	163.9 (18.8)	188.8 (27.3)	F=6.8 ** amb < middle, late and middle < late
N5-N1	813.5 (102.1)	1038.3 (82.2)	1019.8 (38.3)	1077.2 (52.0)	F=18.4 ** amb < early, middle, late
N2-N1	272.8 (24.0)	330.1 (19.3)	317.7 (24.7)	320.8 (18.5)	F=7.2 ** amb < early, middle, late

Average values are presented with the standard deviations given in brackets. The 'least-significant difference' test was used for the post-hoc analyses

Table 4. The number of loud calls per day and percentage of days with morning calls of males in different life stages

	All-male band	Early-tenure	Middle-tenure	Late-tenure
Nr of calls per day	no data	6.9 (2.2)	6.2 (2.7)	7.4 (5.8)
% days with morning calls	0.0 (0.0)	0.29 (0.15)	0.38 (0.25)	0.36 (0.23)

Standard deviations are presented in brackets

that males gave morning calls differed significantly between the all-male band phase and the early tenure phase (t-test: n1=6, n2=9, t=-4.79, p=0.002). However, between early and middle tenure and between middle and late tenure phase no differences were found (paired t-test: n=8, t=-1.01, ns and n=10, t=-0.60, ns respectively).

Tenure and testosterone levels

Fecal testosterone levels for the different life phases are shown in figure 2. The testosterone levels rise from the all-male band phase to the early tenure phase, but then remain stable. Statistical analyses showed that the only significant difference in testosterone levels was the increase between all-male band and early tenure (t-test: n1=4, n2=4, t=-3.69, p=0.02). There was no significant difference between early and middle tenure (t-test: n1=4, n2=3, t=0.68, ns) and between middle and late tenure (t-test: n1=3, n2=3, t=-1.84, ns).

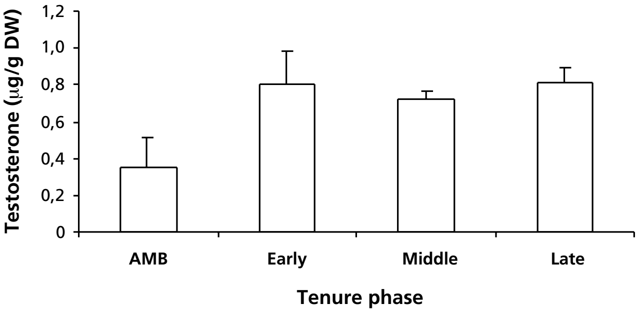

Figure 2. Fecal testosterone concentrations for the different male phases. Values are given as means plus standard deviations.

Discussion

Although several other studies found little or no - developmental changes of loud call characteristics during maturation within primates (Eisenberg 1978; Hodun et al. 1981; Hohmann & Vogl 1991; Mitani & Brandt 1994; review in Seyfarth & Cheney 1997, 1999), the results of this study show that in Thomas langurs, several loud call characteristics do change during the course of development. The discriminant analysis showed that calls could almost perfectly be assigned to the amb-phase. The percentages of correct assignment were somewhat lower for the other three life phases. Further analyses showed that the most notable differences are between the amb phase and the phases in which a male resides in a bisexual group. From the amb-phase to the early tenure phase total call duration increased in combination with an increase in T-units. In addition, an increase was found in most temporal measures from the amb-phase to the early tenure phase . Nevertheless, the number of N-units decreased from the amb phase to later phases, indicating that the duration of N-units increased. No strong pattern in the frequency variables was found, although N1in and N2in have a slightly lower value for the middle/late tenure phase than for the amb/early tenure phase. Overall, these data indicate that in male Thomas langurs loud call structure is under the influence of maturational processes.

An increase in call duration as found in our study when comparing amb males with harem holders could be simply due to an increase in lung capacity during maturation (Snowdon et al. 1997). Such a maturational effect would be in line with the observed fecal testosterone levels, which increase between the amb and early tenure phase, suggesting that amb males are still not fully mature sexually, even though their testes have already descended. Since testosterone is known to influence bird song development and speech development in children (e.g. Groothuis 1993; Titze 1994; Ballintijn & ten Cate 1997; Nottebohm 1999) and is assumed to influence primate calls as well (Snowdon 1988), it could be that testosterone has a direct effect on loud call development in Thomas langurs. This is supported by our finding that the majority of changes in loud call characteristics seen between AMB-males and males in tenure are associated with parallel changes in fecal testosterone levels. An indication for the role of testosterone in vocal development also comes from studies on humans, in which a clear increase in membranous length of the vocal fold and a decrease in the fundamental frequency of the voice during maturation has been reported and supposedly is related to changes in testosterone levels (Titze 1994).

The data also indicate that once individuals are more or less settled in a bi-sexual group loud call structure stays approximately constant. Only a few changes were found in temporal measures between the middle and late tenure phase. This is in accordance with the testosterone levels, which also remain constant from early to late tenure. The finding that loud call characteristics in Thomas langurs thus do not or only slightly change during adulthood are in close agreement with studies on *Presbytis johnii*: (Hohmann & Vogl 1991) and *Cercopithecus mitis* (Butynski et al. 1992), in which also no or little changes in loud call characteristics were found after a male reached adulthood. A similar lack of vocal changes during adulthood has been reported for humans, where the voice appears to be relatively stable over four decades from the age of 20 to 60 (Titze 1994).

The number of loud calls per day did not change over the three tenure phases of a male in a bisexual group. The percentage of days that individuals produced morning calls increased from the amb phase to the early tenure phase and remained stable over the other phases.

Asuggestion often made is that loud calls function in mate attraction (Waser 1977; Whitehead 1987; Steenbeek et al. 1999), and, therefore, should provide cues on which females can base their choice. Thomas langurs are one of the primate species in which the role of female choice has been addressed in some detail (Sterck 1997; Steenbeek 1999). In an earlier paper addressing the role of loud calls and female choice in Thomas langurs (Steenbeek et al. 1999) it was found that males in their late tenure phase participate less in morning call bouts and that extragroup males reacted differently to loud calls from males in the early and late tenure phases than to loud calls from middle tenure males. This latter finding could indicate that extragroup males can hear loud call changes between males in different tenure phases. The lack of further changes in loud call structure once males have reached middle tenure suggests that males base their distintion of late tenure phase males on other cues. We may assume that different reactions of extragroup males to males in differerent tenure phases is mainly due to individual recognition rather than loud call characteristics. Although Steenbeek et al. (1999) found that males in their late tenure phase showed reduced participation in morning bouts, this study, with a larger sample size, did not find differences in the percentage of days that morning calls were produced. Differences in call characteristics and behaviour were found between the amb and early tenure phase. Most importantly, young males produce shorter calls than older males. This could possibly provide females an indication of which males are young and most likely have a long and reproductive carreer ahead. However, since male loud call characteristics hardly change between the middle and late tenure phase it is hard to envisage how females could use loud call characteristics as a cue that their male is nearing his end as a breeding male in a bisexual group.

In conclusion, loud calls in Thomas langur show developmental changes in their loud call characteristics and calling behaviour from the AMB to the early tenure pahse, but remain stable thereafter. These data indicate that females are unlikely to use loud call characteristics to determine when the strength of their current male is waning, but can use loud call characteristics to determine whether young males are in the area.

Chapter 4

Do male "long-distance calls" function in mate defense? A comparative study of long distance calls in primates

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Abstract

Long-distance calls produced by males are common among vertebrate species. Several hypotheses have been proposed to explain features of male long-distance calls and their phylogenetic distribution in primates, but the putative functions of male long-distance calls have yet to be tested comprehensively. We used phylogenetic comparative methods to investigate hypotheses for the function of male long-distance calls. We focused on the mate defense hypothesis, which states that male long-distance calls function in intra-sexual competition for mates, but we also examined factors involving resource defense, mate attraction, and habitat. Phylogenetic reconstruction of male long-distance calls in 158 primate species indicates that the presence of male long-distance calls is the ancestral state. The carrying distance of male long-distance calls is correlated with the size of the home range, which is consistent with the role of male long-distance calls in defending mates, attracting mates, and defending resources. However, measures of male intra-sexual competition were not associated with the evolution of male long-distance calls. Evolutionary transitions were only partly correlated with factors related to mate attraction. Instead, the strongest correlates of male long-distance calls were activity period, body mass, home range, habitat and some measures of resource defense. Our results are consistent with long-distance call production as a costly signal, but detailed study within species is required to assess these costs and the functions of long-distance calls in individual cases.

Introduction

In many primate species, males produce vocalizations that are considered long-distance calls (Waser 1977; Cheney 1987; Hohmann & Fruth 1995). The term long-distance call, also known as long or loud call, refers to the distance over which such calls carry. Long-distance calls, therefore, have the potential to function in extra-group communication among males, particularly in territorial spacing involving mate defense (Waser 1977; Sekulic 1982; Oates &

Troco 1983; Whitehead 1987; Halloy & Kleiman 1994; Cowlishaw 1996; Steenbeek et al. 1999; Oates et al. 2000). This putative function is supported by the observation that long-distance calls frequently are contagious, in that calling by one male stimulates other males to counter-call (Whitehead 1987; Tenaza 1989; Steenbeek et al. 1999). Moreover, long-distance calls may be more common in males than females, which is consistent with a mate defense hypothesis because males are thought to compete for mates while females compete mainly for resources (Emlen & Oring 1977; Nunn 1999). Non-primate animals also exhibit long-distance vocalizations that may have similar functions, including birds and frogs, although different functions may predominate in different clades (Harrington & Mech 1978; Clutton-Brock 1979; Ryan 1985; McComb et al. 1994; Leonard 1995).

Although circumstantial evidence suggests that male long-distance calls function in mate defense, alternative hypotheses exist, and these alternatives are not mutually exclusive of the "mate defense hypothesis." Two alternative hypotheses are most commonly considered. First, male long-distance calls may play a role in attracting mates (Waser 1977; Mitani 1985a; Steenbeek et al. 1999). This "mate attraction hypothesis" can explain counter-calling, because other males would benefit from attracting females that are searching for a mate. The mate attraction hypothesis clearly plays a role in some vertebrates, including frogs (Ryan 1985) and birds (Searcy & Andersson 1986). A second hypothesis for male long-distance calls involves resource defense (Sekulic 1982; Tenaza 1989; Mitani 1990; Wich et al. 2002a, chapter five). This "resource defense hypothesis" might be expected to operate in mating systems characterized by resource defense polygyny, in which males defend resources needed by females (Clutton-Brock 1989; Fashing 2001). Resource defense also may play a prominent role in monogamous mating systems, if males defend resources used by females to invest in their offspring.

Several field studies have addressed possible functions of long-distance calls in one or a few species of primates (see references above and Brown 1989), but few comparative studies have examined general patterns among long-distance calls and socio-ecological variables across a wide array of species (e.g. Hohmann and Fruth 1995; Mitani & Stuht 1998; Nunn 2000). In this paper, we examine the macroevolutionary correlates of long-distance calls produced by male primates. The aim of our paper is to identify the function of male long-distance calls and to test the generality of patterns across primate species. We focus on tests of hypotheses relevant to the mate defense hypothesis, as this appears to be the most general explanation for male long-distance calling. Because this hypothesis and its main alternatives focus on inter-group conflict, we used the operational definition that long-distance calls result in counter-calling by extra-group males (Nunn 2000), as this definition only assumes extra-group communication without assigning a particular function beforehand. In addition, however, long-distance calls may function to reduce predation (Cheney & Wrangham 1987; Gautier-Hion & Tutin 1988; Cordeiro 1992) or to facilitate subgroup re-aggregation (Waser 1977; Wrangham 1977).

Methods

Information on the presence of long-distance calls was obtained from an unpublished comparative database (Nunn 2000) and updated using the published literature and personal communications from field biologists. These and all other unpublished data used in this paper are available upon request or at http://faculty.virginia.edu/charlienunn. Our focus is on extra-group conflict, which we define to include conflict between males resident in different bisexual groups (inter-group conflict) as well as conflict between resident males and potential immigrants (e.g. from all-male bands). We obtained information on long-distance calls by males and females, using sources that provided information on counter-calling by same-sexed individuals outside the group. A species was classified as not producing such calls if either of two conditions were met: (1) long-distance calls were not reported, or (2) it was stated that counter-calling to long-distance calls did not occur. Using this definition excludes vocalizations that function purely for within-group communication or as an alarm call. For example, long-distance calls in baboons (*Papio spp.*) generally function as alarm calls (except in *Papio papio*; Byrne 1981). Among vervets (*Cercopithecus aethiops*), calls produced during inter-group encounters, like the wrr and chutter, are not audible over long distances, and counter-calling from extra-group males is not mentioned explicitly (Hall & DeVore 1965; Stuhsaker 1967; Buskirk et al. 1974).

We conducted two main sets of tests. First, we focused on the scaling of carrying distance with home range size and body mass. If male long-distance calls function in communication with extra-group males, then we expect that the association between long-distance call carrying distance and home range size should exhibit a positive relationship. An association between carrying distance and home range size has been documented previously, but results were based on a very small sample (Brown 1989). We obtained data on carrying distance, measured as the maximum distance at which a long-distance call is audible to observers, from the published literature and experts on vocal communication for particular species (references provided below). These measurements have often been estimated subjectively, introducing measurement error into the estimates of carrying distance. However, we have no reason to believe that this measurement error biases the analysis. Thus, measurement error is likely to reduce the strength of patterns rather than create spurious relationships (Clutton-Brock & Harvey 1984). Estimates of measurement error currently are unavailable, making it impossible to implement more recent comparative methods that can take this error into account in comparative analyses (Martins & Hansen 1997).

The second set of tests examined the macroevolutionary correlates of male long-distance calls and was used to evaluate the validity and generality of the mate defense hypothesis and its main alternatives. Under the mate defense hypothesis, the strength of male intra-sexual conflict is the primary predictor variable for the presence of long-distance calls. Directly testing this association is complicated by the fact that most species of primates exhibit some level of male competition, but reports often are qualitative rather than quantitative, and the data are rarely comparable across multiple species. Thus, we tested whether male long-distance calls are correlated with morphological measures of male intra-sexual competition, including relative male canine size, body size dimorphism and the socionomic sex ratio (the ratio of adult females to adult males) (Table 1). Relative male canine size was taken from Plavcan et al. (1995), body mass dimorphism from Smith & Jungers (1997) while the socionomic sex ratio was based on values for male and female numbers in the group from Nunn & Barton (2000).

Table 1. **Predicted effects of socio-ecological variables on male long-distance calls**

Hypothesis	Correlates of Male Long-distance Calls
Mate defense Hypothesis	Positive association expected between presence of long-distance calls and (1) body mass dimorphism, (2) relative male canine size, and (3) socionomic sex ratio
Mate-attraction Hypothesis	Long-distance calls should be correlated with female transfer
Resource defense	Male long-distance calling should be associated with territoriality and higher D-index.

We generated further predictions to examine alternative hypotheses. (1) The mate-attraction hypothesis predicts that male long-distance calls are correlated with female transfer between groups, as female attraction to males from other groups is only effective if females can enter the group. Information on female dispersal was updated from Nunn and van Schaik (2000) using the published literature and personal communications. (2) Males also may give long-distance calls if they function in resource defense, but under this hypothesis, females should also produce calls; in fact, the distribution of calling between the sexes should be female-biased, because females are expected to show increased participation in territorial defense of food resources (Emlen & Oring 1977). Data on territoriality were obtained primarily from major review sources, including Mitani and Rodman (1979), Cheney (1987), Grant et al. (1992) and Lowen & Dunbar (1994). (3) The resource defense hypothesis also predicts that the presence of male long-distance calls is associated with a higher defensibility of the home range, which we assayed using the D-index (an index indicating the defensibility of an area based on daily travel distance and home range size, Mitani and Rodman 1979; values were calculated from an unpublished comparative database on primate day range length and home range size, updated from Nunn and van Schaik 2001.

A final hypothesis was not considered above but may explain some of the variance in patterns of long-distance calling across species. It has been hypothesized that long-distance calls are more likely to have evolved in areas where visual displays have little function in communication (i.e. tropical rain forests and other densely wooded habitats; Waser & Waser 1977; DeVore 1979) or where long-distance calls cannot be propagated over large distances due to acoustic properties of the habitat (Waser & Brown 1986). Thus, long-distance calls should be less common in savanna-dwelling species, as compared to species living in forested habitats. Information on habitat characteristics was taken from Nunn and van Schaik (2001). In this test, arboreal species were excluded from the dataset and comparison was made between terrestrial species living in wooded versus open habitats. By focusing on terrestrial species, we controlled for the correlated effects of home range size, group size and body mass, which tend to be smaller in arboreal species (Clutton-Brock & Harvey 1977; Nunn & van Schaik 2001).

Phylogenetic comparative methods

We used methods based on independent contrasts (Felsenstein 1985) and the concentrated changes test (Maddison 1990) to test hypotheses in an explicitly phylogenetic framework (Harvey & Pagel 1991; Nunn & Barton 2001). Independent contrasts are calculated as differences between species or higher nodes. As species differences, these contrasts represent evolutionary change since pairs of taxa last shared a common ancestor. Contrasts therefore test whether evolutionary change in one trait is correlated with change in another trait. They also are useful for examining a combination of discrete and continuous characters, such as the presence of long-distance calls, using the "BRUNCH" algorithm in the computer program CAIC (Purvis & Rambaut 1995). Analyses were based on Purvis' (1995) composite estimate of primate phylogeny. Previous research has revealed that log-transformed data and branch lengths best meet the assumptions for the variables considered here, and so these transformations were used (Garland et al. 1992). We also examined outliers and in some cases repeated tests without these data points, which helps to meet the assumptions of independent contrasts and deals with inflated Type I error rates under an alternative model of trait evolution (Price 1997; Harvey & Rambaut 2000; Nunn & Barton 2001).

The concentrated changes test examines the correlation among discrete traits (Maddison 1990). It tests whether a character state in some hypothesized dependent trait is correlated with a particular character state in an independent trait. We used the computer program MacClade version 4.0 (Maddison & Maddison 1992) to implement the concentrated changes test. Polytomies in the primate phylogeny (Purvis 1995) were randomly resolved prior to running the test, and we based our statistical results on 1000 simulations. We also used MacClade to trace characters, e.g. for calculating the numbers of gains and losses. To examine the effects of different random resolutions and the assumptions of parsimony, we repeated analyses using four different randomly resolved trees and the ACCTRAN and DELTRAN reconstruction algorithms (Maddison & Maddison 1992).

When testing particular directional predictions, as outlined above, we used one-tailed statistical tests with the significance level set to 0.05. One-tailed tests have the advantage of increasing statistical power (Cohen 1988; Sokal & Rohlf 1995) and are therefore appropriate when directional, a priori predictions are made and the statistical power cannot be increased by further sampling (a situation common to comparative biology).

Results

General Patterns

Information on the presence or absence of male long-distance calling in primates was available for 158 species. First, we examined the phylogenetic distribution of male long-distance calls. Using MacClade (Maddison & Maddison 1992), we found that the presence of male long-distance calls is most likely to be the ancestral state (Figure 1). Thus, assuming that gains and losses are equally likely, and focusing on unambiguous transitions, long-distance calls were lost 15-16 times during primate evolution, with 3-4 subsequent reversals depending on resolutions of polytomous nodes. These numbers are unlikely to be exact, given the variety of assumptions involved in reconstructing gains and losses phylogenetically (e.g. Omland 1997; Cunningham et al. 1998). The critical issue for testing the hypotheses that follow, however, concerns the ancestral state and the polarity of trait change in the primate lineages. Based on the distribution of calls across extant primates, we assume that the presence of long-distance calls is the ancestral state for primates. Thus, our phylogenetic tests examine the factors that lead to losses of male long-distance calls rather than gains.

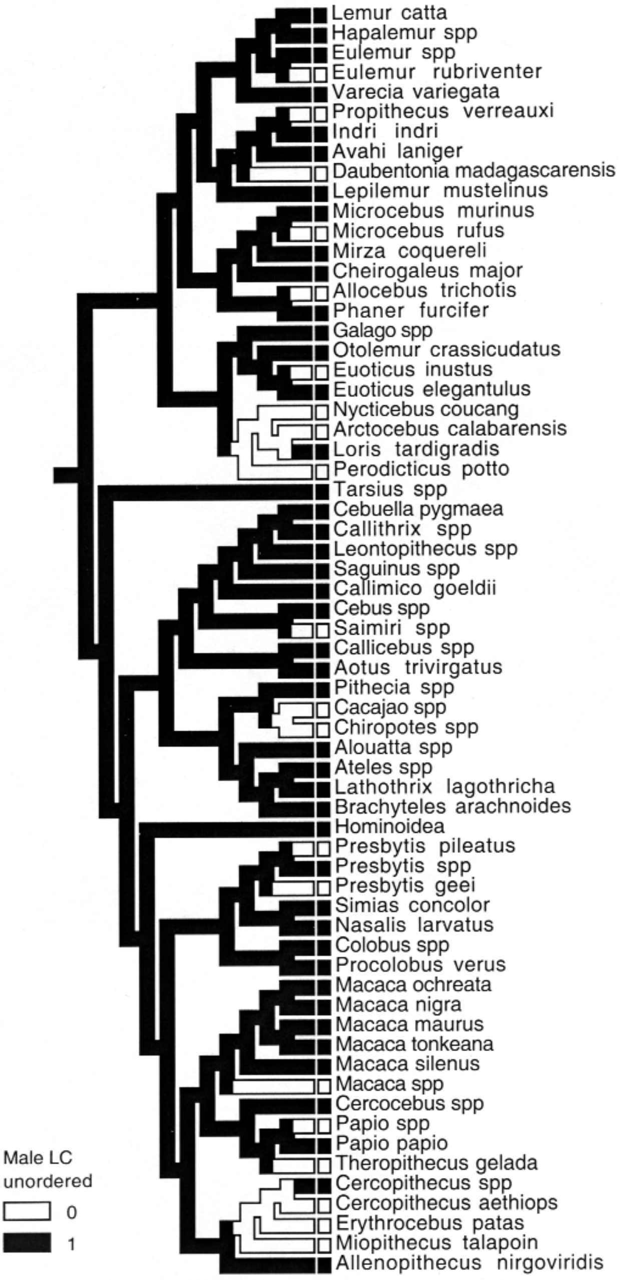

Figure 1. The absence (0) and presence (1) of male long-distance calls (Male LC) mapped onto the Purvis phylogeny (1995). See Purvis (1995) for support indices for particular nodes on this supertree. Species in the same genus that had the same value for male long-distance calls were combined to reduce the size of the tree. Therefore only a limited number of species are presented in this figure.

Prior to testing the hypotheses, we examined the general correlates of long-distance calls and their patterns across species. This is an important step to identify potentially confounding variables and avoid spurious relationships. In our dataset long-distance calls were more common in males than females; in fact, there were no species in which females were classified as exhibiting long-distance calls without males also having long-distance calls (Table 2). With regard to ecological factors, long-distance calls were approximately equally common in simple tabulations of diurnal and nocturnal species (Table 3). However, incorporation of phylogenetic information using the concentrated changes test revealed an association between activity period and losses of long-distance calls, with long-distance call losses concentrated significantly on branches characterized by nocturnal activity period (p=0.03-0.04, based on alternative resolutions of primate phylogeny). This result is largely due to the nocturnal prosimians in which several long-distance call losses occur. Looking across species, long-distance calls are more common in arboreal taxa (Table 3). The concentrated changes test, however, revealed no significant correlation with substrate use and long-distance call production (p=0.20-0.28 based on alternative resolutions of primate phylogeny).

Table 2. Number of species in which males and females produce long-distance calls

	Females: No calls	Females: Long-distance calls
Males: No calls	34	0
Males: Long-distance calls	54	68

Data are available for fewer than the 158 species reported in the text because information was missing on female long-distance calls for two of these species.

Table 3. Number and percentage of species with male long-distance calls for different ecological variables

	Male LC	
Diurnal	107	(79.9)
Nocturnal	16	(69.6)
Terrestrial	13	(50.0)
Arboreal	111	(84.1)

Data are based on 158 species. Numbers refer to absolute number of species exhibiting criteria for having long-distance calls (see Methods), with numbers in parentheses indicating the percentage of species in that category that exhibit calls. Data from Nunn and van Schaik 2001)

Body mass is a covariate in many comparative studies of primates (Clutton-Brock & Harvey 1977), and it is possible that the presence of long-distance calls also correlates with body mass. We found that larger-bodied primates are less likely to produce long-distance calls. Thus, 11 out of 17 contrasts in male body mass were negative over evolutionary transitions to long-distance calls (t_{16}=-1.93, p=0.07). We discuss the implications of this result in what follows.

Long-distance Call Carrying Distance and Home Range Size

All of the hypothesized functions of long-distance calls (mate defense, resource defense, mate attraction) predict that carrying call distance of male long-distance calls should be related to the size of the home range. When focusing on species that were classified as having long-distance calls, we found a significant, positive relationship between carrying distance and home range size using species values ($F_{1,41}$=6.89, p=0.006, one-tailed) and independent contrasts (b=0.20, $F_{1,36}$=5.34, p=0.013, one-tailed: Table 4). The significant result in contrasts analysis, however, relies on removal of three obvious outliers (involving *Colobus polykomos* vs. *C. guereza*, *Macaca nigra* vs. *M. maurus*, and *Aotus trivirgatus* vs. *Callicebus moloch + personatus*). These outliers are on the tips of the primate phylogeny and therefore are likely to reflect the error inherent in estimating carrying call distance and branch lengths rather than confounding variables that also create outliers in contrasts analysis (see Nunn & Barton 2000; 2001).

Table 4. **Home-range size and carrying distance of loud call**

Species	home-range (ha)	Distance call (m)	Source for distance call
Alouatta palliata	43.5	1250	Baldwin and Baldwin 1976; Whitehead 1987
Alouatta seniculus	12.1	1000	Vercauteren Drubbel and Gautier 1993
Aotus trivirgatus	7.1	50	Robinson et al. 1987
Callicebus moloch	5.7	1000	Kinzey 1997
Callicebus personatus	4.7	1000	Kinzey 1997
Callithrix jacchus	13.3	200	Epple 1968
Cercocebus albigena	270.7	1150	Chalmers 1968; Waser 1977; Brown 1986
Cercocebus aterrimus	59	750	Horn 1987; Estes 1991
Cercocebus galeritus	40.7	600	Quris 1980
Cercocebus torquatus	250	1000	Estes 1991
Cercopithecus campbelli	21.5	500	Zuberbühler pers. comm.
Cercopithecus diana	105.5	800	Zuberbühler pers. comm.
Cercopithecus mitis	83.8	685	Waser and Waser 1977; Brown 1986
Colobus badius	57.5	250	Korstjens unpubl. data
Colobus guereza	12.6	750	Marler 1972

Colobus polykomos	36	500	Korstjens unpubl. data
Eulemur mongoz[a]	2.9	100	Curtis pers. comm.
Galagoides demidoff	0.9	100	Charles-Dominique 1974
Gorilla gorilla	2544.5	1600	Schaller 1963
Hylobates agilis	27	1000	Gittins and Raemaekers 1980
Hylobates klossi	21.5	625	Tenaza 1975
Hylobates lar	34.2	1100	Raemaekers and Raemaekers 1984
Hylobates moloch[b]	17	1000	Kappeler 1984
Hylobates muelleri[c]	36	1100	Mitani 1985b
Hylobates syndactylus	26.5	3000	Chivers 1976
Indri indri	22.5	2000	Pollack 1986
Lemur catta	14.4	1000	Jolly 1966
Macaca maurus	25	150	Muroyama and Thierry 1998
Macaca nigra[d]	260	300	N. Bynum pers. comm.
Macaca silenus	50.7	650	Hohmann 1991; Green 1981
Pan paniscus	3475	500	Hohmann and Fruth 1995
Pan troglodytes	1786.8	900	Waser and Waser 1977
Papio papio	1295	2500	Byrne 1981
Pongo pygmaeus	2250	900	MacKinnon 1974; Mitani 1985
Presbytis comata[e]	38	800	Ruhiyat 1983
Presbytis johnii	161.6	450	Poirier 1968
Presbytis potenziani	22	1000	Tilson and Tenaza, 1976
Presbytis thomasi[f]	37.7	700	S. Wich unpubl. data
Procolobus verus	26.5	150	Korstjens unpubl. data
Saguinus fuscicollis	34.3	200	T. Windfelder pers. comm.
Saguinus imperator[g]	30	200	T. Windfelder pers. comm.
Simias concolor	14.4	500	Tenaza 1989
Tarsius spectrum	1	400	Gursky 2000

Home range data are from Nunn and Barton (2000), unless otherwise indicated after species name: [a] Curtis and Zaramody 1998; [b, c] Leighton 1987; [d] Kinnaird and O' Brien 2000; [e] Ruhiyat 1983; [f] Assink and van Dijk; [g] Terborgh 1983. For the carrying distance of loud calls mean loud call distances were calculated when data were available from multiple sources

Another way to test for an association is to examine whether increases in home range size are correlated with increases in long-distance call carrying distance in a non-parametric test. This test makes no assumptions regarding branch lengths and evolutionary model, but simply tests whether the magnitudes of change in the two traits are correlated. Results support the prediction: among the 40 positive contrasts in home range size, 30 show expected increases in carrying call distance, giving a significant result in a sign test ($p<0.005$, one-tailed).

An alternative explanation is that body mass explains the significant association between home range size and carrying call distance, because body mass and home range size show a strong association in our dataset (independent contrasts: b=0.93, $F_{1,35}$=7.72, p=0.009; see also Nunn & Barton 2001). In fact, when body mass is entered as an independent variable in a multiple regression model with home range size in analysis of independent contrasts, only mass is a significant predictor of carrying distance (mass: b=0.64, $F_{1,34}$=15.7, p=0.0004; home range: b=0.14, $F_{1,34}$=1.48, p=0.23). The strong association between body mass and home range size may make it difficult to assess the independent effects of each of these variables in a multiple regression model (i.e., collinearity). In addition, body mass is likely to be measured with less error than home range size; thus, body mass may explain more variation in carrying call distance.

Regardless of the underlying causality, these results suggest a mechanism accounting for losses of long-distance calls over evolutionary transitions to increased body mass. Large-bodied species require larger home ranges (Milton & May 1976; Nunn & Barton 2000), and it may be too energetically costly to produce a call that covers the diameter of a large home range, even in large-bodied species. Two lines of evidence support this proposal. First, not all species produce calls that are audible over one home range diameter. Of the 43 species for which data were available, only 18 have long-distance calls that carry more than one home range diameter, and only eight of these species produce long-distance calls that are audible over more than two home range diameters. Second, the presence of male long-distance calls is negatively related to home range size. Thus, among 14 evolutionary transitions to long-distance calls, 13 corresponded with negative contrasts in home range size (t_{13}=-4.16, p=0.001).

Correlates of Male Long-distance Calls

Mate Defense Hypothesis. If male long-distance calls function in mate defense, then reductions in male intra-sexual aggression should be associated with losses of male long-distance calls. Using data on body mass dimorphism, relative male canine dimorphism, and socionomic sex ratios, however, we found no support for this prediction (Table 5). This analysis may confound competition within groups and competition between groups, because long-distance calling might be expected between groups while either form of competition may lead to dimorphism. Thus, we also examined these patterns after excluding all species characterized as polygynandrous (to exclude competition for females within the group). However, many of the patterns remained opposite to predictions (Table 5).

Mate-Attraction Hypothesis. To examine the hypothesis that long-distance calls function in mate-attraction, we determined whether losses of male long-distance calls were concentrated on branches characterized by

Table 5. **Measures of Male Intrasexual Competition and Male Long-distance Calls**

	Body Mass Dimorphism		Relative male Canine Size		Socionomic Sex Ratio	
	Number of Contrasts Positive	t-statistic	Number of Contrasts Positive	t-statistic	Number of Contrasts Positive	t-statistic
All Species	10/ 16	1.43	4/10	-0.54	5/10	-0.36
Single-Male Only	1 / 6	-2.34	1/3	0.47	1/3	0.49

No results significantly different from 0.

female philopatry. The data (Table 6) indicate that a high percentage of species in which females transfer have male long-distance calls (88.7%), whereas in species without female transfer this percentage is lower (60.0%). However, this difference is not always significant in the concentrated changes test. Depending on the resolution of primate phylogeny the number of losses of male long-distance calls in species where females are philopatric varies from 5-7 with p-values ranging from p=0.02-0.1.

Table 6. **Number and percentage of species with male long-distance calls in relation to female transfer**

	Male LC	
Female transfer	55	(88.7)
No female transfer	24	(60.0)

Resource Defense Hypothesis. Territorial defense of resources may also explain the distribution of long-distance calls across primate species. There is a general trend for non-territorial species of primates to lose long-distance calls, but the association is not perfect (see Table 7).

Among the primates in our dataset, long-distance calling is reconstructed as ancestral, and most losses of male long-distance calls occur on branches characterized by losses of territoriality. Using MacClade, we reconstructed 9-11 losses of male long-distance calls. Depending on the resolution of the polytomies, we found that 7-9 losses of male long-distance calls were concentrated on branches in which territoriality was lost as well. The concentrated changes test showed that this association was significant ($p<0.005$ for all resolutions).

We also examined the patterns using the defensibility index (D-index, Mitani & Rodman 1979) to determine if animals that inhabit more defensible home ranges tend to be more likely to exhibit long-distance calls by males. There was no clear pattern for the D-index to decrease over evolutionary transitions in male long-distance calls (4 of 9 contrasts were negative, $t_8=-0.27$, $p=0.4$, one-tailed). To assess the quality of our data, we tested whether territo-

Table 7. Number and percentage of species with male long-distance calls in relation with territoriality measures

	Male LC	
Territorial	64	(92.8)
Non territorial	19	(50.0)
D-index>1	47	(81.0)
D-index<1	17	(70.8)

riality relates to the D-index and found significant support for this predicted association (12 of 12 contrasts in D-index were positive over transitions in territoriality; t_{11}=3.48, p=0.003, one-tailed). Body mass was negatively related to the D-index (b=-0.48, $F_{1,62}$=31.69, p<0.001, and body mass declined significantly over evolutionary transitions in territoriality (of the 16 transitions, 8 produced negative body mass contrasts: t_{15}=-2.29, p=0.036). These results provide further evidence consistent with the hypothesis that the defensibility of primate home ranges decreases with body mass, potentially explaining the negative associationg between mass and the presence of male long-distance calls.

As a final test for the possible correlation between male long-distance calls and the D-index, species were classified as having a D-index<1 or >1 (following Mitani & Rodman 1979). The concentrated changes test indicates that male long-distance call losses were not likely to have occurred on branches of the tree characterized by a low D-index (p-values range from 0.32-0.34 on alternative resolutions of the tree). These results are therefore contradictory: analysis of territoriality showed an association with male long-distance calling, but the D-index did not, despite a high concordance between the D-index and our measures of territoriality. Moreover, some species also run counter to expectations, since some species have long-distance calls but are not territorial (e.g *Pongo pygmaeus* and *Eulemur fulvus*) or are territorial but lack long-distance calls (e.g. *Eulemur rubriventer* and *Propithecus verreauxi*). These exceptions provide further evidence that factors other than resource defense play a role in explaining variation in long-distance calling across species.

Habitat Use. The data indicate that long-distance calls are indeed more common in species that live in forested habitats. Among terrestrial species, none of those living in open (non-wooded) areas produced long-distance calls, whereas in 13 (68.4%) of the terrestrial species living in wooded areas, males produce long-distance calls. Although male long-distance calls also were lost in species living in wooded areas, there were more losses in species living in open habitats (concentrated changes test: p=0.04-0.03 bases on four random resolutions of polytomies). Moreover, gains were concentrated among species living in wooded areas (e.g. the Guinea baboon).

Discussion

Phylogenetic reconstruction indicates that the presence of male long-distance calls is the ancestral state for primates. Among extant species, long-distance calls more commonly characterize males than females. The major factors that explain this diversity are activity period, body mass, habitat, and home range size. We also found a strong association between home range size and long-distance-call carrying distance. Surprisingly, we found evidence for the mate attraction and resource defense hypotheses in some tests, yet no support for the more widely accepted hypothesis that long-distance calls function in mate defense hypothesis. Recently, Fashing (2001) argued that resource defense polygyny may be an overlooked factor in primate social evolution. Although our results fail to support this function of male territoriality as a general phenomenon in primates, they further highlight the need to investigate such factors within-species. Below, we discuss directions for future research on the mate attraction hypothesis, which has been less thoroughly considered in primates.

What factors can account for our results? First, the presence of male long-distance calls appears to be subject to costs of call production. Most primates produce long-distance calls that carry less than one home range diameter and long-distance calls are lost over evolutionary increases in body mass and home range size. These results suggest that long-distance call production is limited by the costs of producing such calls. In addition, long-distance calls are not found in terrestrial species living in open habitats, which is consistent with vocalizations propagating less efficiently when produced at ground level (Waser & Brown 1986).

Second, our results provide indirect evidence that long-distance call production is sensitive to the benefits. Multiple benefits appear to play a role in explaining the presence of male long-distance calls. Thus, body mass was negatively related to the D-index, and mass declined significantly over evolutionary transitions in territoriality. These results indicate that larger-bodied species experience reduced benefits of territorial defense. In addition, long-distance calls are less common among terrestrial species living in open habitats. Terrestrial species have even larger home ranges for their body mass than arboreal species, increasing the distance between groups and thus reducing the utility of inter-group vocal communication. Males may compete for mates more often within than between groups in these species, which typically have multimale social groups, further reducing the benefits of inter-group communication. This may explain the lack of support for the mate defense hypothesis, because the conditions that favor mate defense, such as increased body mass and a slower life history (Mitani et al. 1996), may also increase the costs of producing long-distance calls or defending a larger home range.

These comparative results highlight the need to combine comparative patterns with detailed study within species. Both types of studies can provide important, and independent, insights to the function of male loud calls. A comparative approach is needed to address the origins of traits and the generality of patterns across species. Moreover, comparative patterns highlight the key variables for more detailed study within species. Thus, our study indicates that body mass, home range size, habitat and defense of resources are key factors to consider in the field. By combining comparative studies of broad evolutionary patterns with detailed analysis of competing hypotheses within species (e.g., Fashing 2001; Wilson et al. 2001; Wich et al. 2002a, b; chapter five, six, and seven), it should be possible to most thoroughly illuminate the multiple factors that influence the costs and benefits of loud call production.

In addition to the possibility that long-distance calls serve multiple functions, several factors could account for the lack of support in our comparative tests. First, our measures of competition (body mass dimorphism, relative male canine size, and socionomic sex ratio) may have been too indirect for testing the mate defense hypothesis. In addition, these measures may be more finely-tuned to patterns of male-male competition within groups, whereas our tests focused on competition among males in different social groups. At present, few alternative measures exist for conducting comparative studies of this type because inter-group competition has not been measured consistently across species. Even when the analyses are restricted to polygynous species, however, results were non-significant.

Second, our analyses may have had insufficient statistical power (Thomas & Juanes 1996). However, this explanation is contradicted by the strong statistical signal that we obtained in some analyses, even with small sample sizes or few evolutionary transitions. Our sample sizes were relatively large compared to other comparative studies in primates. Nonetheless, patterns that were in the predicted direction but not significant, such as analyses of the mate attraction hypothesis may reflect measurement error in predictor variables and thus low statistical power.

Third, social factors may modify the production of long-distance calls. In a previous comparative study, Nunn (2000) used the presence of long-distance calls as a surrogate measure of collective action problems, in which the sharing of benefits leads to a failure to provide the benefit (see also van Schaik 1996; Nunn & Lewis 2001). Consistent with predictions, it was found that the number of males in the group and measures of testes mass were correlated negatively with the production of long-distance calls. To control for social factors such as the collective action problem, we focused on species with particular social organizations in some tests. However, we did not examine this hypothesis directly because our analyses were focused on the function of long-distance calls, and collective action problems can arise under most of the hypotheses that we investigated.

Mate attraction and the costliness of male long-distance calls

Long-distance calls may play a mate attraction role in some species (e.g. *Pongo pygmaeus*, Utami & Mitra Setia 1995; *Presbytis thomasi*, Steenbeek et al. 1999), but there is as yet no experimental evidence that long-distance calls serve a mate-attraction function (orangutan: Mitani 1985a). This hypothesis therefore deserves further scrutiny. For example, a possible prerequisite for long-distance calls to be of relevance in mate defense is that they contain cues to assess the "quality" of the caller, as has been shown for songbirds (e.g. Lambrechts 1992) and anurans (e.g. Ryan & Keddy-Hector 1992). The handicap principle predicts that signals that serve a role in mate-attraction or mate defense are likely to be costly and honest (Zahavi 1975, 1977, Grafen 1991). In addition, females may base their choice on multiple factors, including body condition, intergroup contest competition, and copying other females (Gibson & Hoglund 1992; Keddy-Hector 1992; Sterck 1997; Steenbeek 1999).

Results discussed above regarding body mass and carrying distance provide further evidence that calling is costly, but research is needed to more directly assess the costliness of long-distance-calling. Although several studies have shown that calls are energetically costly to produce (anurans and insects, e.g. Ryan 1988; Prestwich 1994; but see Chappell et al. 1995; Horn et al. 1995 for birds), data on the costliness of primate calls remain sparse. In gibbons, calling rates decreased with altitude (temperature) and during the non-fruiting season (Cowlishaw 1996), consistent with the hypothesis that long-distance calls are costly. It has also been reported that primates give morning calls less often after rainy nights (*Hylobates klossii*: Whitten 1980; *Presbytis thomasi*: Wich unpubl. data). To the extent that both altitude and rain negatively affect body condition (Cowlishaw 1996), these studies are consistent with the hypothesis that long-distance calls are costly in primates.

In summary, our results are consistent with the proposal that primate long-distance-calling is a multi-functional phenomenon (Waser 1977, Whitehead 1987). Although sometimes anecdotal, there is evidence for each of the above hypotheses from field studies, but many of the predicted patterns did not emerge when examining broad phylogenetic patterns. These comparative tests highlight the questions that can be addressed concerning the function of male long-distance calls and the need for detailed (experimental) field studies.

Chapter 5

Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of location

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Abstract

Animals may behave aggressively towards neighbours. For several bird species it has been shown that males react more vigorously towards calls of neighbours from the centre of their home range than from the edge. This is usually explained by assuming that the centre of a home range is of higher value to a male than the edge. To test these ideas for a primate species, we conducted experiments with playbacks of loud calls on wild male and female Thomas langurs (*Presbytis thomasi*). These animals may defend resources in their range or protect their offspring from infanticide and males may defend their females. In natural situations between-group encounters in the centre of a home range by the intruding neighbour are more often accompanied by infanticidal attempts than encounters at the edge. Loud calls of neighbours played back from the centre of the home range caused a more vigorous reaction from the resident male than calls from the edge. However, males in food-containing trees did not respond differently to edge playbacks from males in non-food-containing trees. Although males seem to defend resources and not mates, male behaviour may be best explained by defence of infants against infanticide. Female behaviour is best explained by resource defence.

Introduction

For many bird species that have a resource (nest or food source) in the centre of their home range, responses to song of a neighbouring bird played back from the centre of the test bird's territory are more intense than responses to the same song played back from the boundary of its territory (e.g. Giraldeau & Ydenberg 1987). This phenomenon is known as the centre-edge effect. It has been argued that this effect is the result of the higher value of the centre of a home range than the edge to the territory holder. Consequently, an intruder in the centre will be more fiercely encountered. It has also been suggested that losing the centre of a home range is more likely to lead to the loss of the whole home range and that therefore intruders are more fiercely encountered in the centre of the home range (Giraldeau & Ydenberg 1987).

Like birds, also primates may behave defensively against neighbours. Although the function of range defence may differ for birds and primates (Dunbar 1988), the value of the centre of the range may still be higher than of the edge. Both males and females may be involved in these between-group interactions. Male primates may defend resources, mates (van Schaik et al. 1992) or may defend their offspring against infanticide (van Schaik 1996).). In addition, females may be involved in resource defence and infanticide avoidance (Hill 1994; Starin 1994; Lawes & Henzi 1995; Korstjens 2001).

Several studies have addressed the centre-edge effect in primates (grey-cheeked mangebeys, *Cercocebus albigina*: Waser 1977; gibbons, *Hylobates spp*: Mitani1984; Raemaekers & Raemaekers 1985; spider monkeys, *Ateles geofrroyi*: Teixidor & Byrne 1997; chimpanzees, *Pan troglodytes*: Wilson et al. 2001). Whereas the studies on Hylobates spp. found a stronger reaction to playbacks of duets from the centre than from the edge, the other three studies found no effect. Gibbons defend their home range and have little home range overlap (Preuschoft et al. 1984), whereas grey-cheeked mangebeys have a large home range overlap and do not actively defend it (Waser 1977). Although spider monkeys and chimpanzees are also considered to be territorial (Teixidor & Byrne 1997; Wilson et al. 2001), these species have a fission-fusion social system in which other factors such as groups size might influence the reaction to playbacks (Teixidor & Byrne 1997; Wilson et al. 2001). In addition, stranger instead of neighbouring calls were used in the experiments on the fission-fusion species and are therefore relatively difficult to compare directly with centre-edge experiments in which neighbouring calls are used.

The main aim of this paper is to examine whether males and females of another territorial primate species, the Thomas langur, show a more vigorous reaction to of loud calls from a neighbouring male played back from the centre than from the edge of their home range. Their reaction will be related to the proposed hypotheses.

The Thomas langur is an arboreal foli-frugivore. They typically live in one-male multi-female groups, but solitary males and all-male bands are also found (Sterck 1997). Thomas langur ranges show only about 30% home range overlap and are considered to be territorial (van Schaik et al. 1992). During between-group encounters, males of opposing groups usually behave aggressively towards one another, whereas females do not (van Schaik et al. 1992; Steenbeek 1999a, 1999b). This behaviour might reflect mate defence instead of resource defence, because males try to monopolise access to their females (van Schaik et al. 1992). Nevertheless, nearly two-third of all between-group encounters occur in food-containing trees and the male-male aggression during these encounters indirectly leads to exclusive use of these patches by one of the groups (Steenbeek 1999b). Therefore, in Thomas langurs male behaviour may cause resource defence as a side-effect of mate defence (cf. van Schaik et al. 1992).

Male Thomas langurs are known to commit infanticide (Sterck 1997). Infanticidal attacks occur during between-group encounters, during which the male not resident in the group chases females with infant and tries to kill the infant. When a potentially infanticidal male is chasing the male or females the other females often come close together (group contraction) and collect their young infants (Sterck 1997; Wich, pers. obs.).

Loud calls may have a defensive function (Waser 1977). In Thomas langurs, they are produced exclusively by males (Steenbeek & Assink 1998) and are given under a variety of circumstances: as (pre-) dawn calls, during between-group encounters, during vocal responses to other groups and upon encountering a potential predator (Steenbeek et al. 1999).

If males defend territories for resource defence, males should react more vigorously towards playbacks from the centre than from the edge of their home range (c.f. Wilson et al. 2001)(Table 1). However, if mate defence is important for primate males (c.f. van Schaik et al. 1992; Nunn 2000), males should always repel outsiders, irrespective of location (c.f. Wilson et al. 2001). To further eval-

Table 1. Predicted reactions of males and females to the playback experiments

Test variable	Centre-Control (A)	Centre (C) -Edge (E)	Food-containing (F)-non-food-containing tree (NF)
MALES: latency to 1st loud call	C < A	C < E; C=E	F < NF; F=NF
MALES: number of loud calls	C < A	C > E; C=E	F > NF; F=NF
MALES: latency to 1st move	C < A	C < E; C=E	F < NF; F=NF
MALES: move rate	C > A	C > E; C=E	F > NF; F=NF
MALES: scan rate	C > A	C > E; C=E	F > NF; F=NF
MALES: latency until above speaker	C < A	C < E; C=E	F < NF; F=NF
MALES: duration out of group	C > A	C > E; C=E	F > NF; F=NF
MALES: approach to speaker	C > A	C > E; C=E	F > NF; F=NF
FEMALES: approach to speaker	C≠A	C > E; C < E	F > NF
FEMALES: latency to travel	C < A	C < E	F < NF
FEMALES: decrease of mother-infant distance	C > A	C > E	F=NF
GROUP: decrease of group spread	C > A	C=E; C > E	F=NF

For males the predictions for the resource defence hypothesis are given left and those for the mate defence hypothesis given right in the columns for the centre-edge and food, non-food-containing experiment. For females predictions under the resource defence and infant defence hypotheses differ for some variables in the centre and edge experiment. Where they do, predictions under the resource defence hypothesis are given left and the predictions under the infant defence hypothesis are given right

uate the role of resource defence, edge playbacks were compared for test groups in trees that either did or did not carry Thomas langur food (Table 1). The male was expected to react strongest in a tree containing food. It has recently been suggested that infant defence might also be a factor in male behaviour (van Schaik 1996 van Schaik & Kappeler 1997). However, because in all groups infants were always present we could not specifically address this question.

Although female Thomas langurs are not involved in between-group encounters, females may react differently to centre-edge experiments (Table 1). Two hypotheses can explain such a difference: the resource defence or the infant defence hypothesis. Mate defence is not considered important for females in this species. Under the infant defence hypothesis it was expected that after a centre experiment females would more often not approach the playback site, show group contraction and a reduction of mother-infant distance than after an edge experiment. Under the resource defence hypothesis it was expected that after the centre experiment females more often would approach the speaker and collect their infants, but would not show group contraction than after the edge experiment. Under both hypotheses females should start to travel more quickly after the centre than edge experiment, but in opposite directions. Also female behaviour of groups tested in the edge experiments were compared in food-containing and non-food-containing trees. Under the resource defence hypothesis it was expected that females would approach the speaker site sooner when being in a food-containing than non-food-containing tree

Methods

Study site and subjects

This study was conducted at the Ketambe Research Station(3° 41'N, 97° 39'E), Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia. The study area mainly consists of primary rain forest and was described in detail by Rijksen (1978) and van Schaik and Mirmanto (1985). The langurs in this area have been studied continuously since 1987 onwards (Sterck 1995; Steenbeek 1999a). The history of the Thomas langur study groups is well known and all individuals are well habituated to human presence. The experiments were conducted with 12 bisexual groups with one adult male, 3-6 adult females, 1-4 dependent infants, and several weaned juveniles.

Playback experiments

Playbacks were carried out from February 1997 to July 2000. Three types of playbacks were conducted on each group: a centre (C), an edge (E), and a control experiment (A).

In the centre and edge experiments a test group was subjected to a playback call from a neighbouring group from the centre of the test group's home range (centre experiment) and from the overlap area with that particular neighbouring group (edge experiment). In selecting the playback calls care was taken not to include any calls that were made as a response to a predator. For the control experiment the loud call from a male argus pheasant (*Argusianus argus*) was used and played back from the centre of the test group's home range. The argus pheasant is a common bird in the area, its calls are heard frequently and serve a role in territorial defence (Robson, 2000). The purpose of the control was to determine whether the langurs react purely to a loud sound from a speaker or specifically to the nature of the sound (argus pheasant or Thomas langur male, cf. Raemaekers & Raemaekers, 1985; Wilson et al. 2001). During an experiment the same call was repeated twice with an interval of 20 seconds. This interval was chosen since the natural interval between two consecutive male langur loud calls is 22.9 seconds (n=745 loud call bouts). All test groups were exposed to different langur and argus pheasant calls to avoid pseudoreplication.

A non-random design was chosen to maintain the maximum amount of variation in the sequence of the experiments. Six experimental sequences were made (CEA; ECA; CAE; EAC; ACE and AEC), of which each sequence was assigned to two test groups.

The calls were recorded in the study area a few months before the experiments. Recordings were made with a Sony WM-D6C recorder and Sennheiser MKH 416 p48, Sony ECM-144 and Sony ECM-T140 microphones.

Playback calls were cleaned from disturbing background noises (e.g. harsh bird calls) with the Canary 2.1 software package. Calls were amplified with a Nagra-Kudelski DSM speaker connected to a Sony WM-D6C. The volume of the langur and the argus calls was adjusted to the natural loudness of a calling male (appr. 100dB SPL at 1 meter, Wich, unpub. data). All playbacks were conducted from approximately 75 meters of the test group at a height of two meters. Playbacks were conducted in the morning hours, never on the same test group on consecutive days and never after the test group had encountered another langur group in the hours from the sleeping tree until the experiment.

Data collection

The langur groups were followed from their sleeping tree in the morning until two hours after the presentation of the playback calls. The following data were collected: latency time from the call presentation (defined as the time of the experiment) to the first loud call produced by the test male; number of loud calls in the hour after the presentation; latency from the presentation to the first male move; male move and scan (head movement more than 45 degrees) rate per minute for the first 15 minutes after the presentation; time the male was outside the group (defined as being more than 25 meters away from the group's centre) after the presentation; time from the presentation until the male reached the location of the speaker; male and female approach to the speaker (distance moved to speaker divided by initial distance of group to speaker multiplied by 100); latency from the experiment to the first travel movement by a female; whether or not the group (excluding the male) contracted after the presentation; and whether or not the distance between one or more of the females and their infants decreased. To obtain the female/infant data, one or two females with young infants were observed during the experiment. When both showed an opposite reaction this was taken as no decrease between mother-infant distance. Also noted was whether a group was in a food-containing (producing edible items for the Thomas langur) or non-food-containing tree.

Statistics and analyses

Since the data were not distributed normally non-parametric statistics were used. Paired results were tested with a Wilcoxon signed ranks test or with a Fisher Exact test. A Mann-Whitney-U test was used for the evaluation of the food-containing versus non- food-containing tree experiment (Siegel and Castellan 1988). Significance levels were corrected for by the sharper Bonferroni criterion of Hochberg (1988). Families of related behaviours that needed to be corrected for (e.g. Chandler 1995) were chosen to be male behaviour and female behaviour. Since the same data were used in the control-centre and centre-edge comparison this was corrected for as well with the Bonferroni criterion.

When the male did not reach the speaker or the group did not travel in the hour after the experiment the values of these variables were set at 3600 sec. When the male did not give loud calls, latency to the first loud call was set at 3600 sec. The number of calls and the latency to the first call were significantly correlated with each other and since the number of loud calls is a common used variable in primate playback literature only this variable was presented.

Results

Natural reactions during between-group encounters

In order to evaluate whether neighbouring males in the centre of another home range are not an artificial situation we will first present some observational data on between-group encounter under natural conditions. Of the 104 between-group encounters observed in this study 27 occurred in the centre of a home range of the observed group. On such occasions a neighbouring male entered the home range of the followed group while leaving the rest of his group behind. Of the 27 encounters in the centre 25 involved chases by the intruding male of females with infants. Out of the 77 encounters witnessed on the periphery of a home range only one involved chases of females with infants. Thus, males significantly more often conduct infanticidal attacks during encounters in the centre than during encounters on the edge of a home range (Fisher Exact test: $p<0.00001$).

Centre-Control experiment

A comparison between the centre and control experiments reveals a pronounced difference in reaction between the two treatments. In the centre experiment male and female responses were more intense than in the control experiment (Table 2). Most reactions followed the direction of the predictions (compare Table 1 and 2). In the centre experiment males had a shorter latency time to their first loud call, gave more loud calls, had a shorter latency to their first move, a higher move and scan rate, were sooner above the speaker, longer out of the group and approached the speaker more closely than in the control experiment. Females had a shorter travel time latency and approached the speaker more closely in the centre experiment. Group contraction tended to occur more often in the centre than in the control experiment (Fisher Exact test: $P=0.08$). In the centre experiment a reduction of mother-infant distance occurred significantly more often than in the control experiment (Fisher Exact test: $p=0.0005$).

Table 2. Results of the centre-control playback experiment

Test variable	Centre	Control	Significance
MALE: number of loud calls	4.0 (1.5, 6.8)	0.0 (-, -)	$T^{+}=55$ (2 ties) *
MALE: latency to 1st move (sec)	14.0 (8.3, 36.5)	161.5 (60.0, 900.0)	$T^{+}=78$ **
MALE: move rate (per min)	1.3 (1.0, 1.8)	0.12 (0, 0.5)	$T^{+}=78$ **
MALE: scan rate (per min)	7.3 (3.6, 10.4)	1.0 (0.7, 3.1)	$T^{+}=72$ *
MALE: latency until above speaker (sec)	189.5 (128.0, 363.0)	3600.0 (-, -)	$T^{+}=66$ (1 tie) **
MALE: duration out of group (min)	43.0 (21.5, 56.3)	0.0 (-, -)	$T^{+}=66$ (1 tie) **
MALE: approach (%)	100.0 (80.3, 100.0)	5.0 (0.0, 10.0)	$T^{+}=78$ **
FEMALES: approach (%)	78.0 (64.3, 100.0)	0.0 (-, -)	$T^{+}=55$ (2 ties) *
FEMALES: latency to travel (sec)	60.0 (46.3, 60.0)	1314.5 (510.0, 3600.0)	$T^{+}=78$ *

Median response values are presented here with the 25 and 75 percentiles between brackets. ** = $p<0.01$, * = $p<0.05$ and ~ = $p<0.10$

Centre-Edge experiment

In general the response in the center experiment was more intense than in the edge experiment (Table 3). All but two variables showed a clear significant difference between the experiments and the differences were in the expected direction. In the center experiment males gave significantly more loud calls, had a higher move rate, were sooner above the speaker, longer out of the group, approached the speaker more closely and had a shorter latency to the first loud call than in the edge experiment. In the center experiment males also tended to have a shorter latency to the first movement. Males also scanned more often in the center than in the edge experiment, but this failed to reach significance. In the center experiment females approached the speaker significantly more closely and with a significantly shorter latency than in the edge experiment. This result was expected under the resource defence hypothesis and not under the infant defence hypothesis. Group contraction occurred equally often in both experiments (Fisher Exact test: p=0.705) as expected under the resource defence hypothesis. In the center experiment mother-infant distance reduction occurred significantly more often than in the edge experiment (Fisher Exact test: p=0.004). This latter result was expected under both the infant defence and resource defence hypothesis.

Table 3. Results of the centre-edge playback experiment

Test variable	Centre	Edge	Significance
MALE: number of loud calls	4.0 (1.5, 6.8)	0.0 (0.0, 1.5)	T^{+}=53 (2 ties) *
MALE: latency to 1st move (sec)	14.0 (8.3, 36.5)	44.5 (17.3, 83.8)	T^{+}=54 (1 tie) ~
MALE: move rate (per min)	1.3 (1.0, 1.8)	0.5 (0.4, 0.8)	T^{+}=72 *
MALE: scan rate (per min)	7.3 (3.6, 10.4)	3.3 (1.3, 5.2)	T^{+}=64 ns
MALE: latency until above speaker (sec)	189.5 (128.0, 363.0)	3600.0 (-, -)	T^{+}=66 (1 tie) **
MALE: duration out of group (min)	43.0 (21.5, 56.3)	0.0 (0.0, 0.0)	T^{+}=62 (1 tie) *
MALE: approach (%)	100.0 (80.3, 100.0)	30.0 (15.3, 51.3)	T^{+}=78 **
FEMALES: approach (%)	78.0 (64.3, 100.0)	0.0 (0.0, 15.8)	T^{+}=64 (1 tie) **
FEMALES: latency to travel (sec)	60.0 (46.3, 60.0)	1090.0 (472.5, 3075.0)	T^{+}=72 *

Median response values are presented here with the 25 and 75 percentiles between brackets. ** = p<0.01, * = p<0.05 and ~ = p<0.10

Food-containing versus non- food-containing trees

Six of the experiments on the edge of the home range took place when a test group was in a food containing tree and six in a non-food-containing tree. This allowed us to examine the resource defence component of Thomas langur behaviour more directly. Male reactions did not differ in both situations

(Table 4). However, females approached the speaker significantly more closely when being in a food-containing tree than in a non-food-containing tree and did so also with a shorter latency (Table 4). Group contraction experiments (Fisher Exact test: p=0.772) and the reduction of mother-infant distance experiments (Fisher Exact test: p=0.608) did not differ between these experiments.

Table 4. **Results of the food-containing versus non-food-containing tree**

Test variable	Food-containing tree	Non-food-containing tree	Significance
MALE: number of loud calls	1.0 (0.0, 2.3)	0.0 (-, -)	U=9.0 ns
MALE: latency to 1st move (sec)	37.0 (13.5, 57.5)	73.5 (21.5, 108.8)	U=10.0 ns
MALE: move rate (per min)	0.6 (0.5, 0.8)	0.4 (0.4, 0.9)	U=10.0 ns
MALE: scan rate (per min)	4.9 (1.4, 8.4)	2.4 (1.2, 3.5)	U=9.0 ns
MALE: latency until above speaker (sec)	3600.0 (-, -)	3600.0 (-, -)	U=18.0 ns
MALE: duration out of group (min)	0.0 (-, -)	0.0 (0.0, 13.8)	U=15.0 ns
MALE: approach (%)	20.5 (15.0, 45.8)	35.0 (23.0, 83.8)	U=12.0 ns
FEMALES: approach (%)	15.5 (11.2, 29.5)	0.0 (-, -)	U=3.0 **
FEMALES: latency to travel (sec)	525.0 (285.0, 820.0)	2550.0 (1187.0, 3600.0)	U=0.0 **

Median response values are presented here with the 25 and 75 percentiles between brackets. ** = p < 0.01, * = p < 0.05 and ~ = p < 0.10

Discussion

In this paper two experiments were conducted on wild Thomas langurs. First it was tested whether Thomas langurs react differently when neighbouring calls are played back from the centre or edge of the test group home range. In the second experiment the response of Thomas langurs was measured when they were in food or non-food containing trees during a playback of neighbouring calls from the edge. First we will address male behaviour in the two experiments, then female behaviour and finally we will provide a summary of the results.

Male behaviour

The results of the centre-edge playback experiment are similar to the results that have been found in many bird species (Giraldeau & Ydenberg 1987) and several primate species (Mitani 1984; Raemaekers & Raemaekers 1985). Males responded more vigorously to loud calls from a neighbouring male played back from the centre of the test male's home range than from the zone of overlap between the test male and the neighbouring group: in the centre experiment males gave more loud calls, approached closer to the speaker and with a shorter latency, and remained out of the group for a longer period of time than in the edge experiment. These differences in male behaviour between the centre and edge experiments suggest that a neighbouring male in the centre is perceived as more threatening than a male at the edge of the home range (Falls & Brooks 1975). Males also had a significantly higher move rate in the centre experiment and a higher, although not significant, scan rate. Thus males were in general eager to go after an intruding male in the centre experiment. Male reactions did not differ in the food and non-food containing tree experiment.

Three non-mutually exclusive hypotheses can explain male agonistic behaviour: resource/mate/ and infant defence (van Schaik et al. 1992; van Schaik 1996). Food resources are generally thought to be of more importance for primate females than for males (Wrangham 1980; van Schaik 1989) and food resource defence would a priori be expected to be of minor importance for males. However, following the argument applied by Wilson et al. (2001) in the case of mate defence, males should always repel intruders irrespective of location. Thomas langur males did not react as vigorously in the edge as in the centre experiment and this does not favour a pure mate defence explanation of their behaviour, but rather a resource defence explanation. Since male reactions did not depend on being in a food containing or non-food containing tree, defence of food sources does not seem to be the primary goal of their defence. However, observations under natural conditions indicate that the chances of a neigbouring male committing an infanticidal attempt are significantly higher in the centre than on the edge of a territory. Thus, in anticipation of a possibly aggressive male in the centre a male should try to repel this male before he can attack females with infants. Provided that Thomas langurs suffer little food competition (Sterck 1995; Sterck & Steenbeek 1997; Steenbeek & van Schaik 2001), infant defence might thus be the most parsimonious explanation for the male behaviour found in these experiments.

Female behaviour

Food is considered to be more important as a resource for female than male primates (e.g. Wrangham 1980; van Schaik 1989). Therefore, food is a resource that female, and not male, Thomas langurs are expected to defend. Indeed, Steenbeek (1999b) reports that nearly two-third of the between-group encounters in Thomas langurs occurred in food patches. During natural between-group encounters in a zone of home range overlap females are not involved in chases or aggression and between-group encounters seem more of a male affair. This has been interpreted as a lack of active female resource defence (van Schaik et al. 1992). In our experiments, however, females approached the speaker significantly closer and with a shorter latency in the centre experiment than in the edge experiment. In one of the groups the females even approached the playback site before the male did. This was expected under the resource-, but not the infant defence hypothesis. It indicates that, although during natural circumstances the male alone may guarantee "exclusive" use of food sources as a possible side-effect of home infant defence, when the centre of the area is at stake females also participate in the defence of the area and hence its food sources. Since infanticidal attacks occur mostly outside of the normal between-group encounter context (i.e., the edge experiment), under the infant defence hypothesis group contraction was expected to occur more often in the centre experiment than after the edge experiment. This, however, was not found and again supports the resource defence hypothesis. Although a reduction of mother-infant distance occurred more often in the centre experiment than in the edge experiment, this is can be explained by both the infant defence hypothesis and the resource defence hypothesis. Further support for the resource defence hypothesis came from the significantly closer approach to the speaker and shorter latency of moving towards the speaker that females showed after the "food-containing tree" experiment compared to the "non-food-containing tree" experiment.

In conclusion our results show that male-male antagonistic behaviour in Thomas langurs is most likely due to infant defence. Food defence is, however, likely to be a determinant of female behaviour.

Chapter 6

Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity

With Assink, P.R., Becher, F. & Sterck E.H.M.

(Behaviour 139:79-87)

Abstract

A number of studies on birds and mammals have shown that individuals respond differently to neighbour and stranger call playbacks. This response is generally thought to be adaptive, because differentiating calls from neighbours and strangers can prevent the costs of unnecessary contests. In addition, it has recently been suggested that female lions use call recognition to avoid infanticidal males. In this paper we show that Thomas langur males react more vigorously towards calls from strange than neighbouring males. It is hypothesised that, although differentiating between calls from different males can be useful to reduce unnecessary contests between the males, discriminating between individual calls is important because it might reduce the risk of infanticide.

Introduction

A well-established effect in many animals species is the so-called neighbour-stranger (or dear enemy) effect (e.g. birds: Ydenberg et al. 1988; Stoddard 1996; ground squirrels, *Spermophilus richardsonii*: Hare 1998; cichlid fish, *Cichlasoma nigrofasciatum*: Leiser & Itzkowitz 1999; lizards, *Platysaurus broadleyi*: Whiting 1999). In general, animals react more intensely to simulated unfamiliar (stranger) calls from the border of their home range than to simulated familiar (neighbour) calls from that area (e.g. Ydenberg et al. 1988; Stoddard 1996). The recognition of differences between familiar and unfamiliar calls is considered useful, because distinguishing between them would save energy and time spend on "unnecessary" contests with already established neighbours and would ensure appropriately strong reactions to a stranger searching for a territory and possibly attempting a take-over (Weeden & Falls 1959; Emlen 1971; Ydenberg et al. 1988; Whiting 1999).

Also in primates males may be recognised by their call alone, because individual differences in primate calls have been shown for a variety of species (e.g. chimpanzees, *Pan troglodytes: Marler & Hobett 1975;* vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth 1982; Thomas langurs, *Presbytis* *thomasi*: Steenbeek & Assink 1998). Few primate studies, however, have assessed the neighbour-stranger effect. Notable exceptions are Waser's (1977) classic playback study on the grey-cheeked mangabeys (*Cercocebus albigena*), Mitani's (1985) study on the Mueller's gibbons (*Hylobates muelleri*) and the study of Teixidor and Byrne (1997) on spider monkeys (*Ateles geoffroyi*). All three studies report no significant differences in behavioural responses of the test groups toward neighbour and stranger playbacks.

The ability to discriminate between individually different calls has recently been linked to infanticide in an elegant playback study on lions (*Panthera leo*) by McComb et al. (1993). These authors have shown that female lions discriminate between roars of strange (potentially infanticidal) and resident (non-infanticidal) males and they hypothesise that lionesses with cubs gain direct fitness benefits by avoiding potentially infanticidal males.

The aim of this paper is to investigate whether Thomas langurs discriminate between loud calls from neighbour and strange males and discuss this with respect to infanticide.

Thomas langurs are a medium sized (7-8 kg, Sterck 1997) arboreal endemic colobine species living in Northern Sumatra, Indonesia. These primates are foli-frugivores with limited food competition and weakly differentiated intra-group social relationships (Sterck 1995, 1997; Sterck & Steenbeek 1997; Steenbeek and van Schaik, 2001). Populations consist of one-male, multi-female groups, as well as a smaller number of all-male bands and solitary males (Sterck 1997). Males always leave their natal group, whereas females show a strong preference for staying in a familiar habitat, but sometimes leave both the familiar home range and familiar conspecifics. To describe this system, Steenbeek (1999a, 1999b) introduced the term "flexible" philopatry. During between-group encounters males of opposing groups can behave aggressively towards one another, whereas females do not (van Schaik et al. 1992; Steenbeek et al. 1999). Infanticide by extra-group males occurs and is considered to be a major influence on the Thomas langur social organisation (Sterck 1997; Steenbeek 1999).

For the neighbour-stranger experiment loud calls from neighbours and strangers were played back from the zone of home range overlap. Since male infanticide occurs in Thomas langurs and unfamiliar males more often conduct infanticidal attempts (Sterck 1997; Steenbeek 1999; Wich, pers. obs.), it was expected that males would react more vigorously and females more cautiously to the playback of a call of a stranger than a call from a neighbouring male (Table 1).

Table 1. **Expected reactions on the playback experiments**

Test variable	Neighbour-Stranger
MALES: latency to first loud call	N > S
MALES: number of loud calls	N < S
MALES: latency to first move	N > S
MALES: move rate	N < S
MALES: scan rate	N < S
MALES: duration until above speaker	N > S
MALES: duration out of group	N < S
MALES: approach to speaker	N < S
FEMALES: approach to speaker	N > S
FEMALES: latency to travel	N≠S
FEMALES: decrease of mother-infant distance	N < S
GROUP: decrease of group spread	N < S

For female latency to travel no direction was given for the expectation in the neighbour-stranger experiment because females sometimes quickly move towards neighbouring groups after loud calls and in the case of a stranger call were expected to quickly move away from the playback site. This would therefore yield no difference in the direction of the latency time

Methods

Study site and subjects

This study was carried out at the Ketambe Research Station (3° 41' N, 97° 39' E), Gunung Leuser National Park, Leuser Ecosystem, Indonesia. This study area mainly consists of undisturbed primary rain forest and was described by Rijksen (1978) and van Schaik and Mirmanto (1985). The langurs in this area have been studied continuously since 1987 onwards (Sterck 1995; Steenbeek 1999a). The history of the Thomas langur study groups is well known and all individuals are well habituated to human presence. Groups consisted of one adult male, 1-6 adult females, 1-4 dependent infants and several weaned juveniles.

Playback experiment

Playbacks were carried out from February 1998 until June 2000. Test groups were subjected to two sets of loud calls. One set consisted of two loud calls from a neighbouring male and the other set consisted of two calls from a strange male. In both loud call sets there was an interval of 20 seconds between the two consecutive calls. This is similar to the natural time lapse between loud calls. Both loud call sets were played back from the overlap area of the test group with the neighbouring group from where the call originated. A test group was only subjected to one loud call set per day.

A non-random design was chosen to maintain a maximum amount of variation in the sequence of the experiments. Six of the 12 test groups were exposed to a stranger call set first and then on a different day to the neighbour calls, whereas the six other groups were exposed to the opposite sequence.

To avoid pseudoreplication all groups were subjected to different stranger and neighbour calls. Stranger calls were recorded in an area 2-3 km away from the study area on the other side of the Alas River (not crossed by the langurs in this area), whereas neighbour calls were recorded in the study area a few months before the experiments. Recordings were made with a Sony WM-D6C recorder and Sennheiser MKH 416 p48, Sony ECM-144 and Sony ECM-T140 microphones. The playback calls were equally distributed over the three microphone types and detailed inspections of the spectrographs did not show any differences between the microphone types.

Playback calls were cleaned from disturbing background noises, such as bird sounds, with the Canary 2.1 software package. Calls were amplified with a Nagra-Kudelski DSM speaker connected to a Sony WM-D6C tape recorder. The volume was adjusted to the natural loudness of a calling male (appr. 100dB at 1 meter, Wich unpubl. data). All playbacks were conducted from about 75 meters of the test group at a height of two meters. Playbacks were conducted in the morning hours when the test group was in the overlap area with the neighbour chosen for the experiment. A test group was never tested on consecutive days. In addition, the experiment was not conducted when a test group encountered another langur group before the experiment commenced.

Data collection

The langur groups were followed from their sleeping tree in the morning until two hours after the experiment. The following data were collected: latency time from the presentation (defined as the time of the start of the first experimental call) to the first loud call produced by the test male; the number of loud calls in the hour after the presentation; the latency from the presentation to the first male move; the male move and scan (head movement more than 45 degrees) rate per minute for the first 15 minutes after the presentation; time the male was outside the group (defined as being more than 25 meters away from the group's centre) after the presentation; time from the presentation until the male reached the location of the speaker; male and female approach to the speaker (distance moved to speaker divided by initial distance of group to speaker multiplied by 100); latency from the presentation to the first travel movement by any female of the group; whether or not the group (excluding the male) spread was reduced after the presentation (as measured by the group spread directly before and directly after the playback); and whether or not the distance between one or more of the females and their infants decreased.

Statistics and analyses

Since the data were not normally distributed non-parametric statistics were used such as the Wilcoxon signed ranks test and the Fisher Exact test (Siegel & Castellan 1988). Levels of significance were corrected for by the sharper Bonferroni criterion of Hochberg (1988). Families of related behaviours were corrected for by the sharper Bonferroni criterion (e.g. Chandler 1995) were chosen to be male behaviour and female behaviour.

When the male did not reach the speaker, did not give any loud calls, or the group did not travel in the hour after the experiment the values of these variables were set at 3600 sec.

The latency to the first loud call and the number of loud calls were significantly correlated and only the number of loud calls is presented in the results as this variable has often been used in primate papers on playbacks. A significant correlation was also found for the percentage of male approach to the playback site with the move rate and with the time in which the male reached the playback site. The results on male percentage of approach are presented, since approach measures are also commonly reported in other papers on playbacks (e.g. Waser 1977). A Bonferroni correction was applied to all variables before the correlated variables were excluded.

Results

The neighbour-stranger experiment shows significant differences between the two treatments for some of the behavioural categories (Table 2). Males called and scanned significantly more often in the stranger than in the neighbour experiment. The latency to move tended to be shorter in the stranger experiments than in the neighbour experiment. On average males also stayed out of the group longer and approached the speaker closer in the stranger experiment, but these differences failed to reach significance.

The latency for female travel was significantly shorter in the neighbour than in the stranger experiment. In the neighbour experiment females moved towards the speaker, whereas in the stranger experiment they stayed quietly at their location or moved in the direction opposite to the playback site. Group contraction occurred in 2 out of 12 cases in the neighbour experiment and in 4 out of 12 cases in the stranger experiment (Fisher Exact test: n.s.). Reduction of mother-infant distance was observed significantly more often after the stranger than the neighbour experiment (Fisher Exact test: $p=0.008$).

Table 2. Results of the neighbour-stranger playback experiment

Test variable	Neighbour	Stranger	Significance
MALE: number of loud calls	1.0 (0.0, 2.8)	5.5 (0.8, 6.0)	T^+=45 (3 ties) *
MALE: latency to 1st move (sec)	20.5 (6.3, 91.8)	8.5 (5.0, 8.8)	T^+=57 ~
MALE: scan rate (per min)	2.0 (1.3, 5.3)	6.3 (2.3, 7.8)	T^+=72 *
MALE: duration out of group (min)	0.0 (0.0, 1.5)	14.5 (0.0, 38.8)	T^+=33 (4 ties) ns
MALE: percentage approach	26.0 (0.0, 88.3)	87.0 (73.0, 100.0)	T^+=41 (2 ties) ns
FEMALE: percentage approach	0.0 (0.0, 44.5)	0.0 (-, -)	not testable (8 ties)
FEMALE: latency to travel (sec)	175.0 (112.5, 375.0)	2255.0 (315.0, 3600.0)	T^+=66 (1 tie) **

Median response values are presented here with the 25 and 75 percentiles between brackets. ** = $p<0.01$, * = $p<0.05$ and ~ = $P<0.10$

Discussion

In the neighbour-stranger experiment a stronger reaction of the test male to the stranger call was expected, because strangers are less familiar than neighbours (e.g. Ydenberg et al. 1988; Stoddard 1996). Females were expected to react more cautiously to the stranger than to the neighbour playbacks due to the risk of group take-overs and infanticide. Thomas langur males gave significantly more loud calls and scans in the stranger experiment. In addition, males also tended to show a shorter latency time to their first move in the stranger experiment. All other male measures, however, showed no significant differences, but averages were in the predicted direction. Overall, it seemed that males reacted more alert towards the stranger call than the neighbour call and they may actually initiate a conflict more often with stranger than neighbouring males.

The behaviour of females also differed between the two experiments. Although group contraction did occur as often both after the neighbour and the stranger experiment, a reduction in mother-infant distances was observed more often after the stranger experiment. Females started moving significantly earlier after the neighbour than stranger experiment and on a few occasions during a neighbour experiment went directly to the location where the speaker was placed. This closely resembles the natural reaction, when females also head towards a neighbouring group after calls have been exchanged by the males, whereas they either stay at the same location or move in the direction opposite to the stranger when meeting a strange male (Wich pers. obs.). In the stranger experiment females remained at the same location or moved away from the location of the playback. Both the decrease in mother-infant distance and the earlier movements could indicate that strange "unfamiliar" males are perceived as more threatening by mothers and infants. This reaction may be related to infanticide avoidance as infanticide by extra-group males is a real threat in the Thomas langurs (Sterck 1997; Steenbeek 1999a).

The three other studies on primates that investigated the neighbour-stranger effect found no stronger reaction from males and females to the stranger call playback (grey-cheeked mangabyes: Waser 1977; Mueller's gibbons: Mitani 1985; spider monkeys: Teixidor & Byrne 1997). Although it has been suggested that in all three species there is a risk for infanticide (van Schaik 2000), it is likely that males in these species follow the typical pattern and only commit infanticide after becoming resident in a group (Sterck & Korstjens, 2000). In addition, it has been suggested that the low inter-group encounter rates in gibbons and spider monkeys explain the lack of difference in response to calls of familiar and unfamiliar males (Mitani 1985, Teixidor & Byrne 1997). Mitani (1985) suggests that under such circumstances "selection might be relaxed for vocal discriminination".

In conclusion, this experiment shows that both males and females distinguish loud calls from neighbour and strange males. These results indicate that differentiating between calls from neighbour and strange males may reduce unnecessary initiation of contests with a familiar male. Females may protect their infants by retrieving them and avoiding the unfamiliar male. Thus, discriminating between familiar and unfamiliar calls may reduce the risk of infanticide.

Chapter 7

Male loud call playbacks to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of age

With Assink, P.R. & Sterck E.H.M.

(Animal Behaviour in review)

Abstract

The ability to differentiate between individual calls or call types has been shown for a number of animal species. Several functions have been suggested. One hypothesis, developed for lions, is that the ability to distinguish between call types (neighbour and stranger calls) is linked to the avoidance of infanticidal males. This hypothesis will be evaluated for the wild Thomas langurs (*Presbytis thomasi*) in Ketambe, Indonesia. Thomas langurs are capable of differentiating between calls of neighbouring and strange males. Such an ability could reduce the aggression between neighbouring males or lead to the avoidance of infanticidal males. In this paper, we experimentally test the infanticide hypothesis by examining whether Thomas langurs can differentiate between male loud calls from young adult (likely infanticidal) and old adult (unlikely infanticidal) males. The results of our playback experiment show that Thomas langur males respond more vigorously to playbacks of calls from young adult males than to calls from old adult males. Females show a more cautious response to the calls from young adult males than to the calls from old adult males. Both these reactions are in accordance with the infanticide hypothesis and indicate that it is therefore functional to differentiate between loud calls of young and mature males.

Introduction

Individual differences in primate vocalisations have been shown for a variety of species (e.g. chimpanzees: *Pan troglodytes*: Marler & Hobett 1975; vervet monkeys: *Cercopithecus aethiops*: Cheney & Seyfarth 1982; Thomas langurs: *Presbytis thomasi*: Steenbeek & Assink 1998) and several studies have shown individual recognition based on calls (Kaplan et al. 1978; Cheney & Seyfarth 1982; Symmens & Biben 1986). Such individual discrimination is generally thought to be important in primate mother-infant relationships (Kaplan et al. 1978; Cheney & Seyfarth 1982) or in distinguishing between males of different groups (Steenbeek 1999a). In addition to individual recognition, the recognition of call types, such as those from neighbours and strangers, has been found in large variety of animals (birds: Stoddard 1996; Primates: Wich et al. 2002b, chapter 5, ground squirrels, *Spermophilus richardsonii*: Hare 1998; cichlid fish, *Cichlasoma nigrofasciatum*: Leiser & Itzkowitz, 1999; lizards, *Platysaurus broadleyi*: Whiting 1999). The ability to differentiate between call types (neighbour and strange) has typically been linked to the reduction of unnecessary contests between neighbours (Ydenberg et al. 1988; Stoddard 1996).

Recently, the ability to discriminate between different call types has also been linked to infanticide in an elegant playback study on lions (*Panthera leo*) by McComb et al. (1993). These authors show that female lions discriminate between roars of strange (potentially infanticidal males) and resident (the fathers of the cubs) males and suggest that this has direct fitness benefits for the females since they can avoid the potentially infanticidal males.

For primates a similar suggestions has been made Thomas langurs where individuals also distinguish loud calls from neighbouring and strange males (Wich et al. 2002a).

Thomas langurs are a medium sized (7-8 kg, Sterck 1997) arboreal endemic colobine species living in Northern Sumatra, Indonesia. These primates have been characterised as foli-frugivore with limited food competition and weakly differentiated intra-group social relationships (Sterck 1995, 1997; Sterck & Steenbeek 1997). Populations consist of one-male, multi-female groups, as well as a smaller number of all-male bands and solitary males (Sterck 1997). Males always leave their natal group, whereas females show a strong preference for staying in a familiar habitat, but sometimes leave both the familiar home range and familiar conspecifics. To label this system, Steenbeek (1999a) introduced the term "flexible" philopatry. During between-group encounters males of opposing groups can behave aggressively towards one another, whereas females do not (van Schaik et al. 1992; Steenbeek 1999a).

There is evidence that in Thomas langurs infanticidal attacks and harrassments of mothers with babies by extra-group males occur regularly (Sterck 1995; Steenbeek 1997). Since in Thomas langurs the majority of such attacks are from non-neighbouring extra-group males (i.e. strangers), the ability to differentiate between the familiar and unfamiliar loud calls may derive its adaptive significance from this (Wich et al. 2002a). Moreover, in Thomas langurs most infanticidal attacks come from young adult males (Sterck 1997; Steenbeek 1999; Wich unpubl. data). Young adult males produce loud calls of shorter duration than old, fully matured, adult males and this could be an important cue for both males and females to base their reactions upon (chapter 2).

The aim of this paper is to determine whether Thomas langurs discriminate between loud calls of young adult strange (possibly infanticidal) and old adult strange males (less likely to be infanticidal). We conducted an experiment in which test groups were subjected to two types of calls from strange males: from an old adult male and from a young adult male. Because mostly young adult males were witnessed to commit group take-overs and infanticide (Sterck 1997; Steenbeek 1999; Wich, unpubl. data), we reasoned that group members would respond to these calls with a stronger reaction, which is in accordance with avoidance and defense (Table 1).

Table 1. Expected reactions to the playback experiment

Test variable	Young-old adult stranger
MALES: latency to first loud call	U < M
MALES: number of loud calls	U > M
MALES: latency to first move	U < M
MALES: move rate	U > M
MALES: scan rate	U > M
MALES: duration until above speaker	U < M
MALES: duration out of group	U > M
MALES: approach to speaker	U > M
FEMALES: approach to speaker	U = M
FEMALES: latency to travel	U < M
FEMALES: decrease of mother-infant distance	U > M
GROUP: decrease of group spread	U > M

Methods

Study site and subjects

This study was carried out at two locations (Ketambe and Bukit Lawang) in the Gunung Leuser National Park, Leuser Ecosystem, northern Sumatra, Indonesia.

Ketambe: The Ketambe research area (3° 41' N, 97° 39' E) mainly consists of undisturbed primary rain forest and was described by Rijksen (1978) and van Schaik and Mirmanto (1985). The langurs in this area have been studied continuously since 1987 onwards (Sterck 1995; Steenbeek 1999a). The history of the Thomas langur study groups is well known and all individuals are well habituated to human presence. Groups consisted of one adult male, 1-6 adult females and offspring.

Bukit Lawang: This area is located around 3° 30' N, 98° 6' E on the eastern part of the Leuser Ecosystem. The area in which the data were collected was covered by a matrix of rubber plantations (*Hevea brasiliensis*) and primary forest. The area has an elevation of around 100m a.s.l. All sampled langur groups ranged within plantations and primary forests and were well habituated to human presence. A more detailed description of the area is provided Gurmaya (1986).

Playback experiment

In the experiment 10 test groups were subjected to one set of loud calls from a young adult stranger male and one set of loud calls from an old adult stranger male. To avoid pseudoreplication, each group was exposed to a different set of young and mature calls. Four groups were tested in the Ketambe area and six at the Bukit Lawang site. Each set of loud calls consisted of two calls with a 20sec interval, which is similar to the natural interval between loud calls (Wich et al. 2002b). Both loud call sets were played back from a zone in the home range of a test group where this overlaps with the range of another group. Five groups were first presented the young loud call set and then on a different day the mature loud call set, and the other five groups were presented with the opposite sequence.

Typical young adult stranger calls were selected. In these most of the (tonal) T-units are lacking that normally make up the second half of a fully developed call and they are of much shorter duration than the calls of mature males (for a spectogram of loud calls from young and old adult Thomas langur male see Wich et al. ms). All old adult stranger calls were of normal composition (chapter 3).

All stranger calls were recorded in areas sufficiently far away from the study groups to exclude the possibility that they were known (Ketambe: 2-4km on the other side of the Alas River, Bohorok: 3-10km away on the other side of the Bohorok River).

Recordings were made with a Sony WM-D6C recorder and Sennheiser MKH 416 p48, Sony ECM-144 or Sony ECM-T140 microphones.

Playback calls were cleaned from disturbing background noises, such as bird sounds, with the Canary 2.1 software package. Calls were amplified with a Nagra-Kudelski DSM speaker connected to a Sony WM-D6C tape recorder. The volume was adjusted to the natural loudness of a calling male (appr. 100dB at 1 meter, Wich, unpubl. data). All playbacks were conducted from around 75 meters of the test group at a height of two meters. Playbacks were conducted in the morning hours of days when the test group was in the overlap area. Never was a test group tested on consecutive days. Experiments were cancelled on days when the test group had a between group-encounter with another langur group in the course of the morning.

Data collection

The langur groups were followed from their sleeping tree in the morning until two hours after the experiment. The following data were collected: the time latency from the presentation (defined as the time of the start of the first experimental call) to the first loud call produced by the test male; the number of loud calls in the hour after the presentation; the latency from the presentation to the first male move; the male move and scan (head movement more than 45 degrees) rate per minute for the first 15 minutes after the presentation; the time the male was outside the group (defined as being more than 25 meters away from the group's centre) after the presentation; the time from the presentation until the male reached the location of the speaker; male and female approaches to the speaker (distance moved to speaker divided by initial distance of group to speaker multiplied by 100); the latency from the presentation to the first travel movement by any female of the group; whether or not the group (excluding the male) spread was reduced after the presentation (measured in terms of the group spread directly before and directly after the playback); and whether or not the distance between a mother or other females and an infant decreased.

Statistics and analyses

Since the data were not distributed normally non-parametric statistics were used. The paired results were tested with a Wilcoxon signed ranks test or with a Fisher Exact test (Siegel & Castellan 1988). Levels of significance were corrected for by the sharper Bonferroni criterion of Hochberg (1988). Families of related behaviours that needed to be corrected for by the sharper Bonferroni criterion (e.g. Chandler 1995) were chosen to be male behaviour and female behaviour.

When the male did not reach the speaker, did not give any loud calls, or the group did not travel in the hour after the experiment the values of these variables were set at the maximum value of 3600 sec.

The latency to the first loud call and the number of loud calls were significantly correlated and only the number of loud calls is presented in the results as this variable has often been used in primate papers on playbacks. A significant positive correlation was also found for the percentage of male approach to the playback site and the time in which the male reached the playback site. The results on male percentage of approach are presented, since approach measures are also commonly found in other papers on playbacks (e.g. Waser 1977).

Results

The males reacted more vigorously towards calls of the young than old adult males (Table 2). In the experiment of the young adult calls, males gave more loud calls, had a shorter latency time to the first move, made more movements, scanned more, went out of the group longer, and approached the speaker more closely than in the experiment with the old adult call. All these measures differed significantly in the expected direction.

Females did not approach the location of the speaker at all in both experiments, but moved away from their own position significantly sooner in the young adult stranger male experiment than in the old adult stranger male experiment (Table 3). In both experiments the direction of travel was always away from the location of the speaker. Group contraction occurred significantly more often in the young than old male stranger call experiment (Fisher Exact test: p=0.005). A reduction of mother-infant distances (Fisher Exact test: p=1.0) occurred equally often in the two different type of experiment.

Table 2. Results of the playback experiment of loud calls from young and old adult stranger males

Test variable	Young adult Stranger	Old adult Stranger	Significance
MALE: number of loud calls	5.0 (4.0, 6,3)	2.0 (1.8, 3.3)	$T^{+}=55$ *
MALE: latency to 1st move (sec)	8.0 (5.0, 10.3)	22.5 (10.5, 31.8)	$T^{+}=52.5$ *
MALE: move rate (per min)	2.0 (1.5, 2.9)	1.2 (0.7, 1.4)	$T^{+}=55$ *
MALE: scan rate (per min)	7.6 (6.9, 8.1)	4.9 (4.0, 5.5)	$T^{+}=55$ *
MALE: duration out of group (min)	28.0 (20.3, 33,5)	14.0 (8.0, 18.8)	$T^{+}=54$ *
MALE: percentage approach	97.5 (88.8, 100.0)	57.5 (30.5, 69.5)	$T^{+}=55$ *
FEMALES: percentage approach	0.0 (-, -)	0.0 (-, -)	not testable (10 ties)
FEMALES: latency to travel (sec)	131.0 (64.8, 230.8)	2026.5 (1612.8, 2535.0)	$T^{+}=55$ **

Median response values are presented here with the 25 and 75 percentiles between brackets. Significance levels were denoted as: ** = p<0.01, * = p<0.05, and ~ = p<0.1

Discussion

In this paper we examined whether Thomas langurs differentiate between loud calls from young adult and old adult strange males. Young adult strange males are more often responsible for infanticidal attacks than old adult strange males. For Thomas langur males and females it would therefore be functional to discriminate between loud calls from young adult and old adult strange males. Since loud calls from old adult males have a longer duration that loud calls from young adult males (chapter 3) there seems to be variation that other individuals can use to distinguish these calls.

The results of the experiment showed that the male reaction was more vigorous to the playback of the call of a young male stranger than of a mature stranger. Males gave significantly more loud calls and approached the speaker significantly more closely in the young call experiment. In addition, they scanned with a significantly higher rate and stayed out of the group significantly longer after the young male than after the mature male call experiment. The latter indicates that test males searched the area more thoroughly after the young than mature call experiment.

This experiment also shows that females were more cautious in response to the young male loud call than to the mature male loud call. In none of the experiments did females approach the speaker, but in the experiment with the young male call females moved away significantly earlier than in the experiment with mature calls. In addition females showed group contraction more often after the young than mature playback experiment. All this that a stranger with a young call is being perceived as more threatening than a stranger with a fully matured loud call. Mother-infant distance reduction occurred as often in both experiments, which indicates that females always consider strange males as being dangerous.

These results that both males and females differentiate between calls from young and old adult males and that these results can be interpreted as being functional to reduce infanticide. A similar interpretation has been applied to the ability of female lions to differentiate between male roars (McComb et al. 1993). Our study is the first for primates to suggest a similar function. Since infanticide is such a widespread phenomenon in primate species (van Schaik & Janson, 2000), this hypothesis should be evaluated in more primate species both with and without infanticide pressure to evaluate its generality.

Chapter 8

The audience effect in Primates: an experimental study on male calls in response to a tiger model

With E.H.M. Sterck

(Proceedings of the Royal Society of London B in review)

Abstract

The traditional view in animal communication research asserts that animal vocalisations merely express emotion and are not under voluntary control. Recent research, however, indicates that animal vocalisations can refer to objects in the outside world and that call production can be under control of the sender depending on the type of audience. Our research on wild male Thomas langurs (Primates: *Presbytis thomasi*) shows that these males call as a response to a tiger model when they are in a group but do not call when they are solitary. This is the first experimental primate study showing that the presence or absence of an audience influences calling behaviour. Our results indicate that call production in primates is under control of the callers and not merely express emotion.

Introduction

Since Darwin (1872), the control over expression of emotion by humans has been contrasted with uncontrolled expressions by animals, including non-human primates. Such a view is still expressed in claims that animal calls are "quite automatic and impossible to suppress" (Bickerton 1990) or not much more than just "groans of pain" (Griffin 1981). Two major lines of evidence challenge this view. First, an increasing body of research shows that primate vocalisations refer to objects, especially predator types, in the outside world (Struhsaker 1967; Seyfarth et al. 1980; Zuberbühler et al. 1997; Zuberbühler 2001). Second, some studies indicate that the likelihood that an individual vocalises depends on the presence and identity of the listeners (such as kin or no kin, and sex), the so called "audience effect" (Sherman 1977; Cheney & Seyfarth 1985, 1990; Gyger et al. 1986). Most detailed experimental work on the audience effect concerns birds (Marler & Mitani 1988). In primates the audience effect has received little attention. However, it has been shown that the identity of the listeners affects call rates in vervet monkeys (*Cercopithecus aethiops*, Cheney & Seyfarth 1985) and anecdotes exist for this species that the presence of an audience affects call rates (Cheney & Seyfarth 1990). Our study is the first to experimentally investigate the influence of the presence or absence of an audience on the production of vocalisations in a wild primate.

Our study object was the medium sized arboreal Thomas langur (*Presbytis thomasi*). This primate is endemic in the tropical rain forest of northern Sumatra, Indonesia (Sterck 1997). Thomas langurs live in one-male, multi-female groups (called mixed-sex groups), but solitary males also occur (Sterck 1997). Both males in groups and solitary males produce a so-called loud call (Steenbeek & Assink 1998) that plays a role in inter-group communication (Wich et al. 2002a, b). Loud calls are also given in reaction to the presence of predators, such as tigers (*Panthera tigris*, Steenbeek et al. 1999). An encounter of Thomas langurs with a tiger was observed twice. On one occasion the langurs ascended to the canopy and left the encounter location, on the other occasion the females ascended and left, while the male followed the tiger over a short distance (S. A. Wich, pers. obs., S. E. Koski, pers. comm.). The different grouping constellations provided an opportunity to study the audience effect for a wild primate in its natural habitat.

Methods

Experiments were conducted in two study areas in the Leuser Ecosystem, northern Sumatra, Indonesia. The Thomas langurs in one area (Ketambe 3°41'N, 97° 39'E) have been studied continuously from 1988-2001 and all individuals of the study population were individually recognised and were well habituated to the presence of human observers. The Ketambe area consists of primary tropical rain forest (Rijksen 1978; van Schaik & Mirmanto 1985). At Ketambe six mixed-sex groups and four solitary males were tested. The Thomas langurs in the other area (Bukit Lawang, 3 30'N, 98 6'E) were studied in the early 1980s (Gurmaya 1986) and have been studied by us since 1998. This area consists of a mosaic of primary and secondary forest with rubber plantations on its fringes (Gurmaya 1986). The mixed-sex study groups (n=6) and solitary males (n=3) were well habituated. Data from these two populations were lumped for the analyses.

Our experiments consisted of two parts. First, we aimed to establish that loud calls are produced in reaction to the presence of predators and are not simply an emotional reaction to novel objects of similar size and shape. To this end, mixed-sex groups were exposed to a fake tiger skin and a white cotton blanket with coloured stripes. Second, we examined whether the presence of an audience affected the production of loud calls by exposing solitary males to the tiger skin and the blanket. For each experiment we recorded the number of loud calls produced, whether the group or solitary male ascended or descended the trees, and whether they approached of retreated from the stimulus (tiger skin or blanket). The fake skin and blanket were exposed to the monkeys by a human observer carrying the skin or blanket over his shoulders and the rest of his body while walking on all fours. When one of the monkeys was observed to notice the stimulus by staring at it, the human observer carrying the fake skin or blanket slowly moved out of sight. Two other observers collected the behavioural data. All experiments were conducted between 1998 and 2001. Groups were never exposed to more than one stimulus on the same day or on two consecutive days. Six of the mixed-sex groups and four solitary males were first exposed to the fake tiger skin and then to the blanket, whereas the other six groups and three solitary males were exposed to the opposite sequence. The order of stimulus presentation did not affect the results. Statistics were one-tailed, because we expected that males reacted more strongly to the fake tiger skin than the blanket and that males in mixed-sex groups called but that solitary males remained silent.

Results

The results of the first experiment on mixed-sex groups indicate that loud calls were produced as a reaction to a predator. The males produced significantly more loud calls in response to the fake tiger skin than to the blanket (Wilcoxon signed rank test: p=0.002, n=12 groups, Table 1). After being exposed to the tiger skin the monkeys also significantly more often ascended the trees (11 out of 12 cases) than after exposure to the blanket (5 out 12 cases)(Fischer's Exact test: p=0.02). In addition, the males significantly more often avoided the tiger skin (10 out of 12 cases) than the blanket (4 out of 12 cases)(Fischer's Exact test: p=0.02).

When the fake tiger skin and blanket were exposed to solitary males (2nd experiment, n=7 males) no loud calls were made in either of the experiments (Wilcoxon-signed rank test: 7 ties. p=1.0). Nevertheless, after being exposed to the tiger skin the solitary males tended to ascend the trees (7 out of 7 cases)

Table 1. Results of tiger model exposure to solitary males and males in groups

	Fake tiger skin	Blanket
Males in group (n=12)	2 (1, 3)	0 (0, 0)
Males solitary (n=7)	0 (0, 0)	0 (0, 0)

Table 1. Median number of loud calls given by males in the experiments. Median values are presented here with the 25th and 75th percentiles between brackets.

more often than when exposed to the blanket (4 out of 7 cases)(Fischer's Exact test: p=0.10). Similarly, they retreated significantly more often from the location of the fake tiger skin (7 out of 7 cases) than when exposed to the blanket (3 out of 7 cases)(Fischer's Exact test: p=0.10).

Although the behavioural response (ascend/descend and approach/retreat) is the same for group living males and solitary males, loud calls were only given to the fake tiger skin by group-living males (Mann-Whitney-U test: n1=12, n2=7, U=3.5, p=0.0003). Thus, the fake tiger skin is perceived as a real threat.

Discussion

These experiments convincingly show an effect of the presence or absence of an audience on call production by wild Thomas langur males. Solitary male Thomas langurs do not make loud calls when exposed to a predator model, whereas those in mixed-sex groups do. Hence, Thomas langur males can manipulate their response and loud call production is under voluntary control (Marler & Evans 1996). In addition, these experiments also indicate that loud calls are produced to warn conspecifics (Zuberbühler et al. 1997) and not to alert the predator (Zuberbühler et al. 1997, 1999), since in the latter case calls are always expected when the fake tiger skin is presented and not only by males in groups.

Thus, in contrast to Darwin's view (1872), Thomas langurs show that primates may control the expressions of their emotions and oppose Bickerton's (1990) opinion than animal calls are "impossible to suppress".

Chapter 9

Female transfer and the influence of male quality in Thomas langurs (*Presbytis thomasi*)

With Willems, E.P., van Hooff, J.A.R.A.M. & Sterck, E.H.M.

(Behavioral Ecology in review)

Abstract

Female dispersal is found in a number of primate species. Several ultimate hypotheses have been proposed to explain it: reduction of predation risk, reduction of food competition, inbreeding avoidance and infanticide avoidance through mate choice. This study set out to test all hypotheses on female dispersal and, in addition, investigated parameters of male quality possibly used by females in transfer decisions.

Data were collected on a wild population of Thomas langurs over a 12 year period at the Ketambe Research Station, Sumatra, Indonesia. Nulliparous females were found to transfer only when their father was still resident at the time of maturity. Parous females transferred to the youngest interested adult male. These new, early tenure males provided better protection to offspring against predation and infanticide than the old, late tenure males. The dispersal pattern of nulliparous females was thus best explained through inbreeding avoidance, whereas dispersal by parous females was interpreted as an expression of mate choice. Characteristics of male behaviour influencing mate choice remain unclear. No significant differences in loud call or between-group interaction rates were detected between the late and early tenure males, nor over a male's tenure. Other clues, such as male behaviour during between-group interactions are likely candidates to affect in mate choice by Thomas langur females.

Introduction

In most mammal species, females tend to be more philopatric than males (Greenwood 1980). This is thought to reflect different selective pressures acting on the sexes. It is generally accepted that female reproductive success depends directly upon ecological factors, such as access to food and predation pressure, whereas male reproductive success is limited by sexual access to females (Trivers 1972; Emlen & Oring 1977; Dunbar 1988). Access to food and protection against predation are best obtained in a well-known area and, accordingly, females show a reluctance to disperse (Greenwood 1980). Consequently, males are forced to leave a familiar area to increase mating opportunities with unrelated females (Pusey & Packer 1987).

In contrast to this general mammalian dispersal pattern, female dispersal is rather frequently observed in the primate taxon (Moore 1984; Pusey & Packer 1987; Pusey 1992; Sterck & Korstjens 2000).

In gregarious primates, female dispersal is only expected when females gain little from establishing dominance hierarchies or coalitions, i.e. when between-group competition for resources is low and within-group competition is of the scramble type (Wrangham 1980; Terborgh & Janson 1986; van Schaik 1989; Isbell & van Vuren 1996; Sterck et al. 1997; Sterck 1998). Under these conditions, the main cost for females to dispersal is a loss in reproductive time. Dispersal may entail a group change as well as a change in site, both bringing about specific additional costs (Isbell & van Vuren 1996; Sterck 1998). In the current study transfer was defined as social dispersal between-groups.

Several ultimate hypotheses have been proposed to explain female dispersal: reduction of predation risk, reduction of food competition, inbreeding avoidance and infanticide avoidance through mate choice (Table 1). Groups below optimal size suffer from high predation risk, whereas groups above optimal size constrain female fitness through increased within-group food competition (van Schaik 1983). Thus, to reduce predation risk females are expected to transfer to larger groups (Cheney & Wrangham 1987),

Table 1. Hypotheses that may explain female transfer in the Thomas langur and their predictions.

ultimate hypotheses	proximate predictions
predation risk	- females transfer to larger groups
food competition	- females transfer to smaller groups
	- females transfer when nutritional demands are high (i.e. when lactating)
inbreeding avoidance	- natal nulliparous females transfer when father is still resident
	- females transfer when male kin gains reproductive status
	- females transfer to unrelated male
mate choice	
- offspring protection	- transfer to best male
• predation	• juvenile survival is higher after, than before transfer
• infanticide	• - infant survival is higher after, than before transfer - females transfer without infant - females without dependent offspring transfer first

and to reduce within-group food competition females should transfer to smaller groups (where only adult numbers are considered). Females can also reduce food competition by dispersing whenever nutritional demands are high, that is, when lactating.

Close inbreeding might be prevented through transfer by natal nulliparous females in species in which males are still resident at the time of maturity of their daughters (Clutton-Brock 1989). Under the same hypothesis, parous females are expected to transfer whenever male kin gains reproductive status and to abstain from immigrating into a group with a related resident male (van Hooff & van Schaik 1992).

Transfer may also be an expression of female choice. Females have been suggested to join high quality males that are better protectors of future offspring than the old male (Harcourt et al. 1976; Marsh 1979; Watts 1989; van Schaik 1996). Males may offer protection against infanticide and against predation. The latter is thought to be especially vital for juveniles (Treves & Chapman 1996), whereas protection against infanticide is crucial for infants. The infanticide avoidance hypothesis predicts that females transfer without dependent offspring. It furthermore implies that females with older, independent offspring will leave a lower quality male before females with younger, dependent.

The inherent premise of the mate choice hypothesis is that females are able to assess male quality. Previous analyses indicated that the rate of male loud calls and between-group interactions change over a male's tenure (Steenbeek & Assink 1998; Steenbeek et al. 1999) and, therefore, may reflect male quality (Table 2).

Male loud calls are assumed to be costly to produce (review: Prestwich 1994; Cowlishaw 1996) and high quality males may have higher call rates. This especially holds true for morning calls, as these are energetically the most costly (Whitten 1982; Cowlishaw 1996). Total call rate and morning call rate therefore seem particularly suitable as honest indicators of male quality (Grafen 1990; Maynard Smith 1991).

Table 2. Possible parameters of male quality in the Thomas langur and their predictions.

parameter	predictions
male loud calls	rate of old male at late tenure < rate of new male at early tenure
	rate of old male at late tenure < rate of old male at middle tenure
between-group	rate in old late tenure group > rate in new early tenure group
interactions	rate in old late tenure group > rate in old middle tenure group
male age	females transfer to youngest adult male

A resident male's ability to keep rival males from harassing his group and the rival males' ability to do just so, might be the most obvious indicators of male quality available to females (Wrangham 1979; Cheney 1987). Hence, a low rate of between-group interactions might indicate high male quality.

Moreover, females are expected to prefer young males. These will have a long tenure ahead and accordingly, are likely to keep females from having to transfer in the near future.

In the study population of wild Thomas langurs both male infanticide and female transfer occur, and a relationship between the two was described by Sterck (1997) and Steenbeek (1999). In order to rightfully ascribe the observed transfer pattern to mate choice however, all ultimate advantages associated with dispersal were considered before investigating what parameters of male quality females might use in their transfer decision making. This study is partially a constructive replication (confer Martin and Bateson 1993) of previous projects on the same population, using a larger dataset than previously available to allow more conclusive results.

Methods

Study site and population

The study was conducted at the Ketambe Research Station, Gunung Leuser Ecosystem, Sumatra, Indonesia (3°41'N, 97°39'E). The area consists of approximately 200 ha undisturbed primary rainforest, as described by Rijksen (1978) and van Schaik & Mirmanto (1985). At any given time the study population consisted of five to six bisexual groups, along with a small number of solitary males and all male bands. In total, 20 bisexual groups were studied over an almost continuous time span from September 1987 to May 2000. Data were collected by 42 different observers, under supervision of C.P. van Schaik (September 1987-August 1988), E.H.M. Sterck (November 1988-October 1992), R. Steenbeek (November 1992-March 1996), A.H. Korstjens (March 1996-March 1997) and S.A. Wich (April 1997-May 2000).

Group characteristics

Bisexual groups typically consisted of one resident male with one to seven females and offspring. They ranged in size from 3 to 15 individuals. In the course of the whole project, 162 different langurs were individually recognised. Group identity was linked to male residency as female group membership was far more variable due to female dispersal. Three different phases in the lifespan of bisexual groups were distinguished: the early, middle, and late tenure phase (Steenbeek 1999). The early phase of a male's tenure started with the association of at least one adult female and lasted until the first offspring was born. The last 12 months of a male's residency in a bisexual group, was defined as the late tenure phase. The stable period between the birth of the first offspring and this last year of a male's tenure, was called the middle tenure phase.

New groups were generally formed according to two basic mechanisms: female split-merger and male take-over (Fig. 1). Female split-merger implied voluntarily female transfer and led to gradual group formation (Sterck 1997). Both nulliparous and parous females transferred between-groups. In the event of a male take-over, an extra-group male invaded an existing group and expelled the resident male. In many primate species, male take-overs are the main social contexts in which infanticide occurs (Hrdy 1977; review: Hausfater & Hrdy 1984). In the Thomas langur however, infanticide was also observed in periods without male take-over (Sterck 1997; Steenbeek 1999).

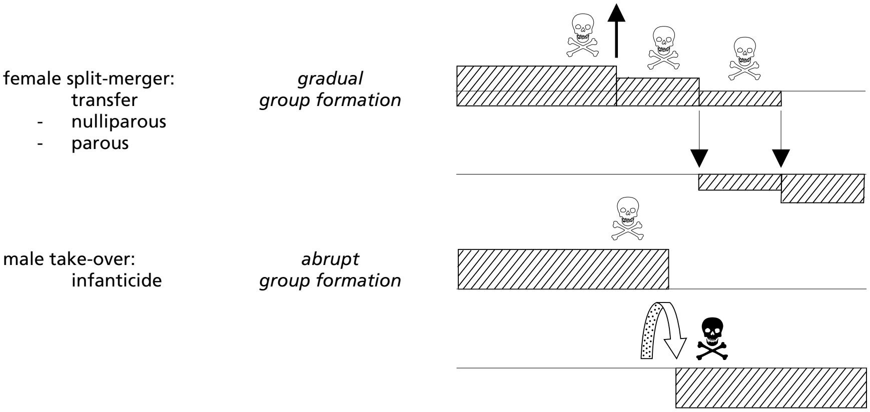


Figure 1. **The group formation processes observed in the study population. Thickness of bars represents female numbers, solid lines and dotted lines represent different males. Skulls indicate infanticide attempts by extra-group males. The black skull marks the period during which infanticide is most likely to occur in other primate species**

Age classes

Three age classes were distinguished: infants, juveniles and adults. Infants were thought to be dependent upon their mother for survival. Weaning age averaged around 18 months, yet when deprived from their mother, infants were frequently observed to survive at much younger ages. Therefore, and consistent with Sterck (1997), 14 months was deemed the last month of infancy. Juveniles were individuals older than 14 months, but not yet sexually mature. Females were considered adult at an age of 60 months, i.e. roughly one year before the average age at which first infants were born (74 months, n=8). This also coincided with the youngest age at which a female in the study population gave birth. A distinction was further made between nulliparous females (young adult females that have not had offspring yet) and parous females (adult females that already have had offspring). Males were regarded sexually mature when their testicles had descended and complete loud calls were produced. Average age of maturity for males is not known, but is reckoned to be over 60 months.

Female reproductive status was either reproductive (caring for an infant) or non-reproductive (not caring for an infant). The gestation period is not known and was not considered in the analyses, thus yielding more conservative tests in respect of the infanticide avoidance hypothesis.

Data collection

Groups were followed from dawn until dusk, usually for several days in succession each month. In this way, a total observation time of 197.75 female-years was acquired. Female-years are the summed number of years that females were observed (Sterck 1997).

Female transfer was defined as dispersal of an adult female from one bisexual group to another. The potentially associated cost in terms of loss in reproductive time, was recorded over the whole female population (both nulliparous and parous females). When females transferred together, this was treated as one event in order to assure independency of measurements. The groups of origin and destination, female reproductive status and parity as well as the age of possibly present offspring were known in all events included in the analyses.

The number of loud calls per day (male loud calls from all contexts) and the proportion of days on which a male produced morning calls (loud calls before 6:30 h, from the sleeping tree) were calculated over the three month period before and after the first female transfer event. This resulted in a cross-sectional comparison between the old -late tenure- male and new -early tenure- male. Furthermore, a longitudinal comparison over the old male's tenure was made between the rates preceding the first female transfer and a three month period during the old male's middle tenure phase. The same cross-sectional and longitudinal comparisons were made for between-group interaction rates.

Two types of between-group interactions were distinguished: between-group encounters (BGE's) and silent encounters (SE's). BGE's were encounters during which two or more bisexual groups approached each other to within 50 m. During a silent encounter, a lone extra-group male would silently approach and invade a bisexual group and chase or try to injure one of the group members. Thus, SE's were by definition aggressive and included infanticide attempts.

The exact ages of males that had interactions (whether BGE's or SE's) with a group during the three month period preceding transfer, were not always known. In most cases however, the youngest individual of these interested males could be identified.

Statistics

The Mann-Witney U test was used to detect the loss in reproductive time for transferring females compared to non-transferring females. With the Wilcoxon signed rank test group size and composition before and after transfer were compared. The Wilcoxon signed rank test was also used to detect possible differences in the between-group interaction and male loud call rates. Female reproductive status at the time of transfer was analysed with the binomial test. Distributions in the contingency table of nullipartous female transfer were analysed with the Fisher Exact test (Mehta & Patel 1992). The Kaplan-Meier Survivalship analysis (de Vries, pers. comm.) was used to test for differences in offspring survival between the last cohort before transfer and the first cohort after transfer.

All analyses were carried out using the statistical packages SPSS 9.0 for Windows and Statxact for DOS, and made use of non-parametric two-tailed tests. The significance level was preset at $p<0.05$ though Bonferroni corrections were applied where appropriate. Only data from complete follow days were used.

Results

Female transfer

General dispersal pattern

During the 12 year observation period 12 new groups were formed, 6 of which through female split-merger, 4 by an aggressive male take over and 2 through the association of a male with a group that had recently lost its resident male by unknown causes. In compliance with the definition, 24 independent events of parous female transfer occurred. In total, female Thomas langurs dispersed at least 39 times. Of these, 26 involved parous, 8 involved nulliparous and 3 involved juvenile females. Reproductive status and parity were not known for 2 dispersing females. In addition to the 39 dispersing females, another 5 disappeared. These either had dispersed to unhabituated groups, or had died. Not taking these females into account, a conservative female dispersal rate was estimated at 0.20 females per year (Fig. 2). Thus, a typical female in the study population dispersed roughly once every 5 years.

Figure 2. **Calculation of the estimated female dispersal rate.**

$$\frac{\text{39 females (26 parous + 8 nulliparous + 3 juvenile + 2 unknown)}}{\text{197.75 female-years (total female observation time)}} = \text{0.20 female per year}$$

Reproductive cost of transfer

Female transfer is known to have consequences for female reproduction. For nulliparous females no difference was found in the age of first reproduction between transferring and non-transferring individuals (Mann-Whitney U test: n1=4, n2=3; Z=-1.41; p=0.16).

The average inter-birth interval of parous females was 34 months for transferring females and 25 months for non-transferring females when the last infant survived to juvenality. This loss in reproductive time of 9 months was highly significant (Mann-Whitney U test: n2=12, n2=30; Z=-3.18; p=0.001).

Group size and composition

The sizes of the group that females left before transfer and the group they subsequently entered after transfer, were investigated (Fig. 3). When considering total group size, females transferred to smaller groups (Wilcoxon signed rank test: n=24, Z=-2.26, p=0.02). They joined groups with fewer immatures, but equal numbers of adult females (Wilcoxon signed rank test: Z_{juv}=-3.68, p<0.001, Z_{inf}=-2.48, p=0.01 and Z_{fem}=-1.59, p=0.11).

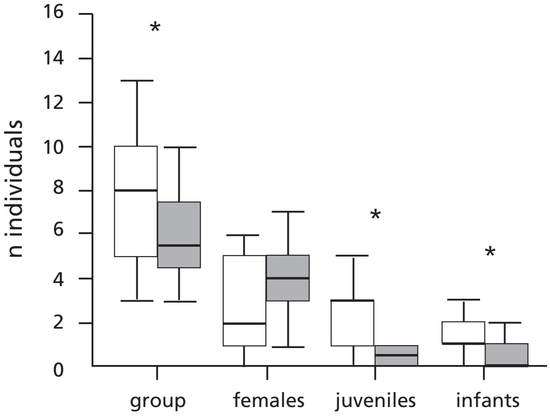


Figure 3. **Median and percentiles for total group size, number of adult females, juveniles and infants before and after the transfer events. Asterisks indicate a significant difference (white coloured bars = before transfer; grey bars = after transfer).**

Reproductive status of transferring parous females

When examining reproductive status of parous females, it was found that females were reproductive during 47.8% of their adult lives. This percentage was obtained by dividing the time females were observed to have dependent offspring (94.5 female-years), by the total female observation time (197.75 female-years).

Of the 26 parous females that transferred 22 were not reproductive (i.e. not caring for an infant), whereas only 4 were. Thus, females transferred significantly more often when not reproductive (binomial test: observed=4:22, expected=12.4:13.6, p=0.001).

Nulliparous transfer

Nulliparous females were expected to transfer when they matured in their natal group and their father was still the resident male. 8 out of 9 nulliparous females indeed transferred under these conditions, whereas none of the 3 females that had transferred as a juvenile and thus matured in a group with a resident male other than their father, did. The probability of obtaining this distribution as a result of chance is 0.02. (Fisher Exact test: n=12)

Offspring survival

The cohorts directly preceding and following female transfer comprised a total of 44 infants. Of these, 10 were excluded from the analyses as they were either stricken by an epidemic (n=8) or died as a consequence of their mothers' inability to raise them (n=2).

Survival of the last offspring cohort of the old male (late tenure), was compared to the survival of the first offspring cohort of the new male (middle tenure) (Fig. 4). Overall offspring survival after transfer was found to be significantly higher than before transfer (Kaplan-Meier: n= 34, d.f.=1, Tarone-Ware statistic=15.8, p=0.0001). This was also found considering infant and juvenile survival separately (Kaplan-Meier: n_{infant}=34, df =1, T-W statistic= 3.94, $p<0.05$; $n_{juvenile}$=26, df=1, T-W statistic=12.6, $p<0.0005$).

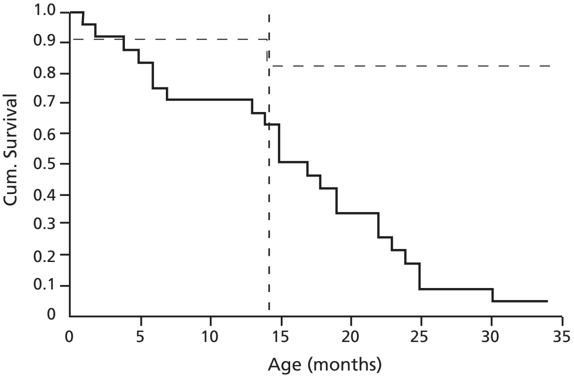
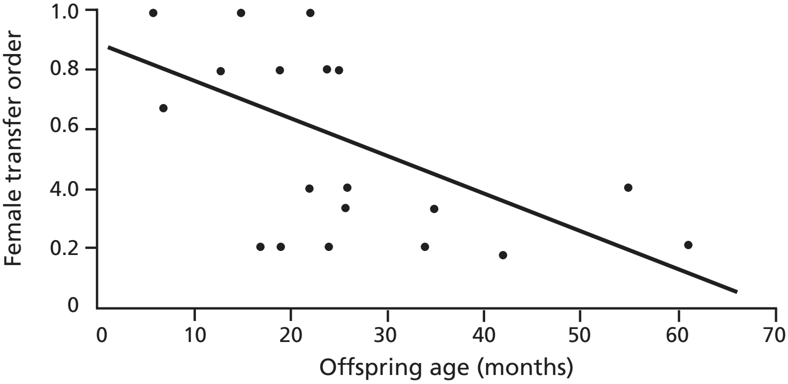


Figure 4. **Offspring survival before and after transfer. On the y-axis cumulative survival is depicted, representing the proportion of offspring within a cohort that is still alive at any given age, presented on the x-axis. The dashed line at 14 month marks the last month of infancy (unbroken line = before transfer; broken line = after transfer) .**

Transfer order and offspring age

The infanticide protection hypothesis predicted that the transfer order of females from a group depends upon the age of a female's offspring (Fig. 5). The transfer order on the y-axis was calculated by assigning a transfer rank to females within a group and dividing it by the total number of females in that particular group. This was done for all groups. The thus acquired measure made it possible to analyse female transfer order in relation to offspring age in the last cohort over the whole population. Offspring age at the moment upon which the last adult female left the group is depicted on the x-axis. Females with the oldest offspring in the last cohort were the first to leave their group (Spearman's correlation: n=22, r=-0.56, p=0.007).

Figure 5. **The relation between female transfer order and offspring age at the time of group end.**



Male quality

General description

During the total observation period, 11 females were the first of their group to transfer to a particular new male. As females from different groups could associate around the same early tenure male, 6 new groups were formed in this way.

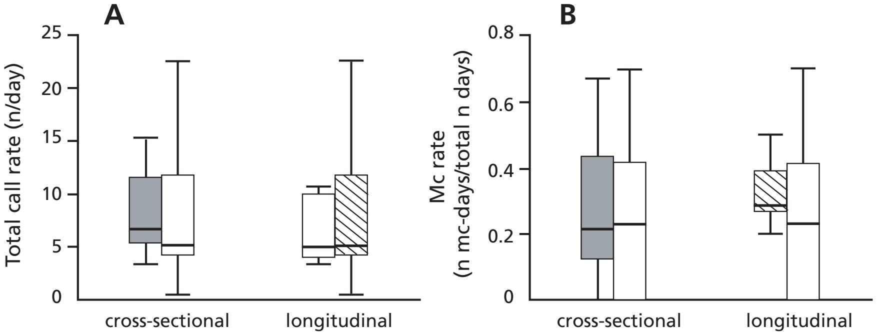
On average, 2.9 extra-group males had interactions with a group in the three month period preceding the first female transfer. This number was calculated by dividing the total number of males that had interactions with a group in the three month period preceding female transfer (n=32) by the number of females that were the first of their group to transfer to a new, early tenure male (n=11).

Male loud calls

Complete data on loud calls of the old and new male were available in 8 of the 11 independent transfer events. Total call rate analyses revealed no significant difference between the old male at late tenure and the new male at early tenure (Fig. 6a; Wilcoxon signed rank test: n=8, Z=-0.70, p=0.48). Likewise, no difference was found between the old male's middle and late tenure phases (Wilcoxon signed rank test: n=8, Z=-1.12, p=0.26).

The same was found in the morning call analyses (Fig. 6b): no differences were revealed in either the cross-sectional analysis between the old and new

Figure 6. **Comparison of the median and percentile values of male vocalisation rate between the old male at late tenure and the new male at early tenure (cross-sectional) and over the old male's tenure (longitudinal). Total call rate (a) and morning call (mc) rate (b) were considered separately (grey coloured bars = new male at early tenure; white bars = old male at late tenure; hatched bars = old male at middle tenure)**



male (Wilcoxon signed rank test: n=8, Z=-0.14, p=0.89) or in the longitudinal analysis over the old male's tenure (Wilcoxon signed rank test: n=8, Z=-.84, p=0.40).

Between-group interactions

Complete data on between-group interactions, were available in 9 of the 11 independent transfer events.

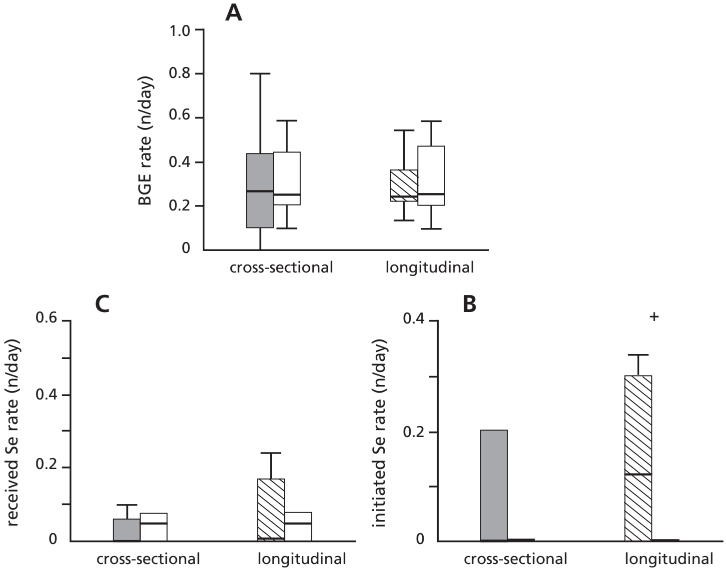
Between-group encounter rates (Fig. 7a) did not differ significantly in the cross-sectional analysis between the old, late tenure male and the new, early tenure male (Wilcoxon signed rank test: n=9, Z=-0.28, p=0.78). Significant differences were also absent in the longitudinal analysis between the old male's middle tenure and late tenure phases (Wilcoxon signed rank test: n=9, Z=-0.30, p=0.77).

Silent encounters were differentiated into silent encounters that the group received (Fig. 7b) and silent encounters initiated by the resident male (Fig. 7c). The received silent encounter rate revealed no significant differences in either the cross-sectional (Wilcoxon signed rank test: n=9, Z=-0.842, p=0.40), or longitudinal analysis (Wilcoxon signed rank test: n=9, Z= -.70, p=0.48), although the differences were in the expected direction. Rates of initiated silent encounters also revealed no significant difference in the cross-sectional analysis (Wilcoxon signed rank test: n=9, Z=-1.46, p=0.14), the difference however was in the expected direction. The longitudinal analysis showed a significant trend for the old male to initiate less sneaky attacks during his late tenure phase than during his middle tenure phase (Wilcoxon signed rank test: n=9, Z=-2.02, p=0.04; Bonferroni corrected).

Male age

The exact age of a male was not always known. In 9 out of the 11 first

Figure 7. **Comparison of the median and percentile values of between-group interaction rate between the old male at late tenure and the new male at early tenure (cross-sectional) and over the old male's tenure (longitudinal). Between-group encounter rate (a), initiated silent encounter rate (b) and received silent encounter rate (c) were considered separately. The plus-sign marks a trend (Bonferroni corrected). (grey coloured bars = new male at early tenure; white bars = old male at late tenure; hatched bars = old male at middle tenure)**



transfers to a new male however, it was possible to make out which of the extra-group males that had interactions with a female's group in the three month period preceding her transfer, was the youngest. The 2 cases in which the youngest male could not be identified, were conservatively treated as transfers to another than the youngest male. Since on average, 2.9 extra-group males had interactions with a group in the three month period preceding the first female transfer, the probability of a female choosing the youngest out of these interested males was estimated at 0.34 (1/ 2.9). In at least 9 of the 11 independent first transfer events, females joined the youngest interested male. Therefore females transferred significantly more often to the youngest interested male (binomial test: observed=9:11, expected=3.8:7.2, p=0.002).

Discussion

Causes of female transfer in Thomas langurs

New groups in the study population were formed through either female split-merger, which implied voluntarily female transfer, through aggressive male take-over, or through the association of an extra-group male with a group that had recently lost its resident male. Thomas langur social organisation thereby resembles that of other colobines (Struhsaker & Leland 1987; purplefaced langurs: Rudran 1973; Hanuman langurs; Newton 1987; capped langurs; Stanford 1991; Tana river red colobus; Marsh 1979), mountain gorillas (Harcourt 1979; Stewart & Harcourt 1987; Watts 1990, 1992) and, to a lesser extent, howlers (Crockett 1984).

Both nulliparous and parous females transferred between social groups. Transferring parous females suffered from an increased inter-birth interval, whereas transfer did not affect the age of first conception of nulliparous females. Below, all possible causes of female transfer are discussed.

Predation risk and food competition

Predation risk is assumed to be lowest in large groups whereas food competition is taken to be lowest in small groups (Alexander 1974; Wrangham 1980; van Schaik 1989). If female transfer were influenced by predation risk or food competition, females were expected to transfer to groups with more, respectively fewer adults than their previous group. The food competition hypothesis also predicts that females will transfer when nutritional demands are high, i.e. when lactating.

Female Thomas langurs transferred to groups with an equal number of adult females as in their old group and transferred when nutritional demands were low. These findings yield no support for either the predation risk or food competition hypotheses and are in line with previous studies on the same population (Sterck 1997; Steenbeek 1999).

Females however, appeared to prefer groups with fewer immatures. The significance of this remains unclear, but it might reflect a female preference for relatively new groups. These groups mostly contained a young resident male, so the apparent preference for groups with fewer immatures might actually be a preference for young males.

Inbreeding avoidance

Female dispersal has been be related to inbreeding avoidance (Clutton-Brock 1989; Pusey & Packer 1987).

In the study population, nulliparous females only transferred from a group when they matured in a group where their father was still the resident male. Since reproductive costs of transfer were not found for nulliparous females, the reluctancy to transfer when maturing in another than their natal group, may reveal additional costs to transfer,.

The inbreeding avoidance hypothesis could not be statistically tested for parous females. Nevertheless, parous females were never observed to copulate with adult sons when these were present in the group, consistent with the hypothesis.

The inbreeding avoidance hypothesis alone can not account for all female transfers. It may explain dispersal of nulliparous females from natal groups, but can not explain dispersal of parous females from a male with whom they have been reproducing. It is evident that other causes underlie transfer of parous females.

Mate choice

Females in non-female bonded primate species are hypothesised to associate with a male on basis of his abilities to protect offspring (Sterck et al. 1997; van Schaik & Kappeler 1997; van Schaik 2000). In support of this hypothesis, offspring survival was found to be higher in the first cohort after female transfer than in the last cohort before female transfer. The new (early tenure) male thus seems to provide better protection to his offspring than the old (late tenure) male. Apparently, females are able to detect these differences in male quality and transfer from a late tenure male to an early tenure male. They preferably do so, when the costs of dispersal are minimal (Sterck 1995; Steenbeek 1999). This pattern of female transfer from low quality males to high quality males is found in other primate species as well (mountain gorilla: Harcourt et al. 1976; Watts 1989; red colobus: Marsh 1979; red howler: Crockett 2000). Most of these studies interpret the female transfer pattern as support for the infanticide protection hypothesis. By looking at infant and juvenile survival separately, this study was able to distinguish between protection of offspring by the resident male against infanticide and protection against predation. Both infant and juvenile survival increased after the transfer to an early tenure male. Therefore, these males were not only better protectors against infanticidal extra-group males, as found by higher infant survival, but also against predators, as illustrated by higher juvenile survival. Moreover, the difference in offspring survival was most striking for juveniles. This may suggest that in the Thomas langur, male protection of offspring against predation is of more importance than male protection against infanticide.

Through the timing of mate choice, females actively contribute to the protection of offspring against infanticide as well. In the study population females with the oldest offspring in the last cohort of late tenure males, were the first to transfer to a higher quality male. Their offspring simply was the first in the group to reach an age at which it was safeguarded from infanticidal attacks by extra-group males. Females therefore only seem to transfer when the infanticide risk for present offspring is minimal. This also explains why females transferred more often without dependent offspring; a new and unrelated male is a potential killer of any infant he did not sire.

Male quality in the Thomas langur

Previous studies (Sterck 1995; Steenbeek 1999) and the results of this study, revealed that females are able to assess male quality. It was argued that females base their transfer decisions on behavioural indicators of male quality.

Likely parameters of male quality are male loud call rate, between-group interaction rate and male age. These parameters are investigated below.

Male loud call rate

Two categories of male loud call rates were distinguished; the number of loud calls per day and the proportion of days on which a male made morning calls. Neither however, revealed a difference between late tenure males and the early tenure males, nor over a male's tenure. One resident male in the study population even never produced morning calls at all. Nevertheless, three females from a neighbouring late tenure group successively transferred to this male, adducing further evidence to the finding that morning call rates are not used as indicators of male quality (contra Steenbeek et al. 1999).

In general, the relation between loud calls and any possibly associated ultimate advantage in primates is unclear, but resource- and mate-attraction likely functions for a wide variety of primate species (chapter four). Loud calls may serve several functions (Waser, 1977) and have been reported to play a role in mate competition, relative male quality and female choice in some species (red howler: Sekulic 1982; brown howler: Chiarello 1995; gibbon: Cowlishaw 1996), but not in others (orangutan: Mitani 1985a; chimpanzee: Mitani & Nishida 1993). Vocalisation rates and characteristics are likely to be influenced by a number of factors, such as the ecological and social situation in a group or population (Prestwich 1994), making it very difficult to identify possibly associated functions.

Male loud call rates in Thomas langurs, do not seem to serve as indicators of male quality. Characteristics of male loud calls in this species are known to encompass information about male identity, call context and male age (Steenbeek & Assink 1998; Koski 2000; van der Post 2001; chapter two & three). Nevertheless, females can probably not use loud calls as a measure to determine when to leave their current residant male (chapter four)

Between-group interaction rate

Two types of between-group interactions were distinguished: between-group encounters and silent encounters. The only significant result in the analyses of these parameters was a trend for a male to initiate silent encounters less often during his late tenure phase than during his middle tenure phase. In a previous study Steenbeek (1999) found significant differences in between-group encounter rates, but not in silent encounter rates. In her study, however, repeated measurements of the same subject (the resident male) were treated as independent of one another, i.e. a pooling fallacy (Martin & Bateson 1993). Therefore the current approach seems more appropriate.

The decrease in initiated silent encounter rate may reflect a decline in male aggression towards the end of his tenure. Male aggression might be an essential trait to keep females associated, whether through sexual coercion - herding- or through direct male-male competition (Smuts & Smuts 1993). The significance of the detected trend remains unclear, however, as between-group interaction rates are influenced by population density and other, more complex factors (Cheney 1987).

Male age

Young males are preferred over older ones. This may be due to the fact that young males are likely to have a long tenure ahead. Females indeed were found to transfer to the youngest interested adult male, thereby increasing the interval between two successive transfers and thus reducing the loss of reproductive time.

Young males can be identified through call characteristics (van der Post 2001), which may be the most likely mechanism underlying female choice in Thomas langurs. By choosing a young male, females join a group with fewer immatures than their previous group and most likely have chosen for a male with a long tenure ahead.

Conclusion

Female transfer in the Thomas langur is caused by social rather than ecological factors (Janson 1992; Janson & Goldsmith 1995), as the costs in terms of food competition are minimal (Sterck 1995; Sterck & Steenbeek 1997; Steenbeek 1999). Both nulliparous and parous females disperse, although the proximate causes differ. Nulliparous females transfer to avoid inbreeding, whereas parous females use transfer as an expression of mate choice. Parous females choose high quality males that offer protection to future offspring against predation and infanticide. They prefer young males that are likely to have a long tenure ahead and thus maximize the interval between two successive transfers. This is an adaptive strategy to reduce the loss in reproductive time, which is inherent to transfer behaviour.

Male characteristics that influence female choice in the Thomas langur remain unclear. A previous study (chapter four) revealed that recently matured, adult males can be identified by their loud call characteristics. This is the most likely parameter used by females to determine which male to associate with. It can not explain however, how females determine when to leave their resident male. Further investigation of especially male behaviour during between-group interactions are desirable to come to a deeper understanding of the proximate mechanism underlying female choice, not only in Thomas langurs, but in non-female bonded primate species in general.

Chapter 10

Summary

Summary

This study has addressed the acoustical structure of male Thomas langur loud calls and their function in Thomas langur social organisation.

Thomas langurs are medium sized arboreal foli-frugivores (Sterck 1995) that live in three social constellations: mixed-sex groups, all-male bands and as solitary males (Sterck 1997; Steenbeek 1999a). Mixed-sex groups typically consist of one resident male and several females with usually a number of immatures. Individuals of both sexes disperse and females also show secondary transfer (Sterck 1997; Steenbeek 1999a; Sterck & Korstjens 2000). Females are observed to associate with new males in two ways. First, they can transfer to an existing mixed-sex group (or solitary male) or second, they can be in a group that is taken over by a new male. Thomas langur males go through four distinct life-stages after leaving their natal group. They first reside in an all-male band after which they can start their own group. At the start of such group a male is defined to be in his early tenure phase. This starts when females associate with a new breeding male. The middle phase of a male tenure starts when females begin to reproduce and the first offspring is born. During the late phase of a male's tenure, females leave the male to associate with a new breeding male. This often results in leaving behind an all-male band consisting of the former breeding male and his male offspring (Steenbeek et al. 2000).

In the introduction I have suggested that females have to make two major choices when considering transfer to a new group. The first is how to determine whether the current resident male is losing strength and whether or not he currently is or for some time to come will be a good protector for the next offspring. The second choice, once a female has decided to transfer, is where to move to. More specifically: to which male from the neighbouring males or other (solitary) males should she move? Since infant survival is significantly higher in the first cohort of infants born in the group of the new male than in the last cohort of infants born in the group of the old male (chapter nine), these are not just trivial matters for a female and her offspring.

For several animal species, including various primate species, it has been suggested that females might use loud calls as a cue for male quality (e.g. Mitani

1985, Ryan 1985, Lambrechts 1992, Steenbeek 1999) and, therefore, use loud calls to base their mate preferences on. For primates, however, there is no conclusive evidence that loud calls are correlated with male quality or mate attraction (e.g. Mitani 1985). This is not surprising, provided that primates are long-lived animals that often live in complex societies in environments where it is difficult to collect the relevant data. Moreover, there are ethical constraints on experiments to evaluate the role of male quality and mate choice. Therefore, it is especially challenging to study primate vocal communication and its relation to male quality and mate choice.

When loud calls play a role in mate attraction it is important that there is variation in these calls between individuals or between classes of individuals. In the second chapter I have shown that both individual and contextual variation exists in Thomas langur loud calls. This indicates that there is variation for females to choose from and that loud call could potentially function in mate attraction. Since Steenbeek (1999a; b) has shown that male strength differs between various life stages and is lower in the late tenure phase, chapter three investigates whether loud calls show clear differences over various male life stages. The analyses show that loud call characteristics do not differ between the early, middle and late tenure phases, indicating that females can not base the decision of when to leave their current male on loud calls characteristics. The analyses, however, did indicate that loud calls in the all-male band life stage were significantly shorter in duration and had less T-units than in the other three life stages. This indicates that females can use loud calls to determine which males are young.

The remainder of this study evaluates possible functions of loud calls in the Thomas langur. Several functions for loud calls have been suggested such as mate-defence, resource-defence and mate-attraction. To evaluate these functions for primates in general a comparative analysis was conducted for a large number of primate species (chapter four). These analysis has shown that the presence of loud calls is correlated with one aspect of resource-defence and also partly with mate-attraction. But other factors such as male body size and activity pattern were also of influence on the presence of loud calls. Several measuers of male mate-defence, however, were not correlated to the presence of male loud calls.

To obtain a better understanding of the function of loud calls in Thomas langurs playback experiments were conducted.

The following experiments (chapter five) evaluate the spacing/resource and mate defence functions of loud calls in Thomas langurs. When resource-defence is important a stronger reaction was expected from the centre of the home range than from the edge from both males and females. When mate-defence is important it was expected that males would react as vigorously in the edge and centre experiment since they would always defend their females

(Wilson et al. 2001). The results show that the location, centre or edge, of a playback of a neighbouring male loud call influenced the reaction of males and females. After hearing a loud call from the centre males reacted more vigorously by giving more loud calls, more scans and by approaching the location of the speaker more closely than after hearing the same loud call from the zone of overlap (edge) of their home range. Females also approached more closely and quickly after the centre than after the edge experiment. The difference in approaching distance to the speaker indicates that the location of the call influences spacing; it illustrates intergroup spacing in the Thomas langurs. The experiments also indicate that resource defence (probably of food sources) is important for both males and females, since males and females approach the speaker more closely in the centre that edge experiment. To examine the resource defence function more explicitly an experiment was conducted in which playbacks from a neighbouring male on the edge were conducted from both a food containing and non-food containing tree. The results show that females, but not males, approach the speaker more closely in the food containing experiment than in the non-food experiment. These results support the hypothesis that food sources are more important for females than for males (e.g. Emlen & Oring 1977). Some researchers (Wilson et al. 2001) have suggested that when mate defence is important for males there should be an equal response of males to loud call playbacks from whichever location in the home range since they should defend their females everywhere. In this strict sense, our experiment does not support the mate-defence hypothesis since males showed a stronger response to playbacks from the centre than the edge. The neighbour-stranger experiment, however, indicated that males do try to defend their mates and offspring when strange males are in the vicinity. This experiment, therefore, supports the mate defence hypothesis for male Thomas langurs.

Chapter six shows that males and females differentiate between calls of neighbouring and strange males that are played back from the edge of the home range of the test group, indicating that loud calls are useful in determining who are familiar individuals. Such differentiation is functional since it can avoid costly and unnecessary fights with neighbours. In addition, I investigated the hypothesis that Thomas langurs can use the ability to recognise between loud call (categories) to defend their infants against infanticidal males. In Thomas langurs stranger males are responsible for the large majority of infanticidal attacks. It is in agreement with this hypothesis that males gave more loud calls, scanned more and approached the location of the speaker more closely in the stranger than neighbour experiment. Also in agreement with this hypothesis females females were hiding after hearing the stranger loud calls and not after hearing the calls from a neighbour.

In order to further evaluate the infant defence hypothesis another experiment was conducted in which groups were exposed to playbacks from young and old adult stranger males (chapter seven). Our observations suggest that young adult males are more often responsible for infanticidal attacks than old males (already established a group or are ex-resident). Therefore, I expected that playbacks from a young adult stranger male would lead to a stronger reaction of the males and a more cautious reaction from the females than playbacks from loud calls of old adult males. Such a response was indeed found. Males seemed to search the area from where the loud call was broadcasted more carefully in the young adult stranger experiment than in the old adult stranger male experiment. Females seemed more cautious after hearing the young adult stranger call and quickly moved in the opposite direction of the speaker location and did not do so after hearing the old strange male playback. This indicates that Thomas langurs can perceive differences between loud calls from young (calls of short duration) and old adult (calls of long duration, chapter three) males and react in such a way that they reduce the risk for an infanticidal attack after hearing the playback from the young adult male.

It has also been suggested that loud calls are given when there is threat from a predator (Waser 1977). This function of loud calls was examined in chapter eight by exposing the langurs to a tiger model (one of their predators). The experiments revealed that loud calls are indeed given after the langurs were exposed to the model tiger. The reponse of males, however, depended on the presence or absence of conspecifics. Solitary males did not respond with loud calls to a model tiger, but did show a similar fleeing behaviour as males in mixed-sex groups. This indicates that loud calls serve to warn conspecifics of the presence of a predator.

Because females are hardly ever found alone, it is impossible to do straightforward playback experiments in Thomas langurs to determine whether loud calls are important in mate choice. Therefore, chapter nine examines which factors determine female transfer and to which groups or males females transferred. In this chapter various hypotheses for female transfer such as food competition, predator-avoidance, and female mate choice are tested. These analyses have shown that females do not choose for smaller or larger troops as expected under the food competition or predator avoidance hypothesis, but transfer to a young male as expected under the female mate choice hypothesis. Transferring to a young male makes sense since young males have a long tenure ahead and females have therefore a good prospect of staying with this male for a few years. Females can potentially use loud calls to determine whether males are young and likely to have a long tenure ahead since loud calls of young adult males are shorter that those of old adult males. Thus females could use a maturational effect, namely the increase in loud call duration, to determine which males are young and where they are.

Nevertheless, loud calls are probably not a good indicator for females to time when to leave their current male. This study shows that loud call characteristics and the number of loud calls given are probably not good indicators of the end of a male's tenure (chapters three and nine). It is more likely that behavioural cues, such a reduction of aggression to other groups by the late tenure male or an increase of aggression to females by extra-group males could serve as a cue to females to time their transfer. More important for a female may be that there is significantly lower offspring survival in the last cohort before transfer than in the first cohort. This could potentially also provide females the necessary cue to leave their current male.

Therefore, it can be concluded that females use behavioural cues to determine when to leave their current male, but can use loud calls to choose which type of male, namely young males to transfer to. How females choose between the several young males that usually are in the area remains unresolved and needs further research.

References

Aich, H., Oos-Heilen, R. & Zimmermann E. (1990). Vocalizations of adult Gelada baboon (*Theropithecus gelada*): acoustic structure and behavioural context. *Folia Primatol.* 55: 109-132.

Alexander, R.D. (1974). The evolution of social behavior. *An. Rev. Ecol. System.* 5: 352-382.

Andersson, M. (1994). *Sexual Selection.* Princeton University Press, Chichester.

Assink, P., & van Dijk, I. (1990). *Social organization, ranging, and density of Presbytis thomasi in Ketambe (Sumatra), and a comparison with other Presbytis species at several South-east Asian locations.* Msc Thesis, Utrecht University.

Baldwin, J.D. & Baldwin, J.I. (1976). Vocalizations of howler monkeys (*Aloutta palliata*) in Southwestern Panama. *Folia Primatol.* 26: 81-108.

Ballintijn, M.R., & ten Cate, C. (1997). Vocal development and its interpretation in a non-songbird: the collared dove (*Streptppelia decaocto*). *Behaviour* 134: 595-621.

Bickerton, D. (1990). *Language and species.* University of Chicago Press, Chicago.

Birkhead, T.R., Fletcher, F. & Pellat, E.J. (1998). Sexual selection in the zebra finch *Taeniopygia guttata: condition, sex, traits and immune capacity. Behav. Ecol. Sociobiol.* 44: 179-191.

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117: 220-241.

Brown, C.H. (1986). The perception of vocal signals by blue monkeys and grey-cheeked mangabeys. *Exp. Biol.* 45(3): 145-165.

Brown, C.H. (1989). The acoustic ecology of East African primates and the perception of vocal signals by grey-cheeked mangabyes and blue monkeys. In: *The comparative psychology of audition: perceiving complex sounds* (R. Dooling & S. Hulse, eds.). Lawrence Erlbaum, Hillsdale, pp. 201-239.

Byrne, R.W. (1981). Distance vocalisations of Guinea baboons (*Papio papio) in Senegal: an analysis of function. Behaviour* 78: 283-312.

Byrne, R.W. (1982) Primate vocalisations; structural and functional approaches to understanding. *Behaviour* 80: 241-258.

Butynski, T.M., Chapman, C.A., Chapman, L.J., & Weary, D.M. (1992). Use of male blue monkey "pyow" calls for long-term individual identification. *Am. J. Primatol.* 28: 183-189.

Chalmers, N.R. (1968). The visual and vocal communication of free living mangabeys in Uganda. *Folia Primatol.* 9: 258-280.

Chandler, C.R. (1995). Practical considerations in the use of simultaneous inference for multiple tests. *Anim. Behav.* 49: 524-527.

Chapman, C.A. & Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Anim. Behav.* 39: 891-896.

Chapman, C.A. & Weary, D.M. (1990) Variability in Spider monkeys' vocalization may provide basis for individual recognition. *Am. J. Primatol.* 22: 279-284.

Chappel, M.A., Zuk, M., Kwan, T.H., Johnsen, T.S. (1995). Energy costs of an avian vocal display: crowing in red junglefowl. *Anim. Behav.* 49: 255-257.

Charles-Dominique, P. (1974). Aggression and territoriality in nocturnal prosimians. In: *Primate aggression, territoriality, and xenophobia* (R.L. Holloway, ed.). Academic Press, New York, pp. 31-48.

Cheney, D.L. (1987). Interactions and relationships between groups. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 267-281.

Cheney, D., and Seyfarth, R. (1982). Recognition of individuals within and between groups of free ranging vervet monkeys. *Am. Zool.* 22: 519-529.

Cheney, D.L. & Seyfarth, R. (1985). Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 93: 150-166.

Cheney, D.L. & Wrangham, R.W. (1987). Predation. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 227-239.

Cheney, D.L. & Seyfarth, R. (1990). *How monkeys see the world: Inside the mind of another species.* University of Chicago Press, Chicago.

Chiarello, A.D. (1995). Role of loud calls in brown howlers, *Alouatta fusca. Am. J. Primatol.* 36: 213-222.

Chivers, D.J. (1976). Communication within and between family groups of siamang (*Symphalangus syndactylus*). *Behaviour* 57: 116-135.

Clark, A. & Wrangham, R. (1993). Acoustic analyses of wild chimpanzee pant-hoots: do Kibale forest chimps have an acoustically distinct food-arrival pant-hoot? *Am. J. Primatol.* 31: 99-109.

Clark, A.P. & Wrangham, R.W. (1994). Chimpanzee arrival pan hoots: do they signify food or status? *Int. J. Primatol.* 15: 185-205.

Clutton-Brock, T.C. & Albon, S.D. (1979). The roaring of red dear and the evolution of honest advertisement. *Behaviour* 69: 145-169.

Clutton-Brock, T.H. (1989). Female transfer and inbreeding avoidance in social mammals. *Nature* 337: 70-72.

Clutton-Brock, T.H. & Harvey, P.H. (1977). Primate ecology and social organisation. *J. Zool. Lond.* 183: 1-39.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences.* Erlbaum Associates, Hillsdale NJ.

Cordeiro, N.J. (1992). Behaviour of blue monkeys (*Cercopithecus mitis*) in the presence of crowned eagles (*Strephanoaetus coronatus*). *Folia Primatol.* 59: 203-207.

Cowlishaw, G. (1992). Song function in gibbons. *Behaviour* 121: 131-153.

Cowlishaw, G. (1996). Sexual selection and information content in gibbons song bouts. *Ethology* 102: 272-284.

Crockett, C.M. (1984). Emigration by female red howler monkeys and the case for female competition. In: *Female primates: studies by female primatologists* (M.F. Small, ed.). Alan R. Liss Inc., New York, pp. 159-173.

Crockett, C.M. & Janson, C.H. (2000). Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: *Infanticide by males and its implications* (C.P. van Schaik & C.H. Janson, eds.). Cambridge University Press, Cambridge, pp. 75-98.

Cunningham, C.W., Omland, K.E. & Oakley, T.H. (1998). Reconstructing ancestral states : a critical reappraisal. *Trends Ecol. Evol.* 13: 361-366.

Curtis, D.J. & Zaramody, A. (1998). Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz. Int. J. Primatol.* 19(5): 811-835.

Darwin, C. (1872). *The expression of the emotions in man and mammals.* Murray, London.

Dawkins, M.S. & Guiford, T. (1991). The corruption of honest signalling. *Anim. Behav.* 41: 865-873.

DeVore, I. (1979). A comparison of the ecology and behaviour of monkeys and apes. In: *Primate Ecology: Problem Oriented Field Studies* (R.W. Sussman, ed.). John Wiley & Sons, New York, pp. 343-361.

Duckworth, R.A., Mendonca, M.T. & Hill, G.E. (2001). A condition dependent link between testosterone and disease resistance in the house finch. *Proc. R. Soc. Lond.* B. 268: 2467-2472.

Dunbar, R.I.M. (1988). *Primate Social Systems.* Croom Helm, London.

Emlen, S.T. (1971). The role of song in individual recognition the indigo bunting. *Zeit. Tierpschychol.* 28: 241-246.

Eisenberg, J.F. (1978). Communication mechanisms in new world primates with special reference to vocalizations in the black spider monkey (*Ateles fusciceps robustus*). In: *Aggression, dominance, and individual spacing* (L. Krames, P. Pliner & T. Alloway, eds.). Plenum Press, New York, pp. 31-48.

Elowson, A.M., Snowdon, C.T., & Sweet, C.J. (1992). Ontogeny of trill and J-call vocalizations in the pygmy marmoset, *Cebuella pygmaea. Anim. Behav.* 43: 703-715.

Elowson, A.M., Tannenbaum, P.L. & Snowdon, C.T. (1991). Food-associated calls correlate with food preferences in Cotton-top tamarins. *Anim. Behav.* 42: 931-937.

Emlen, S.T. (1971). The role of song in individual recognition the indigo bunting. *Zeit. Tierpschychol.* 28: 241-246.

Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223

Epple, G. (1968). Comparative studies on vocalizations in marmoset monkeys. *Folia Primatol.* 8: 1-40

Estes, R.D. (1991). *The Behavior Guide to African Mammals.* University of California Press, USA.

Falls, J.B., & Brooks, R.J. (1975). Individual recognition by song in white-throated sparrows, II. effects of location. *Can. J. Zool.* 53: 1412-1420.

Fashing, P.J. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza): evidence for resource defense mediated through males and a comparison with other primates. Behav. Ecol. Sociobiol.* 50: 219-230.

Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* 125:1-15.

Fischer, J., Hammerschmidt, K., Cheney, D.L. & Seyfarth, R.M. (2001). Acoustic features of female baboon barks. *Ethology* 107: 33-54.

Fitch, W.T. & Hauser, M.D. (1995). Vocal production in non-human primates: acoustics, physiology and functional constraints on "honest" signalling. *Am. J. Primatol.* 37: 191-219.

Garland, T.J., Harvey, P.H. & Ives, A.R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Sys. Biol.* 4: 18-32.

Gautier-Hion, A. & Tutin, C.E.G. (1988). Simultaneous attacks by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatol.* 51: 149-151.

Genevois, F. & Bretagnolle, V. (1994). Male blue petrels reveal their body mass when calling. *Ethol. Ecol. Evol.* 6: 377-383.

Gibson, R.M. & Hoglund, J. (1992). Copying and sexual selection. *Trends Ecol. Evol.* 7: 229-231.

Giraldeau, L.-A., & Ydenberg, R. (1987). The centre-edge effect: the result of a war of attrition between territorial contestants? *Auk* 104: 535-538.

Gittins, S.P. & Raemaekers, J.J. (1980). Siamang, lar and agile gibbons. In: *Malayan forest primates: ten years' study in a tropical rain forest* (D.J. Chivers, ed.). Plenum Press, New York, pp. 63-105.

Gonzalez, G., Sorci, G., Smith, L.C. & deLope, F. (2001). Testosterone and sexual signalling in male house sparrows (*Passer domesticus*). *Behav. Ecol. Sociobiol.* 50: 557-562.

Gouzoules, H. & Gouzoules, S. (1989). Design features and developmental modification of pigtail macaque, *Macaca nemestrina*, agonistic screams. *Anim. Behav.* 37: 383-401.

Grafen, A. (1990). Biological signals as handicaps. *J. Theor. Biol.* 144: 517-546.

Grafen, A. (1991). Modelling in behavioural ecology. In: *Behavioural ecology: an evolutionary approach*, 3rd edition (J.R. Krebs & N.B. Davies, eds.). Blackwell Scientific Publications, Oxford, pp. 5-31.

Grant, J., Chapman, C. & Richardson, K. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behav. Ecol. Sociobiol.* 31: 149-161

Green, S.M. (1981). Sex differences and age gradations in vocalizations of Japanese and lion-tailed monkeys (*Macaca fuscata* and *Macaca silenus*). *Am. Zool.* 21: 165-183.

Griffin, D.R. (1981). *The Question of animal awareness.* The Rockefeller University Press, New York.

Groothuis, T.G.G. (1993). A comparison between development of bird song and development of other displays. *Neth. J. Zool.* 43: 172-192.

Gurmaya, K.J. (1986). Ecology and behavior of *Presbytis thomasi* in Northern Sumatra. *Primates* 27: 151-172.

Gursky, S. (2000). The effect of seasonality on the behaviour of an insectivorous primate, *Tarsius spectrum*. *Int. J. Primatol.* 21(3): 477-495.

Gyger, M., Karakashian, S. & Marler, P. (1986). Avian alarm calling: Is there an audience effect? *Anim. Behav.* 34: 1570-1572.

Halloy, M. & Kleiman, D.G. (1994). Acoustic structure of long calls in free-ranging groups of golden lion tamarins, *Leontopithecus rosalia*. *Am. J. Primatol.* 32: 303-301.

Hammerschmidt, K. & Fischer, J. (1998). The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. *Ethology* 104: 203-216.

Hammerschmidt, K., Newman, J.D., Champoux, M. & Suomi, S.J. (2000). Changes in rhesus macaque 'coo' vocalisations during early development. *Ethology* 106: 873-886.

Harcourt, A.H., Stewart, K.S. & Fossey, D. (1976). Male emigration and female transfer in wild mountain gorilla. *Nature* 263: 226-227.

Harcourt, A.H. (1979). Social relationships among adult female mountain gorillas. *Anim. Behav.* 27: 251-264.

Hare, J.F. (1998). Juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) manifest both littermate and neighbour.stranger discrimination. *Ethology* 104: 991-1002.

Harrington, F.H. & Mech, L.D. (1978). Wolf howling and its role in territory maintenance. *Behaviour* 68: 207-249.

Harvey, P.H. & Rambaut, A. (2000). Comparative analyses for adaptive radiations. *Proc. R. Soc. Lond.* B 355: 1-7.

Harvey, P.H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology.* Oxford University Press, Oxford.

Hauser, M.D. (1989). Ontogenetic changes in the comprehension and production of vervet (*Cercopithecus aethiops*) vocalizations. *J. Comp. Psychol.* 103: 149-158.

Hauser, M. (1993). The evolution of non-human primate vocalizations: effects of phylogeny, body weight and social context. *Am. Nat.* 142: 528-542.

Hausfater, G & Hrdy, S.B. (1984). *Infanticide. Comparative and evolutionary perrspectives.* Aldine Publishing Company, New York.

Henwood, K. & Fabrick, A. (1979). A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *Am. Nat.* 114: 260-274.

Herzog, M. & Hopf, S. (1983). Effects of species-specific vocalizations on the behaviour of surrogate-reared squirrel monkeys. *Behaviour* 86: 197-214.

Hill, C.M. (1994). The role of female diana monkeys, *Cercopithecus diana*, in territorial defence. *Anim. Behav.* 47: 425-431.

Hochberg, Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75: 800-802.

Hodun, A., Snowdon, C. T. & Soini, P. (1981). Subspecific variation in the long calls of the tamarin, *Saguinus fuscicollis. Zeit. Tierpsychol.* 57: 97-110.

Hohmann, G. (1991). Comparative analyses of age and sex specific patterns of vocal behaviour on four species of old world monkeys. *Folia Primatol.* 56: 133-136.

Hohmann, G. & Vogl, L. (1991). Loud calls of male Nilgiri langurs (*Presbytis johnii*): age-, individual-, and population-specific differences. *Int. J. Primatol.* 12: 503-524.

Hohmann, G. & Fruth, B. (1995). Loud calls in great apes: sex differences and social correlates. In: *Current topics in primate vocal communication* (E. Zimmerman, J.D. Newman & U. Jürgens, eds.). Plenum Press, New York, pp. 161-184.

Horn, A.D. (1987). The socioecology of the black mangabey (*Cercocebus atterimus*) near Lake Tumba, Zaire. *Am. J. Primatol.* 12: 218-236.

Horn, A.G., Leonard, M.L. & Weary, D.M. (1995). Oxygen consumption during crowing by roosters: talk is cheap. *Anim. Behav.* 50: 1171-1175.

Hrdy, S.B. (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus) of Abu, Rajasthan. Folia Primatol.* 22: 19-58.

Hrdy, S.B. (1979). Infanticide among animals: A review, classification and examenation of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* 1: 13-40.

Isbell, L.A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav. Ecol.* 2: 143-155.

Isbell, L.A, & van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* 133: 1-36.

Janson, C.H. (1992), Evolutionary ecology of primate social structure. In: *Evolutionary ecology and human behavior* (E.A. Smith & B. Winterhalder, eds.). Aldine de Gruyter, New York, pp. 95-130.

Janson, C.H. & Goldsmith, M.L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behav. Ecol.* 6: 326-336.

Jolly, A. (1966). *Lemur behaviour.* University of Chicago Press, Chicago.

Jolly, A. (1985). *The evolution of primate behavior.* 2nd edition, Mc Millan, New York.

Kappeler, M. (1984). Vocal bouts and territorial maintenance in the moloch gibbon. In: *The lesser apes* (H. Preuschoft, D.J. Chivers, W.Y. Brockelman, & N. Creel, eds.). Edinburgh University Press, Edinburgh, pp. 376-389.

Kinnaird, M.F. & O' Brien, T.G. (2000). Comparative movement patterns of two semi-terrestrial cercopithecine primates: the Tana River crested mangebey and the Sulawesi crested black macaque. In: *On the move: how and why animals travel in groups* (S. Boinski & P.A. Garber, eds.). University of Chicago Press, Chicago, pp. 327-350.

Kinzey, W.G. (1997). *New World Primates: Ecology, Evolution, and Behavior.* Aldine de Gruyter, New York.

Korstjens, A.H. (2001). *The mob, the secret sorority, and the phantoms: an analysis of the socio-ecological strategies of the three colobines of Taï.* PhD-thesis, Utrecht University.

Koski, S.E. (2000). *Individual and contextual variation in Thomas langur (Presbytis thomasi) loud call.* MSc study, Utrecht University

Kraus, C., Heistermann, M. & Kappeler, P.M. (1999). Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxii)? Physiol. Behav.* 66: 855-861.

Lambrechts, M.M. (1992). Male quality and playback in the great tit. In: *Playback and studies of animal communication* (P.K. McGregor, ed.). Plenum Press, New York.

Lawes, M.J. & Henzi, S.P. (1995). Inter-group encounters in blue monkeys: how territorial must a territorial species be? *Anim. Behav.* 49: 240-243.

Leighton, D.R. (1987). Gibbons: territoriality and monogamy. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 135-145.

Leiser, J.K. & Itzkowitz, M. (1999). The benefits of dear enemy recognition in three-contender convict cichlid (*Cichlasoma nigrofasciatum*) contests. *Behaviour* 136: 983-1003.

Leonard, M.L. & Horn, A.G. (1995). Crowing in relation to status in roosters. *Anim. Behav.* 49: 1283-1290.

Lieblich, A.K., Symmes, D., Newman. J. & Shapiro, M. (1980). Development of the isolation peep in laboratory-bred squirrel monkeys. *Anim. Behav.* 28: 1-9.

Lowen, C. & Dunbar, R.I.M. (1994). Territory size and defendability in primates. *Behav. Ecol. Sociobiol.* 35: 347-354

MacKinnon, J. (1974). The behaviour and ecology of wild orangutans (*Pongo pygmaeus*). *Anim. Behav.* 22 : 3-74.

Maddison, W.P. (1990). A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44: 539-557.

Maddison, W.P. & Maddison, D.R. (1992). *MacClade: analyses of phylogeny and character evolution.* Sinauer Associates, Sunderland MA.

Marler, P. (1972). Vocalisations of East African monkeys II: black and white colobus. *Behaviour* 42: 175-197.

Marler, P. & Hobbet, L. (1975). Individuality in a long-range vocalization of wild chimpanzee. *Zeit. Tierpsychol.* 38: 97-109.

Marler, P.M. & Mitani, J. (1988). Vocal communication in primates and birds: parallels and contrasts. In: *Primate vocal communication* (D. Todt, P. Goedeking & D. Symmes, eds.). Springer-Verlag, Berlin, pp. 3-14.

Marler, P. & Evans, C. (1996). Bird calls: just emotional displays or something more. *Ibis* 138: 26-33.

Marler, P.M., Dufty, A. & Pickert, R. (1986). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Anim. Behav.* 34: 194-198.

Marsh, C.W. (1979). Female transference and mate choice among Tana river red colobus. *Nature* 281: 568-569.

Martin. P. & Bateson, P. (1993). *Measuring Behaviour.* 2nd edition, Cambridge University Press, Cambridge.

Maynard Smith, J. (1991). Honest signalling: the Philip Sydney game. *Anim. Behav.* 42: 1304-1305.

McComb, K.E. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus. Anim. Behav.* 41: 79-88.

McComb, K., Packer, C., Pusey, A.E. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo. Anim. Behav.* 47: 379-387.

McComb, K., Pusey, A., Packer, C. & Grinnell, J. (1993). Female lions can identify potentially infanticidal males from thier roars. *Proc. R. Soc. Lond.* B. 252 : 59-64.

Mehta, C. & Patel, N. (1992). *Statxact-Turbo. Statistical software for exact nonparametric inference.* User Manual, Cambridge, Cytel Software Corporation.

Milton, K. & May, M.L. (1976). Body weight, diet and home range area in primates. *Nature* 259: 459-462.

Mitani, J.C. (1984). The behavioral regulation of monogamy in gibbons (*Hylobates muelleri). Behav. Ecol. Sociobiol.* 15: 225-229.

Mitani, J.C. (1985a). Sexual selection and adult male orangutan long calls. *Anim. Behav.* 33: 272-283.

Mitani, J.C. (1985b). Responses of gibbons (*Hylobates muelleri) to self, neighbor, and stranger song duets. Int. J. Primatol.* 6(2):193-200.

Mitani, J.C. (1990). Experimental field studies of Asian ape social systems. *Int. J. Primatol.* 11: 103-126.

Mitani, J.C. & Rodman, P.S. (1979). Territoriality: the relation of ranging patterns and home range size to defendability, with an analysis of territoriality among primates species. *Behav. Ecol. Sociobiol.* 5: 241-251.

Mitani, J.C. & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Anim. Behav.* 45:735-746.

Mitani, J.C., & Brandt, K.L. (1994). Social factors influence the acoustic variability in the long-distance calls if male chimpanzees. *Ehtology* 96: 233-252.

Muroyama, Y. & Thierry, B. (1998). Species differences of male loud calls and their perception in Sulawesi macaques. *Primates* 39(2): 115-126.

Newton, P.N. (1987). The social organisation of forest Hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.* 8: 199-232.

Norcross, J. & Newman, J. (1993). Context- and sex-specific differences in the acoustic structure of common marmoset (*Callithrix jacchus). Am. J. Primatol.* 30: 135-146.

Norcross, J., Newman, J. & Cofrancesco, L.M. (1999). Context and sex differences exist in the acoustic stucture of phee calls by newly-paired common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* 49: 165-181.

Nottebohm, F. (1999). The anatomy and timing of vocal learning in birds. In: *The design of animal communication* (M.D. Hauser & M. Konishi, eds..). MIT press, Cambridge MA, pp. 63-110.

Nunn, C.L. (1999). The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* 46: 1-13.

Nunn, C.L. (2000). Collective benefits, "free-riders", and male extragroup conflict. In: *Primate males: causes and consequences of variation in group composition* (P.M. Kappeler, ed.). University Press Cambridge, Cambridge, pp. 192-204.

Nunn, C.L. & Barton, R.A. (2000). Allometric slopes and independent contrasts: a comparative study of Kleiber's law in primate ranging patterns. *Am. Nat.* 156: 519-533.

Nunn, C.L. & van Schaik, C.P. (2000). Social evolution in primates: the relative roles of ecology and intersexual conflict. In: *Infanticide by males and its implications* (C.P. van Schaik & C.H. Janson, eds.). Cambridge University Press, Cambridge, pp. 388-419.

Nunn, C.L. & Barton, R.A. (2001). Comparative methods for studying primate adaptation and allometry. *Evol. Anthr.* 10: 81-98.

Nunn, C.L. & Lewis, R.J. (2001). Cooperation and collective action in animal behaviour. In: *Economics in Nature: The Evolutionary Biology of Economic Behaviour.* (R. Noë, J.A.R.A.M. van Hooff & P Hammerstein, eds.). Cambridge University Press, Cambridge, pp. 42-66.

Nunn, C.L. & C.P. van Schaik. (2001). Reconstructing the behavioral ecology of extinct primates. In: *Reconstructing behavior in the fossil record* (J.M. Plavcan, R.F. Kay & C.P. van Schaik, eds.). Plenum, New York, pp. 159-216.

Oates, J.F., Bocian, C.M. & Terranova, C.J. (2000). The loud calls of black-and-white colobus monkeys: their adaptive and taxonomic significane in light of new data. In: *Old world monkeys* (P.F. Whitehead & C.J. Jolly, eds.). Cambridge University Press, Cambridge, pp. 431-452.

Oates, J.F. & Troco, T.F. (1983). Taxonomy and phylogeny of black-and-white colobus monkeys: inferences from an analyses of loud call variation. *Folia Primatol.* 40: 83-113.

Omland, K.E. (1997). Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks. *Evolution* 51: 1636-1646.

Plavcan, M.J., van Schaik, C.P. & Kappeler, P.M. (1995). Competition, coalitions and canine size in primates. *J. Hum. Evol.* 28: 245-276.

Poirier, F.E. (1968). Niligiri langur (*Presbytis johnii*) territorial behavior. *Primates* 9: 351-364.

Pollock, J. (1986). The song of the indri (*Indri indri; Primates; Lemuroidea): natural history, form, and function. Int. J. Primatol.* 7: 225-264.

Prestwich, K.N. (1994). The energetics of acoustic signalling in anurans and insects. *Am. Zool.* 34: 625-643.

Price, T. (1997). Correlated evolution and independent contrasts. *Phil. Trans. R. Soc. Lond.* B 352: 519-529.

Preuschoft, H., Chivers, D., Brockelman, W. & Creel, N. (1984). *The Lesser Apes*, Edinburgh University Press, Edinburgh.

Purvis, A. (1995). A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond.* B 348: 405-421.

Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comp. Appl. Biosci.* 11: 247-251.

Pusey, A.E. & Packer, C. (1987). Dispersal and philopatry. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 250-266.

Qurin, R. (1980). Emission vocale de forte intensité chez *Cercocebus galeritus agilis*: structure, caractéristiques spécifiques et individuelles, modes d'émission. *Mammalia* 44: 35-50.

Raemaekers, J.J. & Raemaekers, P.M. (1984). The Ooaa duet of the gibbon (*Hylobates lar*). *Folia Primatol.* 42: 209-215.

Raemaekers, J.J. & Raemaekers, P.M. (1985). Field playback of loud calls to gibbons (Hylobates lar): territorial sex-specific and species-specific responses. *Anim. Behav.* 33: 481-493.

Randall, J.A. (1989). Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis. Anim. Behav.* 38: 620-630.

Rijksen, H. (1978). *A field study on Sumatran orang-utans (Pongo pygmaeus abelli, Lesson 1827): Ecology, Behaviour and Conservation.* Veenman, Wageningen.

Robinson, J.G., Wright, P.C. & Kinzey, W.G. (1987). Monogamous cebids and their relatives: intergroup calls and spacing. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 44-53.

Robson, C. (2000). *A Field Guide to the Birds of South-East Asia*, New Holland, London.

Rudran, R. (1973). Adult male replacement in one-male troops of purple-feced langurs (Presbytis senex senex) and its effects on population structure. *Folia Primatol.* 19: 166-192.

Ruhiyat, Y. (1983). Socio-ecological study of *Presbytis aygula* in West-Java. *Primates* 24: 344-359.

Ryan, M.J. (1985). *The Tungara frog.* University of Chicago Press, Chicago.

Ryan, M.J. (1988). Energy, calling, and selection. *Am. Zool.* 28: 885-898.

Ryan, M.J. & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* 139: S4-S35.

Schaller, G.B. (1963). *The mountain gorilla: ecology and behaviour.* University of Chicago Press, Chicago.

Searcy, W.A. (1992). Song repertoire and mate choice in birds. *Am. Zool.* 32: 71-80.

Searcy, W.A. & Andersson, M. (1986). Sexual selection and the evolution of song. *An. Rev. Ecol. Sys.* 17: 507-533.

Searcy, W.A. & Yasukawa, K. (1996). Song and female choice. In: *Ecology and Evolution of Acoustic Communication in Birds* . (D.E. Kroodsma & E.H. Miller, eds.). Cornell, University Press, Ithaca.

Sekulic, R. (1982). The function of howling in red howler monkeys (*Alouatta seniculus*). *Behaviour* 81: 38-54.

Seyfarth, R.M. & Cheney, D.L. (1986). Vocal development in vervet monkeys. *Anim. Behav.* 34: 1640-1658.

Seyfarth, R. & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Anim. Behav.* 40: 754-764.

Seyfarth, R.M. & Cheney, D.L. (1997). Some general features of vocal development in nonhuman primates. In: *Social influences on vocal development* (C.T. Snowdon & M. Hausberger, eds.). Cambridge University Press, Cambridge, pp. 249-273.

Seyfarth, R.M. & Cheney, D.L. (1999). Production, usage, and response in nonhuman primate vocal develoment. In: *The design of animal communication* (M.D. Hauser & M. Konishi, eds.). MIT press, Cambridge MA, pp. 392-417.

Seyfarth, R., Cheney, D. & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free ranging primate. *Anim. Behav.* 28: 1070-1094.

Seyfarth, R.M., Cheney, D.L. & Marler, P.M. (1980). Monkey response to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210: 801-803.

Sherman, P.W. (1977). Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253 (1977).

Siegel, S. & Castellan, N.J.jr. (1988). *Nonparametric statistics for the behavioral sciences.* McGraw-Hill Book Co, Singapore.

Smith, R.J. & Jungers, W.L. (1997). Body mass in comparative primatology. *J. Hum. Evol.* 32: 523-559.

Smuts, B.B. (1987). Sexual competition and mate choice. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 385-399.

Smuts, B.B. & Smuts, R.W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Study Behav.* 22: 1-63.

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T. (1987). *Primate Societies.* University of Chicago Press, Chicago.

Sokal, R.R. & Rohlf, F.J. (1995). *Biometry.* W. H. Freeman and Company, New York.

Snowdon, C.T. (1988). Communications as social interactions: its importance in ontogeny and adult behaviour. In: *Primate vocal communication* (D. Todt, P. Goedeking & D. Symmes, eds.). Springer-verlag, New York, pp. 108-122.

Snowdon, C.T. & Cleveland, J. (1980). Individual recognition of contact calls by pygmy marmosets. *Anim. Behav.* 28: 717-727.

Snowdon, C.T. & Elowson, A.M. (1992). Ontogeny of primate vocal communication. In: *Topics in primatology*, Volume 1. (T. Nishida, W.C. McGrew, P. Marler, M. Pickford & F.B.M. de Waal, eds.). University of Tokyo Press, Tokyo, pp. 279-290.

Snowdon, C.T., Elowson, A.M. & Roush, R.S. (1997). Social influences on vocal development in new world primates. In: *Social influences on vocal development* (C.T. Snowdon & M. Hausberger, eds.). Cambridge University Press, Cambridge, pp. 235-248.

Stanford, C.B. (1991). Social dynamics of intergroup encounters in the capped langur (*Presbytis pileata), Am. J. Primatol.* 25: 35-47.

Starin, E.D. (1994). Philopatry and affiliation among red colobus. *Behaviour* 130: 253-270.

Steenbeek, R. (1999a). *Female choice and male coercion in wild Thomas's langurs.* PhD thesis, Utrecht University.

Steenbeek, R. (1999b). Tenure related changes in wild Thomas's langurs I: between-group interactions. *Behaviour* 136: 595-625.

Steenbeek, R. (2000). Infanticide by males and female choice in wild Thomas's langurs. In: *Infanticide by males and its implications.* (C.P. van Schaik & C.H. Janson, eds.). Cambridge University Press, Cambridge. Pp. 153-177.

Steenbeek, R. & Assink, P. (1998). Individual differences in long-distance calls of male Thomas langurs (*Presbytis thomasi*). *Folia Primatol.* 69: 77-80.

Steenbeek, R., & Schaik, C.P. van. (2001). Competition and group size in Thomas's langurs: the folivore paradox revisited. *Behav. Ecol. Sociobiol.* 49: 100-110.

Steenbeek, R., Assink, P. R. & Wich, S.A. (1999). Tenure related changes in wild Thomas's langurs II: loud calls. *Behaviour* 136: 627-650.

Steenbeek, R., Sterck, E.H.M., de Vries, H., & van Hooff, J.A.R.A.M. (2000). Costs and benefits of the one-male, age-graded and all-male phase in wild Thomas's langur groups. In: *Primate males* (Kappeler, P. M. ed.). Cambridge University Press, Cambridge, pp. 130-145.

Sterck, E.H.M. (1995). *Females, foods and fights: a socioecological comparison of the sympatric Thomas langur and long tailed macaque.* PhD thesis, Utrecht University.

Sterck, E.H.M. (1997). Determinants of female dispersal in Thomas langurs. *Am. J. Primatol.* 42: 179-198.

Sterck, E.H.M. (1998). Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? *Am. J. Primatol.* 44: 235-254.

Sterck, E.H.M. & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour* 134: 749-774.

Sterck, E.H.M. & Korstjens, A.H. (2000). Female dispersal and infanticide in primates. In: *Infanticide by Males and Its Implications* (C.P. van Schaik & C.H. Janson, eds.). Cambridge University Press, Cambridge, pp. 293-321.

Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997). The evolution of female choice relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* 41: 291-309.

Stewart, K.J. & Harcourt, A.H. (1987). Gorilla: variation in female relationships. In: *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). Chicago University Press, Chicago, pp. 155-164.

Stoddard, P.K. (1996). Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma, & E.L. Miller, eds.). Cornell Press, New York, pp. 356-374.

Struhsaker, T.T. (1967). Auditory communication in vervet monkeys. In: *Social Communication among Primates* (S.A. Altmann, ed.). University of Chicago Press, Chicago, pp. 281-324.

Struhsaker, T.T. & Leland, L. (1987). Colobines: infanticide by adult males. In: *Primate Societies* (B.B. Smuts, D.L., Cheney, R.M., Seyfarth, R.W. Wrangham & T.T. Struhsaker, eds.). University of Chicago Press, Chicago, pp. 83-97.

Teixidor, P. & Byrne, R.W. (1997). Can spider monkeys (*Ateles geoffroyi*) discriminate vocalisations of familiar individuals and stragers? *Folia Primatol.* 68: 254-264.

Teixidor, P. & Byrne, R.W. (1999). The whinny of spider monkeys: individual recognition before situational meaning. *Behaviour* 136: 279-308.

Tenaza, R.R. (1975). Territory and monogamy in Kloss gibbons (*Hylobates klossi*) in Siberut island, Indonesia. *Folia Primatol.* 24: 60-80.

Tenaza, R. (1976). Songs and related behaviour of Kloss' gibbon (*Hylobates klossi*) in Siberut Island, Indonesia. *Zeit. Tierpsychol.* 40: 37-52.

Tenaza, R.R. (1989). Intergroup calls of male pig-tailed langurs (*Simias concolor*). *Primates* 30: 199-206.

Terborgh, J. (1983). *Five new world primates.* Princeton University Press, Princeton.

Terborgh, J. & Janson, C.H. (1986). The sociobiology of primate groups. *An. Rev. Ecol. Syst.* 17: 111-135.

Thomas, L. & Juanes, F. (1996). The importance of statistical power analysis: an example from Animal Behaviour. *Anim. Behav.* 52: 856-859.

Tilson, R.L. & Tenaza, R.R. (1976). Monogamy and duetting in an old world monkey. *Nature* 263: 230-231.

Titze, I.R. (1994). *Principles of voice production.* Prentice Hall, Englewood Cliffs.

Treves, A. & Chapman, C.A. (1996). Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. *Behav. Ecol. Sociobiol.* 39: 43-53.

Utami, S. & Mitra Setia, T. (1995). Behavioral changes in wild male and female Sumatran orangutans (*Pongo pygmaeus abelii*) during and following a resident male take-over. In: *The Neglected Ape* (R.D. Nadler, B.F.M. Galdikas, L.K. Sheeran & N. Rosen, eds.). Plenum Press, New York, pp. 183-190.

Van der Post, D.J. (2001). *Tenure related changes in male Thomas langur (Presbutis thomasi) loud call characteristics.* MSc study, Utrecht University.

Van Hooff, J.A.R.A.M. & van Schaik, C.P. (1992). Cooperation in competition: the ecology of primate bonds. In: *Coalition and alliances between humans and other animals.* (A.H. Harcourt & F.B.M. de Waal, eds.). Oxford University Press, Oxford, pp. 357-389.

Van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120-144.

Van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. In: *Comparative Socioecology* (V. Standen & R.A. Foley, eds.). Blackwell Press, Oxford, pp. 195-218.

Van Schaik, C.P. (1996). Social evolution in primates: the role of ecological factors and male behaviour. *Proc. Brit. Ac.* 88: 9-31.

Van Schaik, C.P. (2000). Social counterstrategies against infanticide by males in primates and other mammals. In: *Primate Males* (P.M. Kappeler, eds.). Cambridge University Press, Cambridge, pp. 34-52.

Van Schaik, C.P. & Mirmanto, E. (1985). Spatial variation in the structure and litterfall of a Sumatran rainforest. *Biotropica* 17: 196-205.

Van Schaik, C.P. & Kappeler, P.M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proc. Roy. Soc. Lond.* B. 264: 1687-1694.

Van Schaik, C.P. & Janson, C.H. (2000). *Infanticide by males and its implications.* Cambridge University Press, Cambridge.

Van Schaik, C.P., Assink, P. & Salafsky, N. (1992). Territorial behavior in south-east Asian langurs: Resource defence or mate defence? *Am. J. Primatol.* 26: 233-242.

Vercauteren Drubbel, R. & Gautier, J-P. (1993). On the occurrence of nocturnal and diurnal loud calls, differing in structure and duration, in red howlers (*Aloutta seninculus*) in French Guyana. *Folia Primatol.* 60:195-209.

Waser, P.M. (1977). Individual recognition, intragroup cohesion and intergroup spacing: evidence from sound playback to forest monkeys. *Behaviour* 60: 28-74.

Waser, P.M. & Waser, M.S. (1977). Experimental studies of primate vocalisations: specializations for long distance propagation. *Zeit. Tierpsychol.* 43: 239-263.

Waser, P.M. & Brown, C.H. (1986). Habitat acoustics and primate communication. *Am. J. Primatol.* 10:135-154.

Wasser, S.K., Risler, L. & Steiner, R.A. (1988). Excreted steroids in primate feces over the menstrual cycle and pregnancy. *Biol. Reprod.* 39: 862-872.

Watts, D.P. (1989). Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81: 1-18.

Watts, D.P. (1990). Ecology of gorillas and its relation to female transfer in mountain gorillas. *Int. J. Primatol.* 11: 21-45.

Watts, D.P. (1992). Social relationships of immigrant and resident demale mountain gorillas I: male-female relationships. *Am. J. Primatol.* 28: 159-181.

Weeden, J.S. & Falls, J.B. (1959). Differential response of male ovenbirds to recorded songs of neighbouring and more distant individuals. *Auk* 76: 343-351.

Whitehead, J.M. (1987). Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta plliata palliata. Anim. Behav.* 35: 1615-1627.

Whiting, M. J. (1999). When to be neighbourly: differential agonistic responses in the lizard Platysaurus broadleyi. *Behav. Ecol. Sociobiol.* 46: 210-214.

Whitten, A. (1980). *The Kloss gibbon in Siberut rain forest.* PhD-thesis, University of Cambridge.

Whitten, A. (1982). The ecology of singing in the kloss gibbons (*Hylobates klossii*) on Siberut island, Indonesia. *Int. J. Primatol.* 3: 33-51.

Wich, S.A., Assink, P.R., Becher, F. & Sterck, E.H.M. (2002a). Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. *Behaviour* 139: 65-78.

Wich, S.A., Assink, P.R., Becher, F. & Sterck, E. H. M. (2002b). Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. *Behaviour* 139: 79-87.

Wich, S.A. & Nunn, C.L. (in review). Do male "loud calls" function in mate defense? A comparative study of long-distance calls in primates. *Behav. Sociobiol. Ecol.*

Wich, S.A., Koski, S., de Vries, H. & van Schaik, C. P. (in review). Individual and contextual variation in Thomas langur male loud calls. *Ethology*

Wilson, M.L., Hauser, M.D. & Wrangham, R.W. (2001). Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim. Behav.* 61:1203-1216.

Winter, P., Handley, P., Ploog, D. & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour* 47: 230-239.

Wrangham, R.W. (1977). Behaviour of feeding chimpanzees in the Gombe National Park, Tanzania. In: *Primate ecology* (T.H. Clutton-Brock, ed.). Academic Press, London, pp. 503-538.

Wrangham, R.W. (1979). On the evolution of ape social systems. *Soc. Sci. Inf.* 18: 335-368.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262-300.

Ydenberg, R., Giraldeau, L. & Falls, J. (1988). Neighbours, strangers and the asymmetric war of attrition. *Anim. Behav.* 36: 343-347.

Zahavi, A. (1975). Mate selection-a selection for a handicap. *J. Theor. Biol.* 53: 205-214.

Zahavi, A. (1977). The cost of honesty. *J. Theor. Biol.* 67: 603-605.

Ziegler, T., Hodges, J.K., Winkler, P. & Heistermann, M. (2000). Hormonal correlates of reproductive seasonality in wild female Hanuman langurs (*Presbytis entellus*). *Am. J. Primatol.* 51: 119-134.

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, Cercopithecus campbelli. *Behav. Ecol. Sociobiol.* 50: 414-422.

Zuberbühler, K., Noë, R. & Seyfarth, R. M. (1997). Diana monkey long-distance call: messages for conspecifics and predators. *Anim. Behav.* 53: 589-604.

Zuberbühler, K., Jenny, D. & Bshary, R. (1999). The predator deterrence function of primate alarm calls. *Ethology* 105:477-490.

Samenvatting

In het algemeen beschikken de meeste apensoorten over een aantal vershillende soorten roepen, waarvan de luide roep het meest opvallend is omdat deze over een lange afstand kan worden gehoord. In het algemeen worden luide roepen door mannetjes in verschillende situaties gegeven. Mannetjes kunnen luide rpeoepn geven om vrouwtjes aan te trekken, om andere mannetjes af te schrikken, om andere groepsgenoten te waarschuwen dat er een predator nabij is, om de predator te laten weten dat hij gezien is door de apen, en om de ruimtelijke verdeling tussen groepen te regelen.. Het doel van deze studie is het analyseren van de structuur en het bepalen van de functie van de luide roep van de Thomas langoer (Presbytis thomasi) mannetjes.

De Thomas langoer is een middelgrootte aap die leeft in de tropische wouden van het noorden van Sumatra, Indonesië. Deze dieren eten voornamelijk blad en onrijp fruit en komen voor in gemende groepen van één mannetje met meerdere vrouwtjes en hun nakomelingen. Groepen bestaande uit onvolwassen en net volwassen mannetjes komen ook voor, evenals solitaire mannetjes. Individuen van beide sekses verhuizen tussen groepen. Mannetjes verhuizen meestal vlak voordat ze volwassen worden naar een groep die alleen uit mannetjes bestaat. Vrouwtjes, daarentegen, kunnen op twee manieren aan een nieuw mannetje komen. De eerste mogelijkheid is verhuizen van hun huidige groep naar een andere groep of met een solitair mannetje een nieuwe groep vormen. De tweede mogelijkheid is dat een mannetje van buiten de groep het huidige mannetje uit de groep jaagt en alle vrouwtjes overneemt. Ook zou het zo kunnen zijn dat mannetjes proberen infanticide te plegen om vrouwtjes naar hun toe te lokken, omdat het laat zien dat het huidige mannetje geen goede beschermer van de kinderen is.

Thomas langoer mannetjes hebben vier verschillende volwassen levensfases. Allereerst de fase waarin zij in zich in een groep met uitsluitend andere mannetjes bevinden. Daarna verkrijgt een mannetje op een van de hierboven beschreven manieren vrouwtjes en is dan in de zogehete vroege fase. Als vrouwtjes dan op een gegeven moment kinderen krijgen gaat het mannetje over in naar zijn middelste fase. De laatste levensfase van een mannetje is gelijk

aan het laatste jaar dat de groep bestaat. In deze laatste fase verhuizen de vrouwtjes uit de groep naar een ander mannetje. Hierna blijft vaak een mannetje achter met zijn mannelijk nageslacht in een zogehete mannengroep.

Een van de centrale vragen in het begrijpen van de sociale organisatie van de Thomas langoer is wat de factoren zijn die de keuze van een vrouwtje voor een nieuw mannetje bepalen en ook het moment waarop vrouwtjes dit doen. Thomas langoer vrouwtjes maken meerdere keuzes indien zij verhuizen naar een ander mannetje. De eerste keuze die ze maken betreft wanneer ze hun huidige mannetje gaan verlaten. Deze keuze zou kunnen samenhangen met wanneer het huidige mannetje kracht verliest en niet meer in staat is de kinderen te beschermen tegen infanticidale mannetjes van buiten de groep. Wanneer vrouwtjes de keuze om te gaan verhuizen eenmaal gemaakt hebben, volgt de tweede keuze: de vrouwtjes kiezen een nieuw mannetje uit de buurmannetjes of solitaire mannetjes. Aangezien het feit dat de overlevingskansen van kinderen in de eerste geboorte groep bij een nieuw mannetje hoger zijn dan die uit de laatste geboorte groep bij het oude mannetje (hoofdstuk negen), geeft duidelijk aan dat het op tijd verhuizen geen triviale aangelegenheid is voor vrouwtjes en hun kinderen.

Voor een aantal diersoorten, waaronder apen, is voorgeteld dat vrouwtjes de roepen van mannetjes gebruiken om te bepalen of een man van goede kwaliteit. In apen is een verband tussen de roepen van mannetjes, keuze van vrouwtje en een verband tussen kwaliteit en de luide roepen van mannetjes nog nooit aangetoond.

Dit is wellicht niet zo vreemd omdat apen over heet algemeen lang leven en in complexe samenlevingsvormen voorkomen in woongebieden waar het verzamelen van gegevens lastig is. Ook zijn er ethische redenen waardoor bepaalde experimenten zoals die met andere diersoorten gebeuren niet met apen gedaan mogen worden. Deze factoren maken het bestuderen van de vocale communicatie en de relatie daarvan met mannelijke kwaliteit en vrouwelijke keuze des te meer een uitdaging

Een van de voorwaardes aan de luide roep van mannetjes om van belang te zijn in het aantrekken van vrouwtjes is dat er akoestische variatie tussen de mannetjes is wat betreft de luide roep. Alleen wanneer er akoestische variatie in de luide roep is kunnen vrouwtjes deze gebruiken om tussen verschillende mannetjes te kiezen. In het tweede hoofdstuk laat ik zien dat er variatie is verschillende akoestische karakteristieken in de luide roepen van mannetjes en dat de luide roep ook verschilt in verschillende contexten zoals de ochtendroep en alarmroep. In elk geval geeft de variatie in de roepen tussen mannetjes dan de vrouwtjes een mogelijkheid om te keizen voor mannetjes op basis van variatie in hun roep.

Eerder onderzoek aan de Thomas langoer toonde aan dat mannetjes verschillen in kracht tussen verschillende levensfases en dat hun kracht lager is in de laatste fase. In dat onderzoek werd het leven van een mannetje ingedeeld in vier levensfasen. In de eerste fase leeft het mannetje nog in een groep met alleen maar andere mannetjes en is pas net volwassen. In de tweede fase start een mannetje een groep door met vrouwtjes samen te gaan leven. In de derde fase leeft een mannetje in een groep met vrouwtjes en hun nakomelingen en in laatste levensfase verlaten de vrouwtjes het mannetje om naar een nieuw mannetje te gaan. Het derde hoofdstuk laat zien dat er weinig variatie is in de luide roep van mannetjes tussen de drie laatste levensfasen, maar dat de luide roep van pas volwassen mannetjes die solitair leven of in groepen met slechts andere mannetjes wel duidelijk te onderscheiden is van die van mannetjes in de andere drie levensfases. Het belangrijkste verschil is dat de luide roep van pas volwassen mannetjes korter is dan die van de mannetjes in de andere drie levensfases. Dit geeft aan vrouwtjes de luide roep van mannetjes niet kunnen gebruiken om te beslissen wanneer ze hun huidige mannetje moeten verlaten, maar wel om een pas volwassen mannetjes te kiezen aangezien deze verschillen wat betreft zijn luide roep van de andere mannetjes.

In de rest van dit proefschrift evalueer ik de verschillende hypotheses voor de functie van de luide roep van de Thomas langoer mannetjes. In het algemeen kan de luide roep van apen verschillende functies hebben zoals het beschermen van het leefgebied tegen andere mannetjes, het beschermen van de vrouwtjes tegen andere manntjes, of het aantrekken van vrouwtjes. Om deze functies te evalueren voor apen in het algemeen heb ik samen met C. Nunn in hoofdstuk vier een vergelijkende studie gedaan naar de functie van de luide roep van mannetjes apen. Deze analyses tonen aan dat er geen functie is die voor alle apensoorten het wel of niet bezitten van een luide roep verklaart. Het blijkt dat mannetjes die in soorten leven waarin verdediging van het woongebied plaatsvindt en/of vrouwtjes tussen groepen verhuizen in het algemeen wel over een luide roep beschikken en dat mannetjes in soorten waarin geen verdediging van het woongebied plaatsvindt en/of de vrouwtjes niet verhuizen tussen groepen niet over een luide roep beschikken.

Maar ook blijken factoren zoals lichaamsgewicht, soort woongebied, en activiteitspatroon van invloed op het wel of niet bezitten van een luide roep.

Om beter inzicht te verkrijgen in de functie van de luide roep bij de Thomas langoer heb ik verschillende terugspeelexperimenten verricht. Bij dit soort experimenten worden eerder opgenomen luide roepen van mannetjes teruggespeeld door middel van een luidspreker die in het bos geplaatst is. Deze terugspeelexperimenten worden in het algemeen gebruikt om te bestuderen welke invloed de locatie van de luide roep op de reactie van apen heeft. Ook kunnen terugspeelexperimenten gebruikt worden om te bepalen of apen anders reageren op luide roepen van verschillende mannetjes.

In hoofdstuk vijf test ik of de luide roep van invloed is op de reisroute van Thomas langoer groepen ten opzichte van andere groepen. Tevens test ik of de luide roep van invloed is op het beschermen van voedselbronnen dan wel vrouwtjes. Ik verwachtte dat als de bronbeschermhypothese waar is mannetjes sterker reageren op het terugspelen van een luide roep van een buurman uit het centrum van zijn (de testgroep) leefgebied dan van de rand ervan. Als de vrouwtjesbescherm hypothese waar is dan zouden mannetjes overal in hun leefgebied even sterk moeten reageren op het terugspelen van een roep van een buurman. De experimenten tonen aan dat mannetjes sterker reageren met meer luide roepen en dichter naderen van de luidspreker op het terugspelen van een luide roep uit het centrum van hun leefgebied dan van de rand van hun leefgebied. Dit steunt de bronbeschermhypothese. Vrouwtjes naderen de positie van de luidspreker ook meer en sneller na het horen van een luide roep uit het centrum van hun leefgebied. Dit steunt het idee dat voedselbronnen belangrijk zijn voor vrouwtjes. Omdat het wel of niet naderen van de luidspreker afhangt van de positie van het terugspelen van de luide roep is de luide roep kennelijk ook van invloed op de positionering van de groepen ten opzichte van elkaar.

Om de bronbeschermhypothese verder te testen heb ik ook bekeken of de reactie van een testgroep verschilt wanneer deze zich wel of niet in een boom met voedsel bevind wanner de luide roep van een buurman teruggespeeld werd. Het valt te verwachten dat wanneer de bronbeschermhypothese waar is, er meer verdediging van de boom plaatsvindt wanneer de apen in een boom met voedsel zitten. Het bleek echter dat mannetjes even sterk reageren in beide situaties, maar dat vrouwtjes de luidspreker sneller naderen als ze zichzelf in een boom met voedsel bevinden. Dit steunt de hypothese dat voedselbronnen belangrijker zijn voor vrouwtjes dan mannetjes.

In hoofdstuk zes richt ik me op de vraag of Thomas langoeren de luide roep van verschillende mannetjes kunnen onderscheiden. Dit doe ik door luide roepen van bekende en onbekende mannetjes terug te spelen aan de testgroepen. Onbekende mannetjes zijn vertonen vaak meer agressief en infanticidaal gedrag dan bekende mannetjes. Wanneer deze mannetjes verschillen in hun luide roep dan zou er een verschil kunnen zijn in reactie van de testgroepen. Ik verwacht dat de luide roep van een bekend mannetje tot minder reactie zal leiden dan die van een onbekend mannetje omdat een bekend mannetje nauwelijks een infanticide risico vormt. Het zou voor een mannetje dus voordelig zijn wanneer hij aan de luide roep kan horen of het om een bekend (weinig infanticidaal) en onbekend (mogelijkerwijs infanticidaal). De resultaten van de experimenten laten zien dat mannetjes meer luide roepen geven, meer op hun hoede waren, en de luidspreker dichterbij naderden nadat de luide roep van een onbekende mannetje teruggespeeld was dan na het terugspelen van de roep van een bekende mannetje. Ook vrouwtjes maken onderscheid, want ze verstoppen zich na het horen van de luide roep van onbekende mannetjes en niet na het horen van de roep van bekende mannetjes. Verder verkleint de afstand tussen moeder en kind vaker na het terugspelen van de onbekende dan de bekende luide roep wat er op wijst dat vrouwtjes na de onbekende luide roep hun kinderen beter willen beschermen. Dus het lijkt erop dat Thomas langoren onderscheid kunnen maken tussen bekende en onbekende mannetjes.

Om in meer detail te onderzoeken of het verdedigen van kinderen gerelateerd is aan terugspelen van luide roepen heb ik groepen luide roepen teruggespeeld van onbekende pas volwassen mannetjes en van al lang volwassen mannetjes (hoofdstuk zeven). Pas volwassen mannetjes hebben een kortere luide roep dan al lang volwassen mannetjes. Ook zijn pas volwassen mannetjes vaker infanticidaal dan al lang volwassen mannetjes. Dit is te verklaren uit het feit dat pas volwassen mannetjes meestal nog geen vrouwtjes om zich heen hebben en er dus baat bij hebben door middel van infanticide vrouwtjes naar zich toe te lokken. Dus verwacht ik dat het terugspelen van de luide roep van pas volwassen mannetjes tot een sterkere reactie zal leiden van de mannetjes en een meer voorzichtiger reactie van vrouwtjes dan het terugspelen van een al lang volwassen mannetje. Alle luide roepen in dit experiment waren afkomstig van onbekende mannetjes. De resultaten van dit experiment laten duidelijk zien dat mannetjes meer zoekgedrag vertonen en vrouwtjes voorzichtiger zijn na het terugspelen van een luide roep van pas volwassen mannetjes dan van al lang volwassen mannetjes. Het lijkt er dus op dat Thomas langoeren verschillen in loud calls kunnen waarnemen en er adequaat op reageren.

Twee andere veel genoemde functies van de luide roep zijn dat deze fungeert als een alarm roep om een roofdier te laten weten dat deze gezien is of om soortgenoten te laten weten dat er een roofdier in de buurt is en er dus gevaar dreigt. Om deze functie te onderzoeken heb ik de langoeren blootgesteld aan een nep tijgervel en een gestreept laken. De Thomas langoeren reageren met luide roep en andere alarm roepen wanneer ze blootgesteld worden aan het nep tijgervel maar niet als na het gestreepte laken. Dit toont aan dat de luide roep ook een alarm functie heeft. Echter solitaire mannetjes gaven geen luide roepen wanneer ze het nep tijgervel zagen, terwijl mannetjes in groepen met vrouwtjes dit wel deden. Dit geeft ook nog eens aan dat de luide roep van mannetjes gericht is op groepsgenoten en niet zozeer op de predator.

Een van de problemen om in de Thomas langoer te bepalen hoe belangrijk de luide roep is voor de keuze van vrouwtjes is dat het niet mogelijk is om directe experimenten te doen. Dit is een gevolg van het feit dat vrouwtjes vrijwel direct overstappen van groep naar groep wanneer ze verhuizen en dus niet een bepaalde tijd solitair leven. Als gevolg daarvan neem ik in hoofdstuk negen een indirecte route om dit vraagstuk op te lossen. In dit hoofdstuk word bekeken welke factoren het verhuizen van vrouwtjes naar een ander mannetje met groep of solitair mannetje bepalen. Hypotheses voor het verhuizen van vrouwtjes zijn het verminderen van predatie risico door te verhuizen naar een grotere groep, het verminderen van voedsel competitie door te verhuizen naar een kleinere groep of vrouwelijke keuze door te keizen voor het beste mannetje wat er in de buurt is. Analyse van 13 jaar gegevens van de Ketambe Thomas langoer groepen laten zien dat de voedselconcurrentie en predatievermindering geen invloed hebben op de verhuiskeuze van vrouwtjes. Want vrouwtjes laten geen voorkeur voor kleine of grootte groepen zien wanneer ze verhuizen maar ze verhuizen naar het jongste volwassen mannetje dat beschikbaar is. Jonge mannetjes hebben een lange carrière voor de boeg en kunnen dus waarschijnlijk nog lang kinderen beschermen. Vrouwtjes kunnen deze mannetjes makkelijk vinden, omdat ze een kortere luide roep hebben dan al lang volwassen mannetjes. Het lijkt er dus op dat vrouwtjes de ontwikkeling van de luide roep van de mannetjes gebruiken om een jong mannetje mee te selecteren

Ondanks dat vrouwtjes de luide roep dus kunnen gebruiken om te bepalen naar welke mannetjes ze willen verhuizen, kunnen ze de luide roep niet gebruiken om te bepalen wanneer ze hun huidige mannetje moeten verlaten. De luide roep veranderd weinig nadat een mannetje eenmaal volwassen is en is daarmee een slechte indicator om te kiezen om te bepalen wanneer een mannetje een minder goede beschermer voor een vrouwtje en haar kinderen gaat worden. Dit is echter mogelijk niet problematisch voor een vrouwtje omdat ze constant bij haar huidige mannetje is en dus veel informatie kan vergaren over zijn conditie en dus ook aan de hand daarvan kan bepalen wanneer deze afneemt en het eigen mannetje geen goede beschermer van de nakomelingen meer is.

Als indicatoren kan een vrouwtje bijvoorbeeld het feit nemen dat een mannetje minder agressie naar andere groepen vertoont in zijn laatste levensfase dan in eerdere fases en ook dat het erop lijkt dat er meer agressie is van andere mannetjes naar een mannetje in zijn laatste levensfase dan in eerdere levensfases. Ook zou een vrouwtje de kindersterfte kunnen gebruiken als indicator voor de conditie van haar huidige mannetje want deze is hoger tijdens de laatste levensfase van een mannetje dan tijdens de andere levensfases van het mannetje.

Al met al kan dus geconcludeerd worden dat vrouwtjes gedragingen gebruiken van het huidige mannetjes om te bepalen wanneer ze een mannetje moeten verlaten en dat vrouwtjes de luide roep gebruiken om voor een jong mannetje te kiezen. Vervolg onderzoek moet echter uitwijzen hoe vrouwtjes kiezen tussen verschillende jonge mannetjes en of de luide roep daarbij een rol speelt.

Ringkasan

Penelitian ini bertujuan untuk menjelaskan struktur suara seruan keras (loud calls) kedih (Thomas langur) jantan dan fungsinya dalam organisasi sosial kedih.

Kedih berukuran tubuh sedang, bergerak di pohon dan pemakan daun serta buah (Sterck 1995) yang hidup dalam tiga kelompok sosial: kelompok yang berlainan jenis kelamin, kelompok semua jantan dan jantan tunggal/sendirian (Sterck 1997; Steenbeek 1999a). Kelompok yang berlainan jenis kelamin, umumnya terdiri dari satu jantan residen dan beberapa betina yang biasanya disertai oleh beberapa anak-anak mereka. Baik betina maupun jantan menyebar dari kelompok asalnya, betina juga dijumpai sering berpindah-pindah (Sterck 1997; Steenbeek 1999a; Sterck dan Korstjens 2000). Bergabungnya betina dengan jantan baru terjadi dalam dua cara. Pertama, mereka dapat bergabung ke kelompok berlainan jenis kelamin yang ada (atau jantan tunggal/sendirian) atau ke-dua, mereka berada di kelompok yang baru saja diambil alih oleh jantan baru. Kedih jantan akan mengalami empat tingkat kehidupan yang berbeda setelah meninggalkan kelompok tempat dia dilahirkan. Pertama mereka akan tinggal pada kelompok semua jantan sebelum mereka dapat membentuk kelompok (berlainan kelamin)nya sendiri. Pada masa awal terbentuknya kelompok baru, jantan dikatagorikan ada pada permulaan masa jabatan (tenure)nya. Tahap dimana beberapa betina bergabung dengan jantan pembiak baru. Masa pertengahan jabatan, dimulai pada saat betina-betina mulai bereproduksi dan anak pertama lahir. Sedangkan pada akhir masa jabatan, betina mulai meninggalkan jantan tersebut untuk bergabung dengan jantan pembiak baru. Kejadian terakhir ini seringkali berakhir dengan terbentuknya kelompok semua jantan yang terdiri dari jantan pembiak lama beserta keturunan jantannya (Steenbeek dkk.2000).

Di dalam pendahaluan saya mengemukakan pendapat bahwa, betina-betina harus membuat dua pilihan besar pada waktu mempertimbangkan untuk pindah ke kelompok baru. Pertama, bagaimana menentukan apakah jantan residen yang sekarang mulai hilang kekuatan dan apakah jantan ini untuk saat ini dan beberapa waktu ke depan akan tetap menjadi jantan yang bagus atau tidak untuk dapat melindungi keturunan berikut. Pilihan ke-dua, sekali betina memutuskan untuk pindah, kemana mereka akan pergi. Lebih tegasnya: ke jantan yang mana, apakah ke jantan kelompok tetangga atau ke jantan (tunggal/sendirian) dia harus pergi?. Karena tingkat kelangsungan hidup anak-anak jelas lebih tinggi pada kelompok tempat anak-anak itu dilahirkan jika dipimpin jantan muda daripada pada kelompok yang dipimpin jantan tua (bab sembilan), hal ini bukanlah suatu hal yang remeh bagi betina dan anaknya.

Bagi beberapa jenis hewan, termasuk berbagai jenis primata, telah dikemukakan bahwa betina mungkin menggunakan seruan keras (loud calls) sebagai isyarat untuk menilai kualitas jantan (mis. Mitani 1985, Ryan 1985, Lamberchts 1992, Steenbeek 1999) dan, karena itu, mereka menggunakan seruan keras sebagai dasar untuk memilih pasangan. Bagi primata, bagaimanapun, belum ada fakta yang meyakinkan kalau seruan keras memang berhubungan dengan kualitas jantan atau daya tarik untuk berpasangan (mis. Mitani 1985). Hal ini tidaklah mengejutkan, mengingat primata adalah hewan yang berumur panjang, hidup dalam sistim sosial yang kompleks di lingkungan dimana kita sulit untuk mengumpulkan data yang relevan. Selain itu, ada batas-batas etika pada eksperimen untuk mengevaluasi peran dari kualitas jantan dan pilihan pasangan. Untuk itu, hal ini menjadi tantangan yang istimewa untuk meneliti komunikasi pada primata dan hubungannya dengan kualitas jantan serta pilihan pasangan.

Pada saat seruan keras memainkan peranan dalam atraksi berpasangan, penting juga dilihat adanya variasi dalam seruan ini, baik diantara individu atau diantara golongan individu. Dalam bab ke-dua, saya memperlihatkan bahwa variasi tersebut diatas dan hubungannya ada pada seruan keras kedih. Hal ini menandakan adanya variasi bagi betina untuk memilih mereka, sehingga seruan keras dapat berfungsi sebagai atraksi memilih pasangan. Sejak Steenbeek (1999a,b) memperlihatkan, bahwa kekuatan jantan berbeda dalam berbagai tingkat kehidupannya, dan yang terendah pada waktu masa jabatan mulai berakhir, bab ke-tiga menginvestigasi apakah seruan keras juga memperlihatkan perbedaan yang jelas dalam berbagai tingkat kehidupan jantan. Hasil analisa memperlihatkan bahwa karakter seruan keras tidaklah berbeda antara permulaan, pertengahan, maupun akhir dari masa jabatan, hal ini mengindikasikan bahwa betina tidak bisa mengambil keputusan untuk pindah ke jantan lain dengan berdasarkan karakter seruan keras. Bagaimanapun juga, hasil analisa mengindikasikan bahwa seruan keras pada kelompok semua jantan adalah lebih pendek dalam waktu dan mempunyai kurang unit-T dibandingkan dengan ketiga tingkat kehidupan lainnya. Hal ini menandakan kalau betina dapat membedakan mana jantan yang masih muda.

Sisa dari penelitian ini adalah mengevaluasi kemungkinan adanya fungsi dari seruan keras kedih. Beberapa fungsi dari seruan keras telah diperkirakan seperti mempertahankan pasangan, mempertahankan sumber dan atraksi memilih pasangan. Untuk mengevaluasi fungsi ini pada primata pada umumnya, analisa perbandingan telah dilakukan pada sebagian besar jenis-jenis primata (bab empat). Hasil analisa memperlihatkan bahwa kehadiran seruan keras berhubungan dengan satu aspek dari mempertahankan sumber dan juga sebagian dengan atraksi memilih pasangan. Tetapi faktor-faktor lainnya seperti ukuran tubuh jantan dan pola aktivitas, juga mempengaruhi kehadiran seruan keras. Beberapa hal yang menjadi ukuran jantan untuk mempertahankan pasangan, bagaimanapun, tidak berhubungan dengan kehadiran seruan keras jantan.

Untuk memperoleh pengertian yang lebih baik akan fungsi dari seruan keras pada kedih, kami melakukan eksperimen putar ulang (playback).

Eksperimen berikutnya (bab lima) mengevaluasi jarak/sumber dan fungsi seruan keras dalam mempertahanakan pasangan pada kedih. Ketika mempertahankan sumber penting, reaksi keras baik dari jantan maupun betina, diharapkan hadir dari tengah-tengah daerah jelajah daripada dari pinggir/perbatasan. Sewaktu mempertahankan pasangan dirasakan penting, diharapkan jantan akan bereaksi penuh semangat baik di pinggir maupun di tengah lokasi eksperimen, karena mereka akan terus menjaga betinanya (Wilson dkk 2001). Hasilnya memperlihatkan bahwa eksperimen putar ulang seruan keras dari jantan tetangga, baik di tengah atau di pinggir lokasi, ternyata mempengaruhi reaksi baik jantan maupun betina. Setelah mendengar seruan keras dari daerah tengah, jantan bereaksi penuh semangat dengan menyuarakan seruan keras lebih banyak, lebih banyak melakukan pengamatan sekitar (scans) dan mendatangi lokasi alat pengeras suara lebih dekat daripada setelah mendengar seruan keras yang sama yang datang dari daerah tumpang tindih (pinggir/perbatasan) dari daerah jelajah mereka. Betina juga datang lebih dekat dan cepat setelah eksperimen di tengah daripada dari pinggir. Perbedaan dalam jarak mendekati pengeras suara, mengindikasikan kalau lokasi sumber suara mempengaruhi jarak; hal ini menggambarkan adanya ruang/jarak diantara kelompok kedih. Uji coba juga mengindikasikan kalau mempertahankan sumber (sumber pakan) penting baik bagi jantan maupun betina, karena jantan dan betina mendekati pengeras suara lebih dekat setelah eksperimen di tengah daripada di pinggir. Untuk menguji fungsi pertahanan sumber lebih jelas/tegas lagi, sebuah eksperimen telah dilakukan, dimana seruan putar ulang dari jantan tetangga di pinggir/perbatasan diputar baik dari pohon pakan maupun dari pohon non-pakan. Hasilnya memperlihatkan hanya betina (jantan tidak) yang mendekati lebih dekat pengeras suara di pohon pakan daripada yang ada di pohon non-pakan. Hasil tersebut mendukung hipotesa, kalau sumber pakan lebih penting bagi betina daripada bagi jantan (mis. Emlen dan Oring 1977). Beberpa peneliti (Wilson dkk 2001) berpendapat, jika mempertahankan pasangan adalah hal penting bagi jantan, maka jantan harus bereaksi sama terhadap seruan putar ulang dari manapun lokasi di daerah jelajah, karena mereka harus menjaga betinanya dimanapun mereka berada. Dalam hal ini, ternyata eksperimen kami tidak mendukung hipotesa pertahanan pasangan, karena jantan memperlihatkan respon lebih kuat terhadap seruan putar ulang yang datang dari tengah daripada yang dari pinggir. Adapun untuk eksperimen tetangga tak dikenal, jantan jelas berusaha untuk melindungi pasangannya dan anak mereka ketika jantan tak dikenal ada di sekitar mereka. Oleh Karena itu, hasil eksperimen ini dapat dikatakan mendukung hipotesa pertahanan pasangan bagi kedih.

Bab enam memperlihatkan kalau jantan dan betina dapat membedakan suara-suara seruan dari tetangga dan jantan tidak dikenal yang diputar ulang dari pinggir daerah jelajah kelompok yang diuji, hal tersebut mengindikasikan kalau seruan keras berguna untuk mengenali individu yang mereka kenal baik. Perbedaan seperti itu fungsionil, karena dapat menghindari kerugian dan ketidak perluan untuk berkelahi dengan tetangga. Untuk tambahan, saya meneliti hipotesa, kalau kedih dapat menggunakan kemampuan untuk mengenali antara seruan keras (katagori) untuk mempertahankan bayi mereka melawan jantan yang ingin membunuh bayi itu. Pada kedih, jantan tak dikenal bertanggung jawab atas sebagian besar serangan pembunuhan bayi. Hal ini sesuai dengan hasil eksperimen, dimana jantan bersuara keras lebih banyak/sering, lebih banyak melakukan pengamatan sekitar (scan) dan mendatangi lokasi pengeras suara lebih dekat pada eksperimen jantan tak dikenal daripada dengan eksperimen jantan tetangga. Juga sesuai dengan hipotesa ini, dimana betina bersembunyi setelah mendengar seruan keras dari jantan tidak dikenal, tetapi tidak setelah mendengar seruan keras dari jantan tetangga.

Dalam rangka untuk mengevaluasi lebih jauh hipotesa pertahanan bayi, eksperimen lainnya telah dilakukan, bagaimana reaksi kelompok terhadap seruan keras dari jantan tak dikenal baik yang muda dan tua (bab tujuh). Hasil observasi kami mengesankan kalau jantan muda lebih sering bertanggung jawab atas serangan pembunuhan bayi daripada jantan tua (sudah mempunyai kelompok atau bekas jantan residen). Oleh karena itu, saya mengharapkan putar ulang seruan keras dari jantan muda tak dikenal akan menarik perhatian lebih dari jantan lainnya dan reaksi hati-hati dari betina, daripada putar ulang seruan keras dari jantan tua. Reaksi seprti itu ternyata benar ditemukan. Jantan sepertinya mencari lokasi darimana seruan keras itu disuarakan lebih hati-hati pada eksperimen jantan muda tak dikenal daripada dengan eksperimen jantan tua tak dikenal. Betina terlihat lebih berhati-hati setelah mendengar seruan dari jantan muda tak dikenal dan secepatnya berpindah ke arah berlawanan dari lokasi pengeras suara, namun tidak berperilaku serupa setelah mendengar seruan putar ulang dari jantan tua tak dikenal. Hal tersebut mengindikasikan kalau kedih dapat merasakan perbedaan antara seruan keras dari jantan muda (seruan dengan waktu/durasi pendek) dengan jantan tua (seruan dengan waktu/durasi panjang, bab tiga), dan memberikan reaksi tertentu dimana mereka dapat mengurangi resiko serangan pembunuhan bayi setelah mendengar putar ulang seruan dari jantan muda.

Telah diperkirakan juga kalau seruan keras disuarakan disaat ada ancaman dari pemangsa (Waser 1977). Fungsi seruan keras ini telah diuji di bab delapan dengan menampakan model harimau (salah satu pemangsa mereka) ke kedih. Pada eksperimen, tampak kalau seruan keras memang disuarakan setelah kedih melihat model harimau. Adapun reaksi jantan tergantung dari ada tidaknya anak-anak. Jantan sendiri/tunggal tidak bereaksi dengan seruan keras terhadap model harimau, namun tetap melakukan perilaku menghindar cepat seperti jantan di kelompok campuran. Hal ini mengindikasikan kalau seruan keras dipakai untuk memperingatkan anggota keluarga akan hadirnya pemangsa.

Karena betina jarang ditemukan sendirian, hal ini tidak memungkinkan untuk melakukan eksperimen putar ulang secara langsung pada kedih untuk mengetahui apakah seruan keras penting dalam pemilihan pasangan. Oleh karena itu, bab sembilan menguji faktor-faktor apa saja yang mempengaruhi betina untuk pindah dan ke kelompok mana. Dalam bab ini aneka hipotesa untuk berpindahnya betina seperti kompetisi pakan, menghidar dari pemangsa, dan pilihan pasangan oleh betina diuji. Dari hasil analisa, memperlihatkan kalau betina tidak memilih besar kecilnya kelompok seperti yang diperkirakan dalam hipotesa kompetisi pakan ataupun penghindaran pemangsa, tetapi pindah ke jantan muda seperti yang diperkirakan dalam hipotesa pemilihan pasangan. Pindah ke jantan muda memang masuk akal, karena jantan muda masih mempunyai masa jabatan yang panjang kedepan dan oleh karena itu, betina punya prospek bagus untuk tinggal dengan jantan ini beberapa tahun kedepan. Betina dapat menggunakan seruan keras untuk menentukan apakah jantan itu muda dan masih mempunyai masa jabatan yang panjang/lama kedepan, karena seruan keras jantan muda yang lebih pendek daripada jantan tua. Oleh karena itu, betina dapat menggunakan efek kedewasaan umpamanya dengan meningkatnya durasi/waktu seruan keras, untuk membedakan mana jantan yang muda dan dimana mereka berada.

Namun demikian, seruan keras kemungkinan bukan indikasi yang baik bagi betina untuk menentukan kapan waktunya mereka meninggalkan jantan yang ada. Penelitian ini memperlihatkan kalau karakter seruan keras dan banyaknya seruan keras yang disuarakan kemungkinan bukan indikasi yang baik untuk menentukan tamatnya masa jabatan jantan (bab tiga dan sembilan). Sepertinya isyarat dari perilaku, seperti berkurangnya agresi dengan kelompok lain oleh jantan diakhir masa jabatan atau meningkatnya agresi terhadap betina oleh kelompok jantan lain dapat dipakai sebagai petunjuk untuk betina saat untuk pindah. Hal yang lebih penting bagi betina mungkin, adanya perbedaan yang nyata, dimana rendahnya tingkat kelangsungan hidup anak pada kelompok terakhir sebelum pindah dibandingkan di kelompok pertama. Hal ini juga dapat dijadikan alasan sebagai suatu isyarat yang potensial bagi betina untuk meninggalkan jantannya saat ini.

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Curriculum vitae

Serge Alexander Wich was born in Athens on the 5th of August 1969. After finishing his secondary school education at the Vossius Gymnasium in 1988 he started his biology study at the University of Amsterdam. In 1989 he obtained his "propedeuse" there and continued at the University of Utrecht for the second part of his study. The first working practice concerned measuring eye-movements in response to arthokinetic influence at the TNO Institute of Human Factors. Although, as a city kid, being a non-naturalist and only able to differentiate between flying birds ("sijs") and floating birds ("drijf-sijs"), several journeys to National Parks in India and Africa kindled an interest in living nature and animal behaviour. To pursue this interest a second working practice was conducted in the tropical rainforest of Ketambe in Indonesia to study the feeding ecology of orangutans under supervision of Jan van Hooff and S.S. Utami. This study resulted in a masters that was obtained in 1995 at Utrecht University. In the same year a study started to study bonobos in the Democratic Republic of Congo for the Max-Planck Institute in Seewiesen, Germany. In 1997 he returned to Ketambe. The research, conducted under the supervision of Jan van Hooff, Carel van Schaik end Liesbeth Sterck, concerned Thomas langurs and has resulted in this thesis. The four year fieldwork period in Indonesia was also partly devoted to a continuation of orangutan fieldwork and especially on several surveys to assess orangutan distribution on Sumatra.

After the PhD work he will return to Indonesia to study orangutan traditions in two populations at Sumatra and Kalimantan for a collaborative project between the universities of Utrecht and Duke, USA. In addition, he is involved in setting up a database for the long-term data on orangutan behaviour and ecology that have been collected at Ketambe since the early seventies.

Publication list

Wich, S. A., Sterck, E. H. M. and Utami, S. S. (1999) Are orangutan females as solitary as chimpanzee females? *Folia Primatologica* 70: 23-28.

Wich, S. A., Steenbeek, R., Sterck, E. H. M., Palombit, R. A. and Usman, S. (1999) Tree mortality and recruitment in an Indonesian rainforest. *Tropical Biodiversity* 6(3): 189-195.

Wich, S. A. and van Schaik, C. P. (2000) The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16: 563-577.

Wich, S. A., Assink, P. R., Becher, F. and Sterck, E. H. M. (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. *Behaviour* 139: 65-78.

Wich, S. A., Assink, P. R., Becher, F. and Sterck, E. H. M. (2002) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. *Behaviour* 139: 79-87.

Wich, S. A., Fredriksson, G. and Sterck, E. H. M. (2002) Measuring fruit patch size availability for three sympatric Indonesian primates. *Primates* 43: 19-27.

Graaf, B. de., Bos, J. E., Wich, S. and Bles, W. (1994) Arthrokinetic and vestibular information enhance smooth ocular tracking during linear (self) motion. *Experimental Brain Research* 101: 147-152.

Utami, S., Wich, S. A., Sterck, E, H, M. and Hooff, J. A. R. A. M. van. (1997) Food competition between wild orangutans in large fig trees. *International Journal of Primatology* 18: 909-927.

Steenbeek, R., Assink, P. and Wich, S.A. (1999) Tenure related changes in wild Thomas's langurs II: loud calls. *Behaviour* 136: 627-650.

Buij, R., Wich, S. A., Lubis, A. H., Sterck, E. H. M. (2002) Seasonal movements in the Sumatran orangutan *Pongo pygmaeus abelii* and consequences for conservation. *Biological Conservation* 107: 83-87.

Buij, R., Fox, E. F., and Wich, S. A. (in press) Birds of the Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia. *Kukila*

Wich, S. A. and Nunn, C. L. (in press) Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. *Behavioural Sociobiology and Ecology*

Wich, S. A., Koski, S. , de Vries, H. and van Schaik, C. P. (in press) Individual and contextual variation in Thomas langur male loud calls. *Ethology*

Wich, S. A., Singleton, I., Utami-Atmoko, S. S., Geurts, M. L., Rijksen, H. D. and van Schaik, C. P. (in review) Present Distribution of the Sumatran Orangutan (*Pongo abelii*). *Oryx*

Wich, S. A., Buij, R., and van Schaik, C. P.(in review) Determinants of orangutan densities in the Leuser Ecosystem. *International Journal of Primatology*

Van Bolhuis, G. H. and Wich S. A. (in review) Prevalence and intensity of intestinal parasites in wild Thomas langurs (*Presbytis thomasi*) in Sumatra, Indonesia *Folia Primatologica*

Wich, S. A., van de Post, D. J., Heistermann, M., Möhle, M., van Hooff, J. A. R. A. M. and Sterck, E. H. M. (in review) Tenure Related Changes in Male Loud Call Characteristics and Testosterone Levels in Wild Thomas Langurs. *International Journal of Primatology*

Wich, S. A., Assink, P. R.& Sterck, E.H.M. (in review) Male loud call playbacks to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of age. *Proceedings of the British Royal Society, London B.*

Wich, S. A. and Sterck, E. H. M. (in review) The audience effect in Primates: an experimental study on male calls in response to a tiger model. *Proceedings of the British Royal Society, London B.*

Wich, S. A., Willems, E.P., van Hooff, J.A.R.A.M. & Sterck, E.H.M. (in review) Female transfer and the influence of male quality in Thomas langurs (*Presbytis thomasi*). *Behavioral Ecology*