BEHAVIORAL ENDOCRINOLOGY OF WILD MALE SIAMANGS
(*SYMPHALANGUS SYNDACTYLUS*)

By

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and approved by

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ABSTRACT OF THE DISSERTATION

Behavioral endocrinology of wild male siamangs (*Symphalangus syndactylus*)

by LUCA MORINO

Dissertation Director:

Ryne Palombit

The goal of my dissertation is to clarify the evolutionary forces shaping the behavioral and hormonal profiles of male primates. I collected more than 4,000 hours of focal behavioral observation and over 700 hormonal samples on five monogamous and six polyandrous groups of wild siamangs (Hylobatidae: *Symphalangus syndactylus*) in Sumatra (Indonesia), between August 2007 and May 2009. I addressed three basic aspects of gibbon sociality:

1. The monogamous social system of gibbons is thought to be maintained by intense male-male intolerance, yet in many populations there are numerous polyandrous groups. I test the hypothesis that dominance relationships regulate the interactions of adult male siamangs. Dominant males could clearly be identified in each group, based on a consistent direction of agonistic interactions, displacements and positional behavior. These males enjoyed greater social access to the resident female and monopolized copulations.

2. I tested the Challenge Hypothesis, which posits a correlation between male androgen levels, male-male aggression, and paternal effort. Results showed no association

between male testosterone and group composition, male rank, or rate of intergroup aggression. Androgen concentrations were positively correlated with rate of intragroup aggression. Males involved in a period of social instability (an aggressive group takeover) had T concentrations twice above average. Males displaying active parental care had significantly lower testosterone concentrations than control males. These results represent a particularly valuable test of the Challenge Hypothesis due to the rarity of monogamous/polyandrous mammal species with paternal care.

3. An analysis of the aggressive takeover of three siamang groups suggests that: 1) variation in this species' characteristic duetting is associated with periods of social instability; 2) takeovers represent a threat to vulnerable infants and forced weaning is used as an anti-infanticide tactic; 3) female 'preferential' social behavior toward one of the contenders influences the outcome of a takeover; 4) a secondary adult male in the group reduces the risk of being evicted for the dominant male.

    This research adds important pieces to our understanding of gibbon social organization, can help assess the generality of some human patterns (such as mate guarding, paternal care), and has important contributions to conservation efforts.

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And if I forgot someone, my shame will be my punishment.

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CHAPTER ONE

INTRODUCTION

The focus of my long-term research is the origin and maintenance of pair bonds in primates. In particular, my dissertation work investigated the physiology, social behavior, and reproductive strategies of siamangs (Hylobatidae: *Symphalangus syndactylus*), small apes that live in monogamous or polyandrous groups.

Four main reasons led me to choose these questions and this study animal. First, many aspects of this species' sociality are still unknown or unclear. For example, before this study, no information was available on the socioendocrinology of male siamangs or any other wild hylobatid in the context of adult mating and social strategies. Second, monogamous and biparental species are rare among primates and mammals. Accordingly, models addressing the interplay of hormonal systems and reproductive strategies in mammals are mostly based on species living in multi-male multi-female societies, and are limited by a lack of comparative hormonal data from monogamous and polyandrous systems (Hirschenhauser and Oliveira, 2006). With the data I collected, I intend to fill this gap. Third, siamangs are the only catarrhine primate that share with humans a set of features that include long lasting pair bonds, the involvement of the putative fathers in the care of the young and some form of mate guarding. Thus, data on this species provide a valuable evolutionary background from which to evaluate studies on these aspects of human behavior.

Finally, the population of siamangs I have studied contains several polyandrous groups, and thus allowed me to test hypotheses on the evolutionary and proximate mechanisms generating and maintaining these rare social systems.

In my investigation I used a three-pronged approach, which is reflected in the structure of this dissertation: after a chapter on general methods, in which I present the study area and population and outline the data collection protocols, I present the three core parts of my research. In the first section I analyze the interactions between adult males living in the same social group. It was thought that the extreme intolerance exhibited by males during intergroup encounters was a crucial proximate mechanism maintaining socially monogamous grouping in gibbons (Tenaza, 1975; Brockelman and Srikosamatara, 1984; Mitani, 1984). I tested the hypothesis that the factor allowing males to co-exist in polyandrous groups is a dominance relationship between them, reducing the chance of (and need for) physical fights.

In the second part, I investigate the endocrinological component of these relationships. Specifically, I test predictions of the Challenge Hypothesis, which is an attempt to explain the complex correlations between testosterone concentrations and male social behavior (Wingfield et al., 1990). To measure testosterone levels I collected hormonal samples non-invasively and assayed them in the Animal Science laboratory at Rutgers University. This is the first time this methodology has been applied to hylobatids, and, with the exception of data on two immature agile gibbons in captivity (Suzuki et al., 2003), I provide the first data on gibbon androgens and social behavior. Much more can be done in this direction, and I outline some of the analyses that could be conducted or are already under way.

After exploring broad, underlying mechanisms, in the third part of this dissertation I focus on the aggressive takeover of a group by an external male. Takeovers are rare events in gibbon populations; nonetheless, they have a great impact on individual reproductive success: males without a territory are highly unlikely to reproduce, infants might die as a result of the tenure change, females might lose their offspring and have to establish a new relationship with a strange male. Although researchers usually report takeovers that they witness, usually only brief descriptions of the context and outcome are provided, and no systematic data collection is carried out due to the unpredictability and infrequency of such events. I describe in detail the takeovers I have witnessed during my study period, analyze their salient features and propose and indicate how they may help our understanding of the strategies and constraints shaping individual gibbons' behavior.

In the final chapter of this dissertation I draw conclusions from the three lines of my research, and outline promising directions for future research to continue decoding siamang sociality.

Ecology of the study area

This research project was conducted at the Way Canguk Field Station, in the Bukit Barisan Selatan National Park, southern Sumatra, Indonesia (lat. 5° 39' S, long. 104° 24' E, 30m asl) (Fig. 1.1., 1.2).

Fig1.1 Map of Sumatra, with the location of the study site indicated by a star (Source: US Army Map Service).

Way Canguk comprises 900 ha of primary lowland rainforest, jointly managed by the Wildlife Conservation Society and the Indonesian Ministry of Forestry. While most of the core study area is composed of undisturbed primary forest, some parts are also subject to occasional poaching and small scale harvesting of forest resources, which do not directly affect the siamang population (except for the clearing of a 7-m-wide path for a planned illegal road across group U's home range). A 165-ha area in the southeast corner was damaged by forest fires in 1997 (Kinnaird and O'Brien, 1998). A grid of trails at 200 m intervals is available in the study area. This location has a mildly seasonal tropical wet climate, with an average annual temperature of 27°C (range 22-35°C) and an annual rainfall between 3000 and 4000 mm (O'Brien and Kinnaird, 2003).

The area, part of a UNESCO World Heritage site since 2004, supports a wide variety of fauna and flora. The forest vegetation is dominated by dipterocarps, and includes several species of fig and epiphytes. Among the primates, in addition to two hylobatid species, the siamang and agile gibbon

(*Hylobates agilis*), it includes Sumatran surili (*Presbytis melalophos*), silvery langur (*Trachypithecus cristatus*), long tailed macaques (*Macaca fascicularis*) pig-tailed macaques (*M. nemestrina*), Sunda slow loris (*Nycticebus coucang*), Western tarsier (*Cephalopachus bancanus*).Several potential predators of the siamang are present in the area, including tiger (*Panthera tigris*), Sunda clouded leopard (*Neofelis diardi*), marbled cat (*Pardofelis marmorata*) and reticulated python (*Python reticulatus*) (O'Brien and Kinnaird, 1996; Morino, 2009; Morino, pers. obs.).

Fig 1.2 Map of the Way Canguk study area (Source: M. Nusalawo).
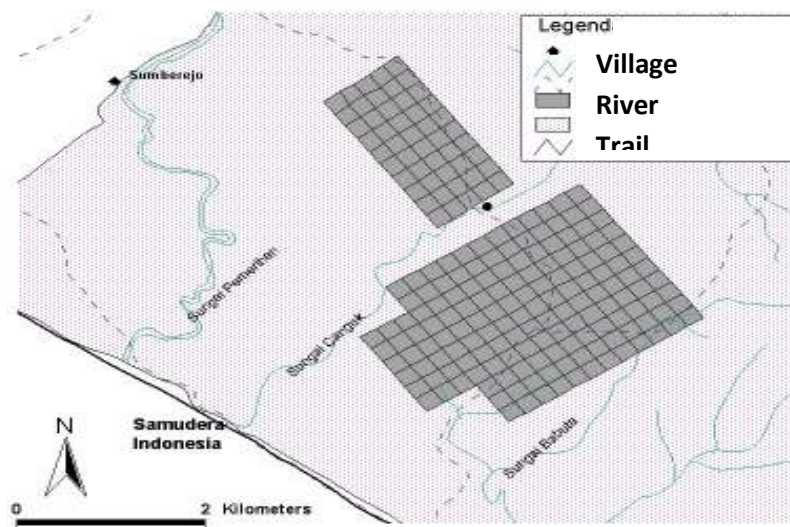
Background information on the hormonal mechanisms addressed in this study

Testosterone (T) is a steroid hormone produced in the testes and adrenal cortex. It regulates the development of male reproductive system and secondary sexual traits, increases muscle mass and bone density, and modulates aggressive, sexual, and parental behavior in vertebrates (Hart, 1974; Griggs et al., 1989; Booth et al., 2006; Wallen and Hassett, 2009). The effects of T on target cells can occur by direct activation of androgen receptors (directly by T or its metabolite 5α-dihydrotestosterone), or by conversion of T into estradiol and activation of estrogen receptors (Hiipakka and Liao, 1998).

While high levels of T confer competitive advantages during the mating season, if they are maintained high for a prolonged period they can also have negative effects: among them, a recent review lists high energetic costs, reduced fat stores, oncogenic effects, increased mortality and risk of injury, interference with parental behavior, suppression of immune function (Wingfield et al., 2001).

While the activating mechanisms and influence of T on sexual traits are relatively well known, the effect of T on social behavior are less well understood. Part of the difficulty is the nature of the hormone/behavior interaction: studies on humans suggest that an individual's behavior is ultimately determined by the interaction of T levels, social context and an individual's past experience, perception and behavioral propensities (Booth et al., 2006).The first step in understanding these complex feedback loops is to establish correlations between hormone levels and social behaviors or circumstances, which is the aim of the research I describe on chapter 3.

CHAPTER TWO

DOMINANCE RELATIONSHIPS AMONG SIAMANG MALES

LIVING IN MULTIMALE GROUPS

Abstract

Intense intolerance among males is considered to be an important mechanism maintaining the uni-male structure traditionally attributed to socially monogamous gibbons. Long-term field work, however, has revealed the existence of stable socially polyandrous groups in various hylobatid populations, raising questions about the mechanism that allows two adult males to co-reside in the same group. I collected 21 months of behavioral data on 7 two-male groups of wild siamangs (*Symphalangus syndactylus*) in southern Sumatra (Indonesia) to test the hypothesis that dominance relationships regulate the interactions of adult male siamangs and ultimately facilitate polyandrous social groups. A dominant male could clearly be identified in each dyad, based on a consistent direction of agonistic interactions (Wilcoxon Signed Ranks test, p=0.04), displacements (p=0.03) and positional behavior (p<0.01). Males identified as dominant enjoyed greater social access to the resident female (p<0.01) and monopolized copulations (N=43). These results suggest that gibbons possess the psycho-social flexibility to regulate intra-sexual aggression and live in non-monogamous social units under some conditions. I also discuss the

effects that relatedness between males and female choice have in determining this grouping pattern.

Introduction

Hylobatids are arboreal Southeast Asian apes typically living in socially monogamous groups (Ellefson, 1974; Gittins and Raemaekers, 1980; Leighton, 1987). Adults of each group actively defend a territory, partly by singing duets that advertise their presence in the area and partly by interacting agonistically with neighbors at their shared range boundaries (Leighton, 1987; Mitani, 1987). Inter-group encounters are mostly characterized by ritualized agonistic behaviors, such as calling and chases (Tenaza, 1975; Leighton, 1987; Reichard and Sommer, 1997), but sometimes male-male confrontations escalate to physical aggression that can generate fatal injuries (Palombit, 1993). Such intense intersexual intolerance is thought to contribute to the maintenance of the monogamous mating system of gibbons (Tenaza, 1975; Brockelman and Srikosamatara, 1984; Mitani, 1984). Nonetheless, long term studies have emphasized the flexibility of gibbon social systems (Palombit, 1994a; Brockelman et al., 1998; Lappan, 2007a, Reichard and Barelli, 2008), and sizeable proportions of stable polyandrous groups (and fewer polygynous ones) are reported in the most intensely studied populations (Lappan, 2007a, Reichard and Barelli, 2008; Malone and Fuentes, 2009).

Given the marked intolerance between neighboring males, how could a stable, long lasting association of two adult males within a group be maintained? Previous

studies documenting polyandrous and polygynous gibbon groups have not provided information on the mechanisms regulating group dynamics.

Dominance is one common mechanism mediating aggression among males living within a social group (Schelderupp-Ebbe, 1922; Zuckerman, 1932; Melnick and Pearl, 1987; Drews, 1993). Once relative ranks are established, there is reduced need to sustain dangerous and energy costly fights for access to valuable contested resources. Dominance relationships are a common feature of primates living in multi-male, multi-female groups (Melnick and Pearl, 1987; Sapolsky, 1993) and have also been documented in monogamous/polyandrous systems (*Leontopithecus rosalia*: Baker et al. 1993; *Propithecus verreauxi*: Kraus et al. 1999).

The aim of this study is to determine whether dominance relationships facilitate the maintenance of long-lasting two-male siamang groups. I address this question by evaluating first the nature of male social relationships and then the association between male dominance status and indirect measures of reproductive success.

Dominance implies a consistent asymmetry in the outcome of a range of different agonistic interactions between two individuals (Dewsbury, 1982; Hinde, 1983; Drews, 1993; Sapolsky, 1993). Interactions typically used to establish dominance among primates include approach/retreat, dyadic aggression and visual/vocal signals (Koyama, 1967; Hausfater, 1975; Strum, 1982; Walters and Seyfarth, 1987; Cowlishaw and Dunbar, 1991; Baker et al., 1993; Chaffa et al., 1995; Bergman et al., 2006). Accordingly, evidence of dominance in this study was obtained by testing the following predictions:

a)   <u>Aggressive behaviors and threat signals</u> will be directed asymmetrically from one (dominant) male toward the other (subordinate) male (Walters and Seyfarth, 1987).

b)   <u>Approach/retreat</u>: the approach of one male will cause the retreat of the other male more often than vice versa. Importantly, the patterning of this interaction will be consistent with the outcomes of aggressive interactions above. That is, if approach/retreat interactions for a particular dyad are asymmetrical, the identity of the 'retreating' individual will be the same as the identity of the victim of aggression in the previous prediction.

c)   <u>Relative canopy height</u>: one male will maintain a higher position than the other male significantly more often than vice versa. In a tridimensional world such as that inhabited by the arboreal gibbons, being higher than an opponent potentially confers a tactical advantage in physical confrontation (in terms of energy conversion during an attack). Observational evidence supports this 'upper hand' advantage: siamangs rarely attack an opponent from below, and are typically at least at the same height of an opponent before lunging (Morino, pers. obs.). At the end of a fight or chase, the 'winning' animal is virtually always higher than the loser (Ellefson, 1974; Morino, pers. obs.). Finally, losing individuals occasionally escape by dropping to the ground (Tenaza, 1975; Palombit, pers. comm.; Morino, pers. obs.) – which is virtually the only context in which I have observed terrestrial movement in gibbons.

Although the correlation between male dominance and reproductive success varies (e.g. Bernstein, 1981; Fedigan, 1983), and although most relevant data come

from catarrhine studies, recent reviews report general support for the hypothesis that high dominance rank confers reproductive benefits (Cowlishaw and Dunbar, 1991; Alberts, in press). A commonly used behavioral proxy for reproductive success is mating success, although the two variables are not always found to be correlated with one another (Packer, 1979; Cowlishaw and Dunbar, 1991; de Ruiter and van Hooff, 1993; Dixson et al., 1993). I test the prediction that the majority of the copulations involving the resident female will be performed by the male who is identified as dominant on the basis of agonistic asymmetries.

In many primate species, (dominant) males consort or mate guard females (Bulger, 1993; Setchell et al., 2005). This is thought to provide several advantages, from the obvious one of keeping competitors away from reproductive females, thus reducing potential sneak mating (Bulger, 1993; Setchell et al., 2005), to more subtle ones such as obtaining information on the reproductive status of the female (Palombit, 1999; Engelhardt et al., 2006; Barelli et al., 2007; Mass et al., 2009). Two related predictions I test are that the dominant male will spend more time than the subordinate close to the resident female, and that the dominant male will be more responsible than the subordinate for maintaining such close proximity.

Methods

Study groups

Data were collected on seven siamang groups containing a single adult female and two adult males (Table 1.1). Four of these groups (A, B, C and F) had been

followed previously by Lappan (2007a). Both males in group F were the same individuals studied by Lappan, and in groups A and C one of the current adult males had been observed as a juvenile. The identities of both males of group B had changed since Lappan's research.

Table 1.1 Composition of study groups.

Group	Male1	Male2	Female	SA/LJ	SJ
A	x	x	x	f	m
B	x	x*	x	f	f
C	x	x**	x	f	m
E	x	x	x	m	f
F	x	x	x	f	f
H	x	x	x	f	f
M	x	x	x	f	f

SA: subadult; LJ: large juvenile; SJ: small juvenile; x: present; f: female; m: male; *: emigrated after 11 months; **: emigrated after six months.

Each group was followed from sleeping-tree to sleeping-tree for 3-4 consecutive days each month, between August 2007 and April 2009, for a total of approximately 4,100 hours of focal follows. A male was defined as 'present' for the day if he was observed for at least two hours within 20 m of the rest of the group (Table 1.2).

Table 1.2 Adult male presence in the group (% of observation days).

Group	Dominant	Subordinate	N days
A	100	84.1	82
B	100	100	42
C	100	100	13
E	100	94.4	89
F	100	78.7	75
H	100	98.2	57
M	100	88.7	53

Behavioral data collection

Data were collected through 10-min continuous focal follows of randomly selected adult individuals, scan observations (every 10 minutes, throughout the day), and *ad libitum* observations (Altmann, 1974).

<u>Agonistic interactions</u>

During continuous focal follows, I recorded all behaviors that could be considered agonistic in nature: open-mouth threats, chases, lunges, and physical aggression (Table 1.3; see Liebal et al. [2004] for an updated siamang ethogram). For comparative purposes, I also report agonism involving the resident adult female and nonadults.

Table 1.3 Operational definitions of agonistic behaviors

Chase	Animal A moves fast after animal B. Fast chases (more than 20m, and always at a very high speed) could be distinguished from slow ones, but in the analysis they were lumped together due to small numbers. Chases are mainly a ritualized agonistic behavior, as they seldom lead to physical aggression (Reichard and Sommer, 1997).
Lunge	Animal A suddenly and brusquely reaches forward, toward animal B.
Open-mouth threat	Animal A briefly opens his mouth wide while silently staring in the direction of animal B.
Physical aggression	Animal A slaps, pulls hair, bites animal B

<u>Approach/retreat</u>

During focal follows, an approach/retreat, or displacement, was coded whenever individual A approached to within 3m of individual B, and individual B moved at least 6m away, or out of the tree, within 5 seconds of that approach. I chose the arbitrary 3 m threshold as the distance at which a physical contact from a siamang could not be prevented.

<u>Relative canopy height</u>

During each instantaneous scan, I recorded which male was higher. Since the potential advantage of being higher than one's opponent becomes less competitively relevant as the distance between two individuals increases, I only include data collected when males were <6m apart (an attack carried out within this distance cannot easily be avoided). Including larger (up to 20m) or shorter (within 3m) inter-male distances in the analysis did not alter the results. For this analysis, I considered one individual to be higher than the other if his position in the canopy was separated from the other by >0.5m in height. If the height difference between males was <0.5m, the two individuals were assigned the same height rank, to control for possible estimating error when animals were high in the canopy.

Copulations

All observed copulations involving the focal animal, and the identity of the mating partner, were noted.

Distance to resident female

Distances among all adults were recorded every 10 minutes. An average of 2,640 (SD=974) instantaneous scans was conducted for each of the seven groups. To determine which male was closer to the female, I calculated the percentage of scans in which each male was nearer or farther than 10m from the female, only including days when both males were present in the group (Table 1.3). Each time distances among all three adults could be collected (47% of the scans), I established which adult individual was closest to the female.

Proximity maintenance

During focal follows, I recorded every time an adult individual 'approached' (moved to within 3m) or 'withdrew' (moved from within 3 m to farther than 3m) from another, in order to evaluate responsibility for the maintenance of proximity, according to the formula (Hinde and Atkinson, 1970):

$$A_1/(A_1+A_2) - W_1/(W_1+W_2)$$

where A is an approach, W is a withdrawal and 1 and 2 are two individuals.

Statistics

One-sample t tests, Wilcoxon Signed Ranks tests and Mann-Whitney U statistics, two-tailed with $\alpha = 0.05$ are reported. All analyses were done using SPSS 17.0 (SPSS Inc.)

Results

Agonistic interactions

Overall, intra-group aggression involving any member of the group was rare, occurring at an average rate of 0.30 ± 0.27 (mean $\pm$ SD; N=7 groups) interactions per group per day. Aggression was typically manifested as brief chases or lunges, which elicited an escape and, at times, a submission call (Lappan's (2005) 'scream') from the recipient. Physical contact was rare, occurring in about 16% of all interactions and never resulting in discernible injury to participants (in contrast to inter-group aggression, see Chapter 3 and 4).

The highest percentage of agonistic interactions was between the two adult males (47.6%; Table 1.4). There was a significant difference in the frequency in which one male threatened the other (N=7 groups, Z=-2.032; p=0.04), such that 90.2% of the interactions were directed by one male toward the other (Table 1.5). This result was not due to a generally higher aggressiveness of the 'dominant' male, as rates of aggression toward all other group members were low for both males. On the other hand, adult females also directed considerable aggression toward 'subordinate' males residing in their group (Table 1.4).

Table 1.4 Distribution of agonistic interactions by dyad (Mean±SD). Percentage of total aggressions from all groups, N=107).

Actor	Recipient				
	Female	**Male1**	**Male2**	**LJ**	**SJ**
Female		**3.2** (±3.9)	**24.7** (±19.0)	**9.3** (±10.0)	**0.4** (±0.9)
Male1	**3.9** (±7.0)		**37.4** (±24.8)	**10.0** (±20.7)	**0**
Male2	**4.5** (±5.5)	**3.8** (±5.1)		**2.8** (±5.0)	**0**

Table 1.5 Daily rates of agonistic behaviors directed by one adult male toward the other (mean ± SD).

Group	Actor				N
	Male1		**Male2**		
A	**0.22**	(± 0.54)	**0.00**	(± 0.00)	15
B	**0.07**	(± 0.34)	**0.00**	(± 0.00)	3
C	**0.15**	(± 0.38)	**0.15**	(± 0.38)	4
E	**0.08**	(± 0.42)	**0.01**	(± 0.11)	8
F	**0.27**	(± 0.71)	**0.03**	(± 0.18)	18
H	**0.00**	(± 0.00)	**0.00**	(± 0.00)	0

M	**0.06**	(± 0.25)	**0.00**	(± 0.00)	3

Approach/retreat

There was a significant difference in the rate at which one male displaced the other (N=7 groups, Z=-2.12; p=0.03; Table 1.6, where "dominant" is based on data from the previous table). The direction of this asymmetry was consistent with that observed for aggression. That is, the males that were displaced more often were the also those who were targeted disproportionally in aggression.

Table 1.6 Daily rates of displacement between adult males (mean ± SD).

Group	Actor Dominant		Subordinate		N
A	**0.10**	(± 0.30)	**0.04**	(± 0.21)	15
B	**0.12**	(± 0.33)	**0.02**	(± 0.15)	3
C	**0.00**	(± 0.00)	**0.08**	(± 0.28)	4
E	**0.06**	(± 0.24)	**0.02**	(± 0.15)	8
F	**0.05**	(± 0.22)	**0.03**	(± 0.18)	18
H	**0.05**	(± 0.23)	**0.02**	(± 0.13)	0
M	**0.11**	(± 0.31)	**0.00**	(± 0.00)	3

Canopy height

The 'dominant' member of a dyad, who threatened and displaced more frequently (see above), also occupied a position higher in the canopy more often than the other, 'subordinate' male (average: 61.4%, t=5.48, df=6, p<0.01) (Fig.1.1). The difference in height was usually not pronounced, but consistently in favor of the dominant male.

Figure 1.1 Canopy height relationships among adult males within each group.
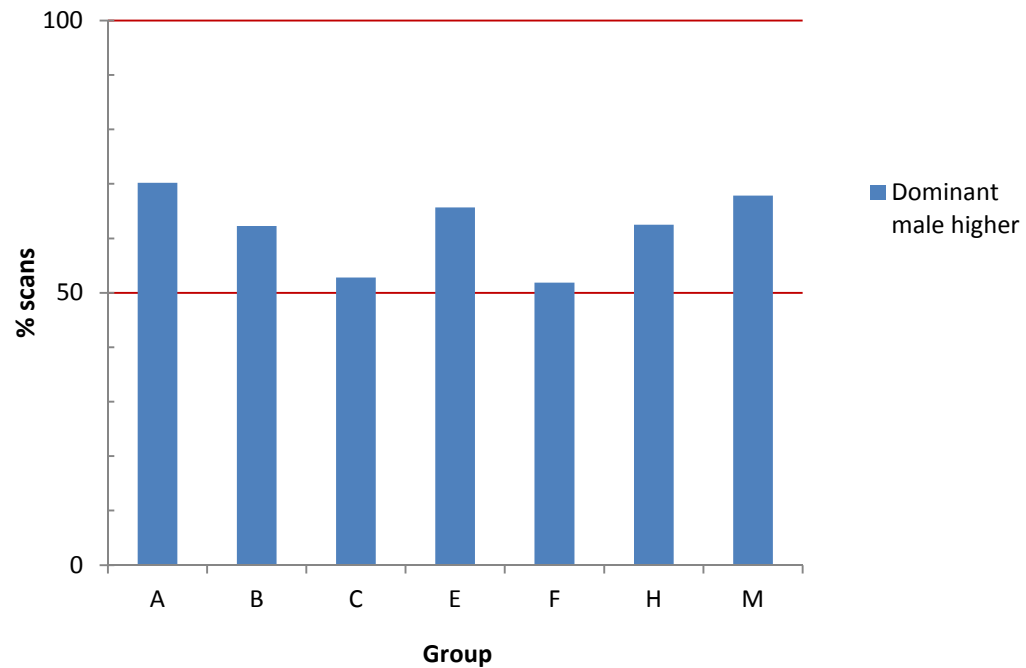
Copulations

    I observed a total of 45 copulations within the focal groups during the study period (Table 1.7). Of these, all the copulations involving the adult female were with the dominant male of her group (N=43); the remaining two matings occurred between subordinate males and subadult females. Copulations never resulted in overt conflict between the males, and in many occasions occurred within sight of the subordinate male. The latter never approached the mating pair or showed any apparent sign of distress, whereas matings were often disturbed by juveniles approaching, inspecting, or trying to separate the copulating pair.

Table 1.7 Observed copulations within study groups.

Group	Dominant male - Adult female	Subordinate male - Adult female	Subordinate male – Subadult female
A	27	0	0
B	7	0	0
C	2	0	0
E	2	0	0
F	2	0	1
H	1	0	0
M	2	0	1
TOT	**43**	**0**	**2**

Distance to resident female

While the dominant male was always present in the group, the subordinate was, in some cases, absent for the whole day (Table 1.3). When both males were present, the dominant male was observed within 10m from the female significantly more often than the subordinate (mean dominant= 72.9, mean subordinate= 54.6; N=7; U=3; p<0.01; Fig. 1.2). The dominant male was also the closest adult to the female significantly more often than the subordinate male (73.5% of the time, average of 7 groups; Wilcoxon signed rank test, Z=-2.37; p<0.01) (Fig. 1.3).

Figure 1.2 Distribution of distances of dominant and subordinate males from female. Percentage of scans males were at various distances from female.
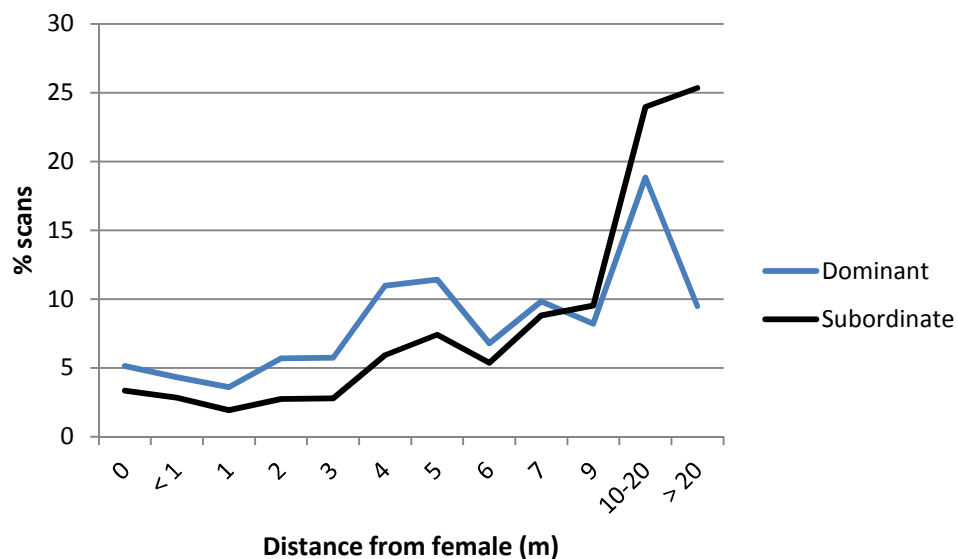
Figure 1.3 Intergroup variation in proximity of males to female. Percentage of scans when each male was nearer to the female.
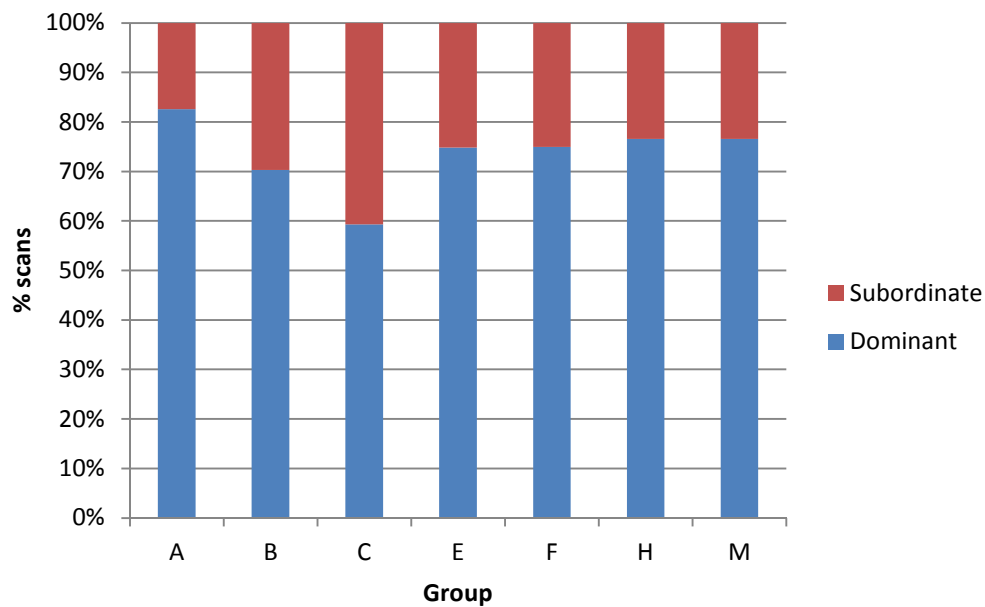
Proximity maintenance

Hinde indices were positive in 12 out of 14 dyads (Fig. 1.4), suggesting that males were more responsible than the female for maintaining proximity. Indices for the dominant males were variable (but positive), while indices for the subordinates highly positive, with the exception of groups C and M (Fig. 1.4). There was no significant difference in the contributions of dominant and subordinate males to maintenance of proximity to the female (N=7; U=18.0; p=0.46). It is possible that the expected pattern was not found because the females in this study were at different reproductive stages, whereas adult mates would likely mate guard only cycling females. Running the analysis after excluding lactating females, however, reveals a trend for dominant males to be less responsible than subordinates for maintaining proximity (p=0.07; Fig. 1.5).

Figure 1.4 Responsibility for maintaining proximity to female by dominant and subordinate male (all data – see text for intepretation).
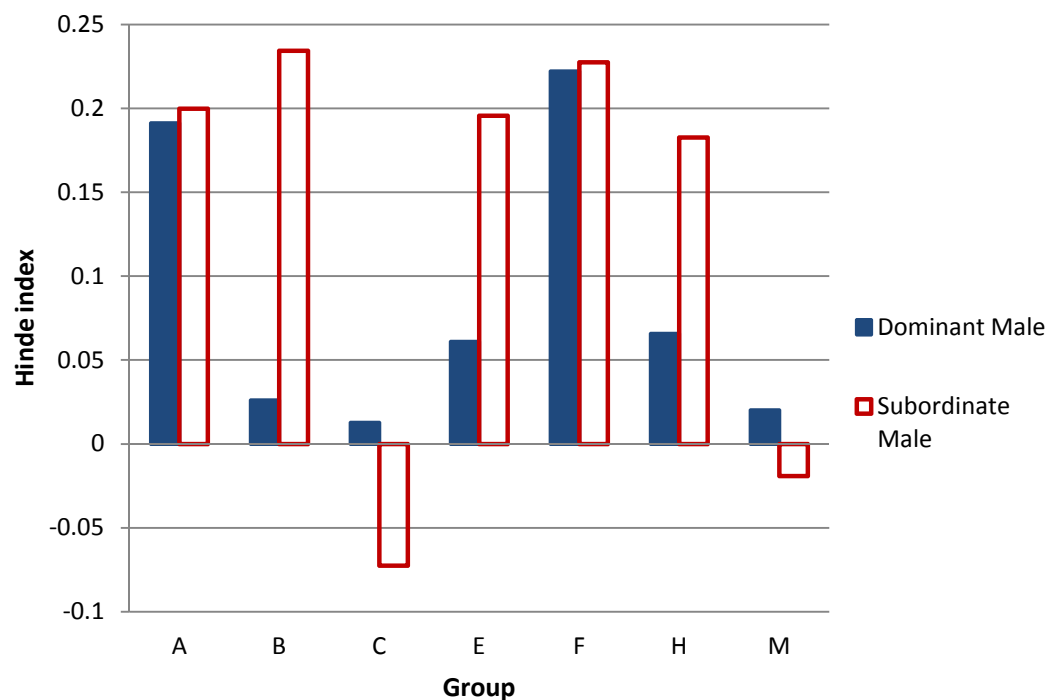
Figure 1.5 Responsibility for maintaining proximity to female by dominant and subordinate male, excluding nursing females (see text for intepretation). Two groups are missing because the female was suckling during the whole study period.
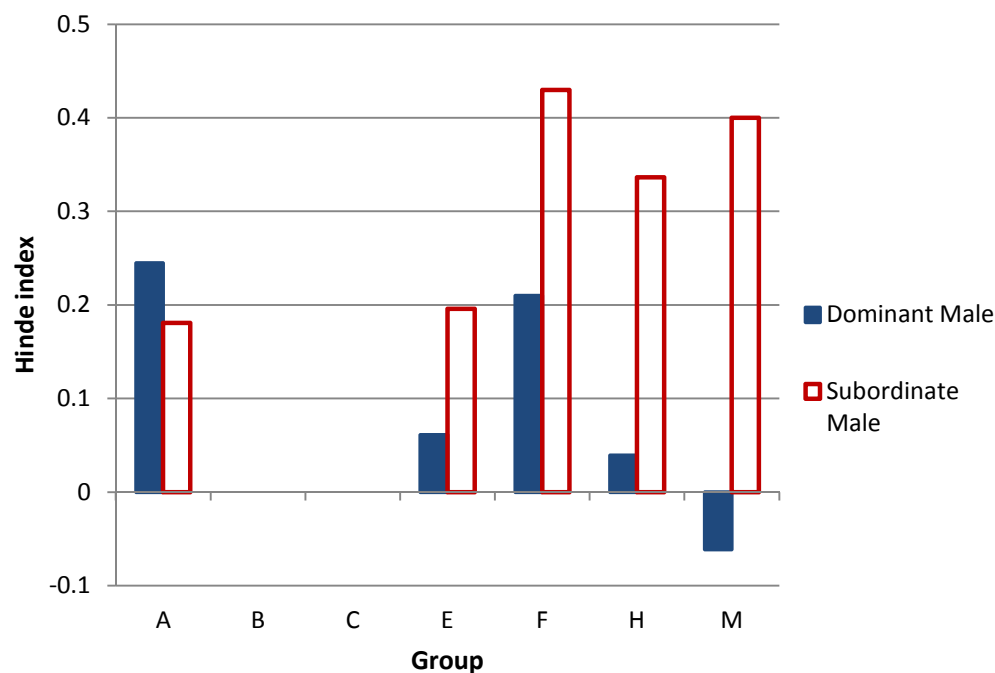
Discussion

The pattern of agonistic interactions in each of the seven study groups indicates

clear dominance relationships between resident males. In spite of a relatively small

sample size, and several potential confounding factors (e.g. age, relatedness, female

reproductive status, and different patterns of male infant-carrying), all three

predictions were supported by the data. First, one male directed aggression toward

the other significantly more often than the reverse. Second, the same male displaced

the other more often than vice versa. Finally, the same male occupied a higher,

strategically advantageous canopy position. The presence of stable two-male groups

in this population, and the results of this study, indicate that gibbons possess the psycho-social flexibility to reduce intra-sexual aggression and live in non-monogamous groups, and that they use dominance hierarchies to regulate social relationships in multi-male groups. Two subsequent chapters will provide additional details on this subject, one documenting group takeovers (when dominance is established) and the other investigating the hormonal correlates of these social changes.

Few aggressive interactions were observed during the study period, with rates almost identical to those reported previously for the same population (Lappan, 2007a), and comparable to those of other 'polyandrous' primate species (Baker et al., 1993; Kraus et al., 1999). The fact that little aggression was observed, however, does not indicate that dominance relationships are not important among siamangs. On the contrary, one of the expected functions of dominance relationships in these stable two-male groups is to reduce the likelihood of costly escalated aggression, which may cause potentially lethal wounds (Palombit, 1993).

The majority of agonistic interactions occurred between the two males, suggesting that they may be competing over long-term access to mating opportunities. The fact that some aggression also occurred between the subordinate male and the female (as well as other dyads), however, raises the possibility that feeding competition could also play a significant role in male-male conflict. Future fine-grained analyses focusing on feeding behavior will help elucidate this point.

Data on copulations unequivocally show a monopoly of mating by the dominant male. This apparent mating exclusivity stands in sharp contrast to the pattern reported by Lappan (2007a), with polyandrous mating in three out of four two-male groups she studied. It is worth noting, however, that for the only pair of males present in both studies (group F), Lappan (2007a) also reported that copulations were monopolized by one male (the dominant one of the present study). It is unlikely that sneaky copulations between the resident female and the subordinate male went unnoticed in the current study, since there seemed to be no particular attempt at concealing matings (Lappan, pers. comm.; Morino, pers. obs.). Genetic relatedness could explain the difference between this study and Lappan's (2007b): it is possible that the subordinate males in this study are related to the dominant males and/or the females in their group, whereas in at least three of the polyandrous groups studied by Lappan (2007b), genetic data indicated that the males could not have been the offspring of the female (but could have been related to each other). In fact, unpublished census data indicate that the dominant males in groups A, B, C, and M are the presumed fathers or brothers of the co-residing subordinates (T. O'Brien, M. Kinnaird, S. Lappan, L. Morino, unpubl. data). If so, these subordinate males may be "helpers at the nest" waiting to obtain a reproductive position (Baker et al., 1993, Lappan, 2008). Close relatedness among these males could contribute to explaining tolerance between males (*sensu* Hamilton, 1964), but it does not rule it out: in one of the two successful takeovers I witnessed, a subordinate male initially dispersed, then returned and ousted the dominant male (his putative brother) after a week of intense physical aggression (Chapter 4). Future research will clarify the genetic relationships

within these siamang groups, and investigate the contributions 'helpers' might offer in exchange for being tolerated within the group.

As predicted, dominant males spend more time than subordinates in close proximity to the female. There seems to be a threshold around 8 m from the female, below which the dominant male is more frequently found than the subordinate one. This could be due to the dominant's intolerance of proximity between the subordinate male and the resident female, which might function to interfere with the subordinate's assessment of the female's sexual status. It is also possible that the female herself does not tolerate the subordinate's proximity. At the same time, subordinate males – who are not mating within the group – are expected to roam farther away in search of breeding opportunities in neighboring territories. This is supported by the fact that subordinate males were the only ones who were sometimes missing during part or all of the observation day.

Contrary to expectations, dominant males were not more responsible than subordinates for maintaining proximity to the resident females. It is difficult to interpret the pattern revealed by the Hinde indices. Subordinate males were highly responsible for maintaining proximity to the resident female in all but two study groups. The females of these groups, Connie and Margaret, were lactating during most of the study period, unlike the females of other groups who could have potentially been cycling. Excluding these lactation periods from the analysis reveals a trend toward dominant males being less responsible than subordinates for proximity maintenance. This goes against the mate-guarding hypothesis, which

would predict an even stronger investment from the dominant in watching carefully the female when she is potentially cycling. This conclusion must be considered to be very tentative, however, because data are unavailable for two groups (whose females were also lactating throughout the study period), the female reproductive state was not directly established, and because the Hinde index for group M was based on few observations. If this pattern were confirmed by additional data, however, it could indicate an important role for female choice in this population, which could also explain the observed pattern of dominance. In several species, female choice influences the outcome of agonistic challenges between males (e.g. hamadryas baboon, Bachmann and Kummer, 1980). Female support should be especially important in hylobatids, where body and canine size in females are as large as in males, and indeed females are often actively involved in physical confrontation during inter-group encounters and, in particular, in cases of attempted male immigration (Chivers, 1974; Palombit, 1994a; Morino, in prep.). The impact of female choice on male rank will be analyzed in a forthcoming paper.

In conclusion, this study confirms that hylobatid males can coexist peacefully within the same social group, and suggests dominance as the mechanism regulating their interactions. Moreover, current evidence suggests dominance status is likely to have reproductive consequences for males.

CHAPTER THREE

SOCIAL CORRELATES OF ANDROGEN LEVELS IN A

MONOGAMOUS APE (SYMPHALANGUS SYNDACTYLUS): A

TEST OF THE CHALLENGE HYPOTHESIS

Abstract

The Challenge Hypothesis (Wingfield, Hegner, Dufty & Ball, 1990) posits a

correlation between male androgen levels and mating system, male-male aggression

in a sexual context, and parental effort. This model has received support across a

variety of taxa, including primates. Most primate studies have focused on multi-male

societies characterized by relatively high levels of male-male aggression and limited

paternal care. To expand this dataset, I tested predictions of the Challenge

Hypothesis in a population of wild siamangs (*Symphalangus syndactylus*), small apes

characterized by intense territoriality, monogamous/polyandrous grouping patterns,

and varying amounts of paternal behavior. Between August 2007 and April 2009 I

collected behavioral data on 11 study groups (five two-male groups and six one-male

groups). I collected 734 fecal samples from 21 adult males and quantified

concentrations of testosterone by radioimmunoassay. Results showed no association

between male androgen concentration and group composition, male rank, or rate of

intragroup aggression. Androgen concentrations were positively correlated with rate

of intergroup encounters, although this result was due to a period of social instability

during a group's aggressive takeover. Males involved in this dispute had T

concentrations twice above average. Males displaying active parental care had

significantly lower testosterone concentrations than control males. The increase in

testosterone during periods of social instability and the decrease associated with

paternal care are consistent with the Challenge Hypothesis. The lack of a correlation

between androgen levels and group composition or rank might be explained by

dominance relationships reducing aggression between adult males residing in the

same social group.

Introduction

Social behavior and hormones have been shown to influence and regulate one

another, generating complex feedback loops (Bercovitch and Ziegler, 2002). In

particular, testosterone (T) is known to play a role in modulating aggressive, sexual,

and parental behavior in vertebrates (Hart, 1974; Harding, 1981; Bouissou, 1983;

Sapolsky, 1983, 1993; Wingfield et al., 1990; Wickings and Dixson, 1992;

Brockman et al., 1998; Klukowski and Nelson, 1998; Nunes et al., 2000; Gray et al.,

2002). The "Challenge Hypothesis" (Wingfield et al., 1990) provides an explicit

theoretical framework for explaining the interactions among mating system,

individual reproductive strategies and patterns of T secretion. This model posits that

T secretion in males is correlated positively with rates of aggressive behavior

associated with mating, intrasexual competition and/or territory defense. At the level

of mating system, polygynous males are predicted to: (1) engage in high levels of

intrasexual competition; and (2) maintain high T levels throughout the mating period

(to facilitate high rates of sexual aggression). In polygynous males (not engaging in paternal behavior), T levels are not influenced by behavioral challenges *per se* (such as territorial disputes or mate guarding) because the baseline T level is already high. Conversely, monogamous males are characterized by: (1) relatively less intense male-male competition; and (2) low baseline T levels, which fluctuate dynamically in response to transitory challenges.

Originally formulated using avian data, the Challenge Hypothesis has received considerable empirical support from studies of a wide variety of taxa (Oliveira et al., 2002; Klukowski and Nelson, 1998; Clark and Galef, 1999; Goymann et al., 2003; Hirschenhauser and Oliveira, 2006). Studies on primates – human and non-human – have provided support for the predicted positive correlations between T secretion and mating-related aggression, mating season, and dominance rank in certain social contexts and taxa (Sapolsky, 1983; Wickings and Dixson, 1992; Higley et al., 1996; Cavigelli and Pereira, 2000; Muller and Wrangham, 2004; Ross et al., 2004; Huck et al., 2005; Marshall and Hohmann, 2005; Archer, 2006; Bales et al., 2006; Beehner et al., 2006; Muroyama et al., 2007; Setchell et al., 2008; Girard-Buttoz et al., 2009; but see Lynch et al., 2002; Ostner et al., 2002; Whitten and Turner, 2004). Another prediction of the Challenge Hypothesis is that high concentrations of T are incompatible with male direct parental care (Wingfield et al., 1990). A negative correlation between male T levels and male parental care has been confirmed in several vertebrates (Oliveira et al, 2002; Reburn and Wynne-Edwards, 1999; Clark and Galef, 1999; but see Trainor and Marler, 2001; McGlothlin et al., 2007; Van Anders et al., 2012). Among primates, some studies report the expected post-partum

decrease in T (Nunes et al., 2000; Storey et al., 2000; Gray et al., 2002; Shur et al., 2008) while in other cases T levels actually increase, possibly in relation to a need to protect infants from infanticide (Dixson and George, 1982; Ziegler and Snowdon, 2000; Ostner et al., 2008; Teichroeb and Sicotte, 2008).

The Challenge Hypothesis has attracted widespread empirical interest in behavioral biology generally and primatology specifically. Nevertheless, with the notable exception of research on callitrichids (Nunes et al., 2000; Huck et al., 2005; Bales et al., 2006), most tests in primates have focused on multi-male societies with high potential for male intrasexual competition and with low levels, or a complete absence, of male parental behaviors (e.g. chimpanzees: Muehlenbein et al., 2004; Muller and Wrangham, 2004; macaques: Rose et al., 1971; Bercovitch, 1993; baboons: Sapolsky, 1993; Beehner et al., 2006). This trend reflects the rarity of monogamous or polyandrous species among primates and in mammals generally. Additional studies of primates with such mating systems are necessary to evaluate the general applicability of the Challenge Hypothesis (Hirschenhauser and Oliveira, 2006).

Siamangs (*Symphalangus syndactylus*), arboreal apes living in South East Asia, are an ideal taxon to improve our knowledge of the relationship between androgen levels, aggression, and sexual and parenting behavior as outlined above, for two reasons: first, they are mostly monogamous, with a sizeable proportion of polyandrous (two-male) groups reported from at least one population (Lappan, 2007a). Second, siamangs are the only hominoid species, besides humans, displaying extensive direct paternal care, with males carrying infants for a considerable (and

variable) amount of time during their second year of life (Chivers, 1974; Gittins and Raemaekers, 1980, Palombit, 1996; Lappan, 2008). In addition, no data are currently available on androgen levels in the siamang, and the only published report on testosterone concentrations in any hylobatid is a developmental study on two agile gibbons (*Hylobates agilis*) (Suzuki et al., 2003).

I collected hormonal and behavioral data from a population of siamangs that contains a large number of stable (>7 years) two-male groups, with the co-residing males being, in most cases, not related maternally to each other or to the resident female (Lappan, 2007b). A clear dominance relationship usually exists between co-resident males, with rather infrequent aggressive interactions (Lappan, 2007a; Morino, in prep). The dominant male occupies a central position in the group and generally monopolizes sexual access to the female (Morino, in prep., but see Lappan, 2007a). In some cases both males provide parental care of the resident infant (Lappan, 2008; Morino, pers. obs.). These characteristics allowed me to investigate the association between androgen profiles and different social conditions (living in one- or two-male groups, having an infant in the group) and challenges (intra- and intergroup agonistic interactions, aggressive takeovers). I tested the following predictions of the Challenge Hypothesis involving these variables.

Relative to conspecific males residing in one-male groups, both males in two-male groups will have higher T concentrations, due to the presence of a potential sexual competitor in these groups. Some primate studies, however, report that T concentration was negatively related to the number of resident males, because males

in smaller groups faced higher pressure from external males (Whitten and Turner, 2004; Rangel-Negrin et al., 2011). Thus, I test this alternative hypothesis and compare rates of intergroup encounters for one- and two-male groups.

The T profiles of dominant and subordinate males in this population should not be significantly different. Several studies have found a positive correlation between rank and T, mainly caused by dominant males having to defend their position with frequent fights, and/or subordinate males being the targets of frequent aggression (Kraus et al., 1999; Klinkova et al., 2004; Setchell et al., 2008; van Belle et al., 2009). Other studies, however, found no difference in T between dominant and subordinate males during stable periods (Sapolsky, 1983). The siamang population I studied is characterized by clear and stable dominance relationships between the males in two-male groups, and extremely low rates of aggression between them (Lappan, 2005; Morino, in prep.).

Adult male T levels will be positively correlated with rates of intergroup agonistic interactions. Since longitudinal observations of extra-pair copulations and mate-switching in hylobatids suggest that neighboring males are potential sexual competitors (reviewed by Palombit, 1994b), the Challenge Hypothesis predicts that in this context intergroup interactions constitute reproductive "challenges" and therefore higher rates of encounter should be associated with elevated T concentrations among male participants.

Testosterone levels will be lower in males actively involved in direct paternal care than in males living in groups without dependent infants, or in males that do not provide paternal care for an infant currently in the group.

Methods

Study population

The study was conducted at the Way Canguk Field Station, in the Bukit Barisan Selatan National Park, southern Sumatra (Indonesia), between August 2007 and April 2009. This area includes about 900 ha of well-preserved primary lowland rainforest, and siamang habitat is near saturation (O'Brien et al., 2003). Subjects came from 11 groups of habituated siamangs. Five of these groups contained only one adult male throughout the study period; 5 groups contained two adult males, and one group (B) contained two males for the first 5 months of the collection period, then had only one male for 5 months, and in the final 4 months was in a state of transition, with several 'challengers' trying to oust the long-term resident (Morino, in prep.).

Behavioral data collection

Behavioral data were collected through 10-min continuous focal follows of randomly selected adult males (Altmann, 1974). An average of 179:06 hours (±8:24 SE) were collected for each male (Table 2.1). Data on the following variables were collected to test the predictions of the Challenge Hypothesis.

Table 2.1 Number of fecal hormonal samples per subject male (see text for details).

Group	Individual	Code	# Hormonal samples	# Focal hours
A	Amang	AM1	54	202
	Arjuna	AM2	43	184
B	Bram	AM1	58	249
	Bimbim	AM2	15	115
	Buster	Challenger 1	7	31
	Bimbim	Challenger 2	12	42
C	Congo	AM	38	226
E	Emile	AM1	55	214
	Edmond	AM2	51	187
F	Fredy	AM1	41	227
	Frank	AM2	37	164
G	Gatot	AM	43	135
H	Hercules	AM1	45	163
	Hugh	AM2	42	142
L	Lony	AM	38	130
M	Masre	AM1	42	187
	Michael	AM2	37	153
S	Sony	AM	36	154
U	Upam	AM	40	172
Total			734	3,077

AM1: Adult male (dominant); AM2: Adult male (subordinate)

Group composition and testosterone

To compare males living in one-male groups versus two-male groups, I calculated for each male the daily average aggression exchanged with all group members, and their average T concentration for the whole study period. To confirm that higher T values were due to aggression between sexual antagonists, rather than increased generalized aggression in larger groups, I compared the rates of intragroup aggression between males, as well as that involving all individuals.

Male rank and testosterone

Male rank was determined on the basis of agonistic interactions, approach/retreats and spatial positioning (Morino, in prep.). The rank relationships within male dyads did not change during the study period. I compared T concentrations of dominant and subordinate males in two ways. First, I averaged T values for each male in a dyad for the whole study period. Second, as a more conservative analysis, I limited this analysis only to days where fecal samples for *both* males in a group were collected.

Intergroup competition and testosterone

To analyze intra- and intergroup aggression, I recorded all agonistic behavior, including open-mouth threats, chases, lunges, bites, slaps (for operational definitions see Morino, in prep.). I defined an 'intergroup encounter' as the period when two groups were within 20m from each other for at least 10 minutes. These periods typically involved counter-singing as well as agonistic interactions (Chivers, 1974; Morino, unpubl. data). I constructed a linear regression model of the relationship between the average T level of a male and the rate at which he was involved in intergroup encounters (encounters/observation day).

Direct challenge to breeding position and testosterone

At the beginning of the study, Group B was a two-male group with dominant male Bram and secondary male Bimbim. The resident female was carrying an infant of approximately 18 months of age. After five months Bimbim left the group, and

Bram remained the sole male. Five months after Bimbim's departure, Bram was challenged by two males in succession. The first challenger, Buster, gave up the challenge after two months of frequent and prolonged fighting with Bram. Within three weeks, Bimbim returned, challenged Bram over a period of four days and finally ousted him, taking over his breeding position (for details, see Morino, in prep.).

During this transition "takeover" period (from the beginning of Buster's challenge to Bram's final ousting: 16 January – 27 March 2009), the outside male (whether Buster or Bimbim) typically kept in close proximity with the group, participated in group calling, and was chased away by the resident male several times a day. Chasing and other agonistic interactions were significantly more frequent than in the preceding stable period, but were also qualitatively more intense than the standard stereotyped displays (Morino, in prep.). Since these takeover attempts undoubtedly represent serious sexual challenges to a resident male, I analyzed T profiles during this period in detail. I compared the average T concentrations of Bram and Bimbim during the instability period with their T concentrations before this period. To avoid the storage time bias (see below), I compared the average T concentration of the three males involved in the takeover (Bram, Buster and Bimbim) to the average of the males who had not been involved in the takeover transition (during the same time period). I also compared the average T concentration of Bram and Bimbim before the takeover, with that of all the other males (excluding those performing paternal behaviors). Finally, I compared Bram's average T level with that of his two challengers.

Paternal care and Testosterone

During the study period, four groups had infants that were in the age range when they are usually carried by males (1-3 years, Lappan, 2008). Three of these study groups were uni-male, and one had two males. The resident male in two of the three uni-male groups was the principal carrier (was observed to carry the infant for more than 50% of the carrying time) throughout the study (group S and U), while the male of the third group (group B) was never seen carrying the infant. In the two-male group (group H), which had an approximately one year old infant, a clear-cut pattern emerged over 13 months of data collection: the principal carrier was the female for the first three months, the dominant male during the subsequent five months, and the subordinate male during the final five months. While other adults sporadically carried the infant, and the female slept next to her, the principal carrier was always easily identifiable.

To determine whether males involved in paternal care had lower T concentration, I first compared the monthly average T concentrations of all males who carried an infant (N=4) with those of the males residing in groups lacking an infant (N=8). I used monthly averages to account for males starting or stopping their carrying during the study period, and to eliminate the storage bias (see below). To test whether it is the male's direct parental contribution that is related to the change in T, I also compared the average T concentrations of males in groups with an infant with those of males in groups without infants, irrespective of who did the carrying. Next, I compared the four caregiver males to the male of group B, who co-resided with an

infant but was never observed to carry it (I excluded from this analysis the period in which this male was involved in the takeover, see above). Finally, I analyzed the T profiles of the two males of group H, each of whom carried the resident infant during different, consecutive periods. The storage time bias did not permit within-individual comparisons of these two males, therefore I compared the monthly average T concentration of the carrying male with that of the non-carrying male.

Fecal samples collection, extraction and storage

Over a 13-month period (March 2008-April 2009), I collected 3-4 fecal samples/month from the 19 males in the 11 study groups, for a total of 734 samples (Table 2.1). Siamangs can be individually recognized using facial and body features, and the six field assistants who helped me collect the fecal samples were well acquainted with all siamang individuals and had been trained by me on the collection protocol. For hormonal sampling and processing I followed a well-established methodology (Whitten et al., 1998; Beehner and Whitten, 2004; Ziegler and Wittwer, 2005). After observing the focal individual defecating, I isolated a portion of fecal material, homogenized it with a spatula, and collected about 0.5 g of it, placed it in 10 ml of a methanol/acetone solution (8:2), and hand-vortexed it for 5 seconds. All samples were collected before 12:30pm to avoid potential error due to circadian fluctuation in hormone concentrations (Czekala et al., 1994; Muller and Wrangham, 2004). I only collected samples I could unequivocally assign to the source male (discarding samples that were within 50 cm of other feces). Ten hours after collection, I filtered 4 ml of the solution through a polytetrafluoroethylene

syringeless filter (0.2 μm; catalogue # EW-29703-10, Cole Parmer, Vernon Hills,
IL), and washed the filter with another 4 ml of methanol/acetone solution. I diluted
the filtrate (1:2) with distilled water. I primed solid-phase extraction cartridges (Sep-
Pak Plus C18, catalogue # WAT020515, Waters, Franklin, MA) according to the
manufacturer's instructions, by slowly pushing through 2 ml of methanol, followed
by 5 ml of distilled water. Then I pushed the diluted filtrate through a cartridge,
followed by 2 ml of sodium azide solution. I placed the solid-phase extraction
cartridges in Whirl-Pak bags with silica beads and preserved them in a dry box at
steady ambient temperature for approximately two weeks, until they could be
transported to a freezer (-20ºC) at the nearby Lampung University. To obtain dry
weight measures, I dried the fecal samples by letting the solution evaporate under a
mesh cover, and removed undigested seeds.

Radioimmunoassay

To verify that the extraction and assay method effectively measured T values in
siamangs, prior to the field study I collected samples from two captive siamangs (one
male and one female) at the National Zoo (Washington, DC). Following the planned
methodology produced the expected results, with male samples significantly higher
than female ones. After transporting (on dry ice in a freezer box) the samples from
Indonesia to the Animal Sciences Endocrinology Laboratory at Rutgers University, I
reconstituted them and quantified free testosterone from samples assayed in
duplicate using DSL-4900 kits (Beckman Coulter, Inc.). The reagent in this kit (^{125}I)
reacts 100% with free T, 0.35% with 19-Nor-T, 0.21% with 17α-
MethylTestosterone, 0.13% with 11-Ox-Testosterone, less than 0.01% with all other

tested compounds. Assay sensitivity was 0.0119 pg/ml. Because of the reliability of the commercial kit used, quality controls were run only once in each assay, therefore intra-assay coefficients of variation could not be calculated. The inter-assay coefficients of variation for Controls I and II were 16.4% and 11.8% respectively.

The monthly average T concentration steadily increased throughout the study (Fig. 2.1). Rather than being a seasonal effect, or due to increases in intragroup or intergroup agonistic interaction (I found no significant correlation with these factors, after removing data from the takeover attempt), this increase in T is probably caused by depletion due to storage time (samples that stayed longer in the freezer had lower T levels).

Figure 2.1 Average T levels across the study period (excluding males involved in the takeover). Above each column are the number of samples and the number of males (on parenthesis).
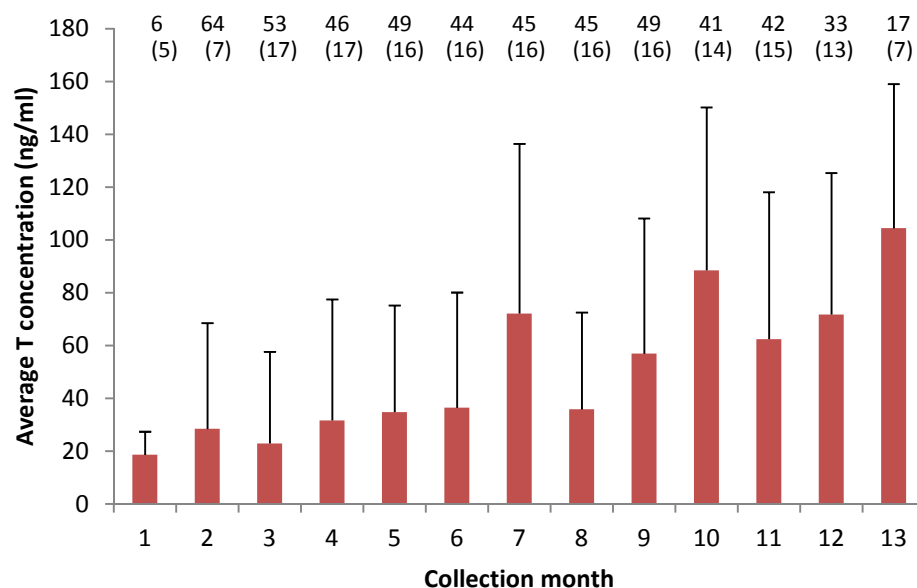
Results

Group Composition and Testosterone

Compared to males in one-male groups, males in two-male groups were predicted to have higher average T levels, because they potentially and actually faced significantly more aggression, due to the continuous presence of a sexual competitor in the group. After excluding the outlier group G (in which the aggression between the recently immigrated male and the adult and subadult females accounted for 39 of the 48 aggressive behaviors recorded for one-male groups; Fig. 2.2 Dixon's Q test, Dean and Dixon, 1951), data showed that males in two-male groups indeed experienced significantly more frequent intragroup aggression than males in one-male groups (U=11.5, p=0.048, N=17; Fig. 2.3). The extra aggression was due to agonistic interactions between the two co-resident adult males, which alone accounted for 47% of all the aggression within two-male groups. After excluding aggression between adult males there was no difference in intragroup aggression between one- and two-male groups (U=17, p=0.17, N=16). Compared to males living in two-male groups, those in one-male groups faced significantly more intergroup encounters (Fig.3; U=9, p=0.01, N=18).The average T concentration exhibited by males living in the two-male social context groups did not significantly differ from that of males in one-male groups (U=36, p=1.0, N=18, Fig. 2.4).

Figure 2.2 Rate of intragroup conflict involving focal males.
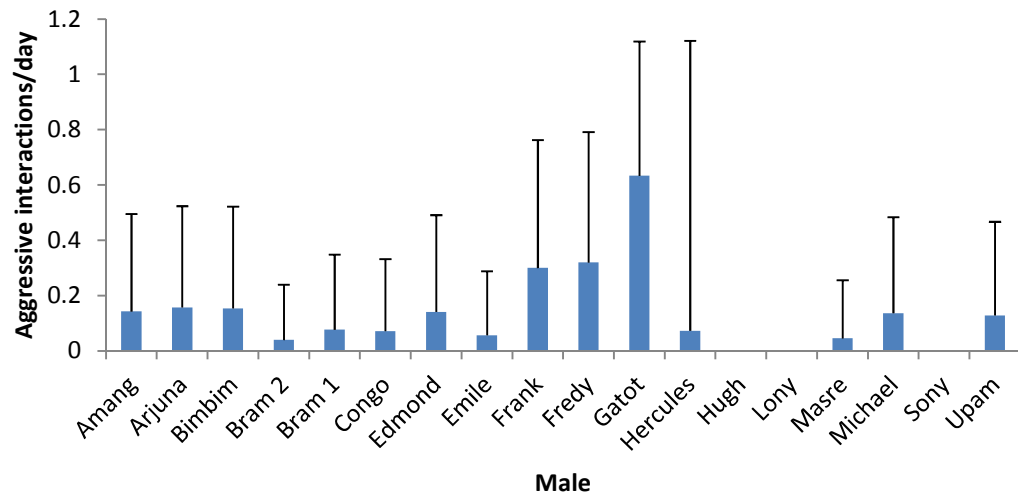
Figure 2.3 Rate of intergroup and intragroup conflict for males residing in uni-male and two-male groups (mean±SD).
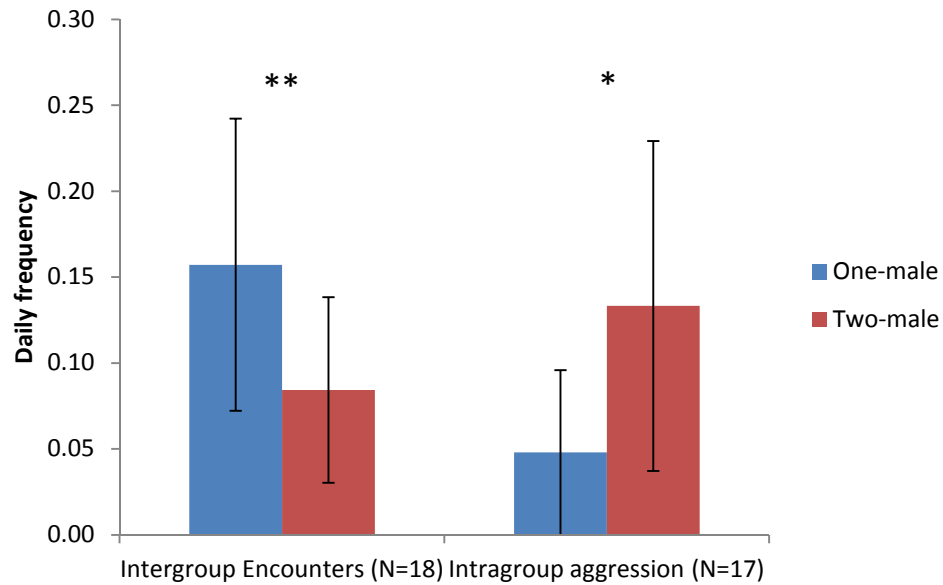
Figure 2.4 Average T concentration of single males, dominant and subordinates (±SE).
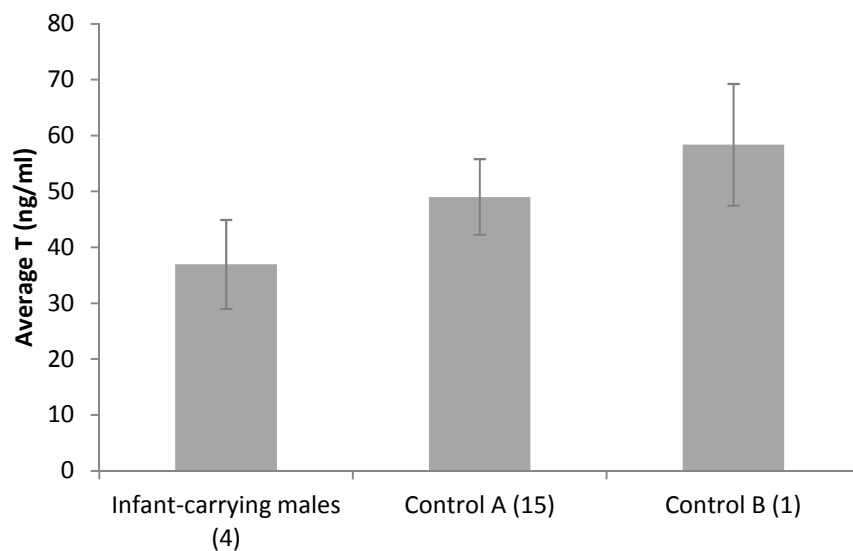
Male Rank and Testosterone

Ninety percent of the agonistic interactions involving co-resident males were directed by the dominant male toward the subordinate one. Nevertheless, there was no significant difference in average T level between dominant and subordinate males living in the same group, both considering all samples (Wilcoxon signed rank test, $Z=-1.6$, $p=0.12$, $N=6$ groups, 357 samples) or when including only days when both males were sampled ($Z=-0.11$, $p=0.91$, $N=6$ groups, 292 samples).

Intergroup Competition and Testosterone

As expected, a male's average T level was positively correlated with the number of intergroup encounters he participated in during the study period ($R=0.86$, $R^2=0.73$, $p<0.001$, $N=18$ males, 572 samples). This result, however, was due to data from the takeover of group B (see below): the correlation disappeared when these

data were excluded from the analysis (R=0.01, R^2=0.00, p=0.98, N=17 males, 529 samples).

Direct challenge to breeding position and testosterone

During the takeover in group B, the challenged resident male (Bram) showed significantly higher average T concentration than he had in the previous 10 months (N=21, U=142, p<0.01; Fig. 2.5). Likewise, the average T concentration of Bimbim was significantly higher during the takeover period than in the preceding period, when he was a secondary male in the stable two-male group B (N=10, U=20.5, p=0.02; Fig. 2.5). The average T concentrations of all three males involved in the takeover attempt were significantly higher than the overall averages of control males – males who were not involved in a takeover during the same time period (Fig. 2.6, Table 2.2). In the period before the takeover, there was no significant difference in T concentration between Bram or Bimbim and the other males (excluding males involved in paternal behavior) (Table 2.2). There was no significant difference between the average T concentrations of Bram's fecal samples and those of his two contenders (ANOVA, F=0.5, p=0.61, Fig. 2.6, Table 2.2).

Figure 2.5 Change in T concentration of males during a direct mating challenge (Group B).
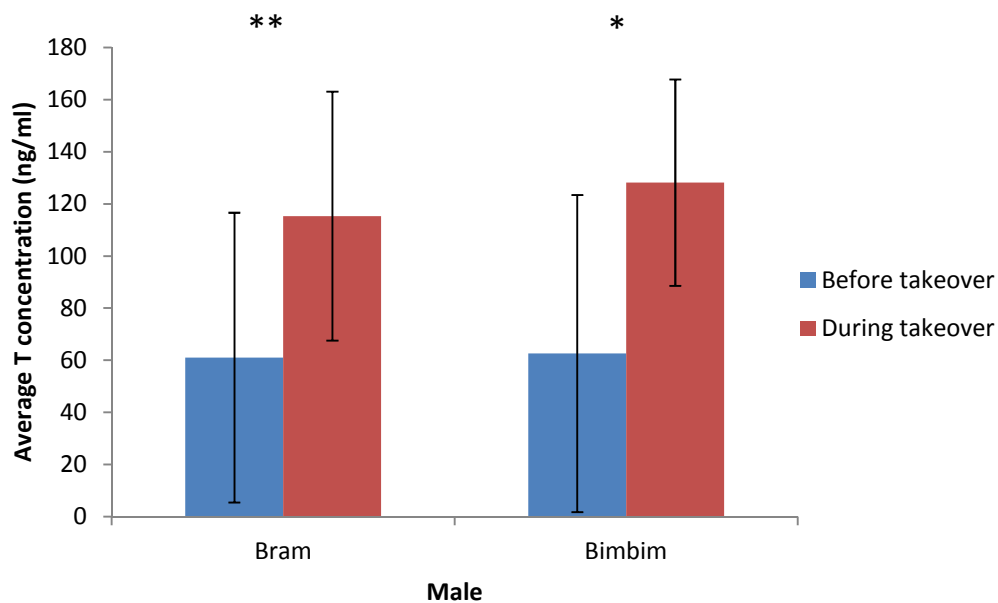
* p<0.05; ** p<0.01

Figure 2.6 Change in male T concentration during a direct mating challenge. Number of samples on parenthesis. Columns with different letters have significantly different values.
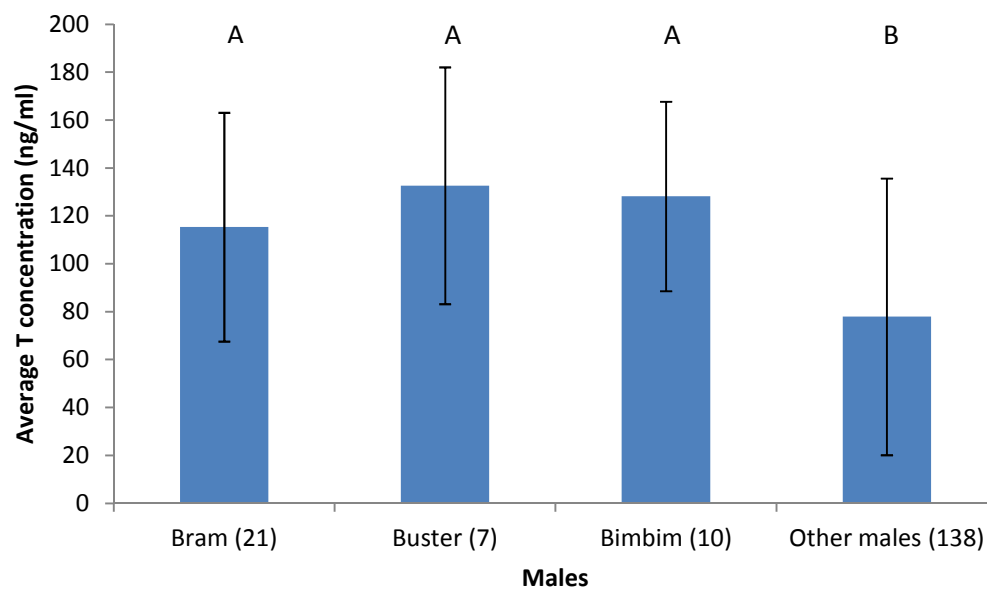
Table 2.2 Testosterone concentration of males before and during a direct mating challenge. Mann-Whitney U test compares males of group B with "other males", which were not involved in the takeover) .

	N samples	Mean (ng/ml)	SD	U	p
Before takeover:					
Bram	28	61.04	55.60	4645.5	0.08
Bimbim	10	62.61	60.83	1532.5	0.17
Other males	412	49.54	53.47		
During takeover:					
Bram	21	115.35	47.76	975	0.014
Buster	7	132.65	49.43	173	0.004
Bimbim	10	128.16	39.56	383.5	0.018
Other males	138	77.92	57.77		

Paternal care and testosterone

The monthly average T concentrations of males regularly carrying infants were consistently lower than those of males with no infants in their group (Wilcoxon Z=-2.04, p=0.041, Table 2.3). Bram, the only male who did not carry an infant of carrying age, also had significantly higher monthly average T concentrations than carrying males (Z=-2.67, p=0.008; Table 2.3). These results are not merely due to the presence of an infant, since there was no difference in the monthly T concentration of males in groups with an infant compared to males without an infant (Wilcoxon Z=-4.54, p=0.65, N=13 months, 534 samples). In group H, where both males were seen carrying the infant in different periods, the carrying male had lower average T values than the male who did not carry at the time (Wilcoxon Z=-2.50, p=0.013; Table 2.4).

Table 2.3 Effect of paternal behavior (carrying) on T concentration. Infant carrying: males who regularly carried an infant; Control 1: males who did not have an infant in their group; Control 2: a male with an infant of carrying age, but who did not carry it.

	N males	N samples	Mean (ng/ml)	SD	Z	p
Infant-carrying	4	84	36.96	27.63		
Control 1	15	450	49.02	23.48	-2.04	0.041
Control 2	1	28	58.37	32.67	-2.68	0.008

Table 2.4 Effect of paternal behavior (carrying) on T concentration: within-group comparison of carrying vs. not carrying males. Note that the identity of the carrier changed during the study period (see methods for details).

Month	N	Carrying male Mean	SD	Non-carrying male Mean	SD
4	2	57.04	-	148.20	-
5	6	7.87	6.76	26.42	10.61
6	6	19.72	14.23	14.43	8.66
7	5	10.00	0.98	51.43	75.82
8	6	15.23	12.88	28.07	14.92
9	7	13.30	1.435	36.35	32.53
10	5	83.45	64.98	112.40	32.57
11	6	109.13	72.52	102.37	84.24
12	4	63.45	5.02	92.90	43.84
13	4	57.50	-	123.73	45.49

Discussion

Several limitations should be taken into consideration when interpreting the results of this study. Some of these are inherent to researching monogamous primates (e.g. small sample size, long life history, arboreality). Others concern variables for which data are unavailable or limited, e.g. relatedness among males, female reproductive status (see below). Nonetheless, these data provide a useful test of the

Challenge Hypothesis in a monogamous/polyandrous ape, and suggests future directions for the understanding of gibbon behavioral socioendocrinology.

Group composition, male rank and testosterone

While the original formulation of the Challenge Hypothesis did not make specific predictions for polyandrous groupings, the presence of two adult males in a group should, *ceteris paribus*, increase sexual competition. Therefore, at the onset of this research male T levels were predicted to be higher in two-male groups than in one-male groups. The data did not support this prediction, however. One intriguing explanation for this finding concerns the possible interaction of the rates of intra- and intergroup aggression. Namely, it is possible that the higher frequency of *inter*group competition in one-male groups might have opposed (and counterbalanced) the corresponding effects of intensified *intra*group conflict in the two-male groups (Fig. 2.3). However, data collected on siamangs living in two-male groups (Morino, in prep.) suggest an alternative interpretation of how the Challenge Hypothesis applies to this population: the clear and stable dominance relationship between males in the same social group, and the (concomitant) extreme rarity of aggression between them, may mean that T profiles should optimally be at or near baseline (since maintaining high T levels has costs – Wingfield et al., 1990). Under such circumstances, T may therefore not differ significantly between the males in two-male groups or between bi-and uni-male groups (in a pattern similar to that described for baboons in stable hierarchies by Sapolsky, 1982). Various factors could alter this equilibrium, internal to the group, or external. Two of these are female reproductive state and kinship.

A female's reproductive state is likely to affect male strategies. While this study did not directly control for this factor, it revealed no difference in the T profiles of males in groups with an unweaned infant (suggesting that the female was not cycling) versus males in groups with a potentially cycling female. A future fine-grained study monitoring female cycles (and focusing on cycling females) could help assess the influence of such factor on male hormonal patterning.

The genetic relatedness of the males in two-male groups was unknown in this study. Kinship potentially explains the low rates of agonistic interaction, but does not preclude high rates and intensities of aggression, as shown by group B's takeover: the male who successfully ousted the resident male was a former subordinate in that group (and presumably a younger brother of the dominant – Morino, in prep.). Future genetic analysis can test whether relatedness affects T profiles in siamangs in a manner similar to that observed in polyandrous golden lion tamarins (*Leontopithecus rosalia*), in which androgen levels of subordinate males were lower than those of dominants that were unrelated to them, but were similar to dominants that were kin (Bales et al., 2006).

Intergroup competition and takeover

Male T levels were positively correlated with the frequency of intergroup encounters, although this result disappeared after exclusion of data from the aggressive takeover of group B. One possible explanation for this finding is that the sampling schedule of this study (3-4 samples/month) did not capture the transient peaks in T corresponding to infrequent inter-group conflicts. Future research should

include a flexible and more intensive sampling schedule to detect short-term

fluctuations in an male's T following agonistic interactions. Another possible

explanation for these results concerns the existence of two different kinds of

intergroup encounter. On one hand, there are encounters with neighboring, already

paired, males. Although these males can attempt to obtain an extrapair copulations

and test the solidity of a male's social/breeding position (Palombit, 1994a, Lappan,

2005, Morino, in prep.), most of these encounters are mainly ritualistic displays, and

may not pose an immediate 'sexual challenge' to a territory holder. Encounters with

unmated or unknown males, on the other hand, are generally genuine, direct

challenges to a male's breeding position, and in fact, in accordance with the

Challenge Hypothesis, T concentrations during an actual takeover were twice as high

as the baseline. This result is coherent with other primate studies, which report

increases in T during social instability (Sapolsky, 1983; Alberts et al., 1992; Setchell

et al., 2008; Teichroeb and Sicotte, 2008).

Paternal Care

The analysis of paternal care data supports the Challenge Hypothesis: males

who carried an infant had lower T levels than males who did not carry or did not

have an infant of carrying age in the group. The male contribution to parental care in

siamangs comprises carrying the infant during group travel as well as grooming and

playing with it on occasion. This care is also quite variable: while some males accept

the role of sole carriers, others do not carry at all, and in some groups the parents and

other group members appear to scramble out of feeding trees to avoid being left

alone with the infant and having to carry it (Lappan, pers. comm.; Morino, pers. observ.). Future research could further investigate how these different parenting 'styles' relate with different T profiles, and seek behavioral correlates that could explain them (e.g., strength of the pairbond).

Conclusions

The results suggest that under socially stable conditions, the T profiles of male siamangs are not affected by group composition, dominance rank or frequency of intra- or intergroup agonistic interactions. Testosterone levels were significantly higher than baseline in males involved in an aggressive takeover, and significantly lower in males who performed parental behavior. These results provide support for the Challenge Hypothesis in a bio-behavioral context heretofore unexamined: a nonhuman, facultatively monogamous ape with paternal care. Future research should explore social factors which could potentially interact with androgen profiles (such as female reproductive state, genetic relatedness), and attempt to detect possible transient peaks in T corresponding to specific, short-term sexual challenges such as intergroup encounters.

CHAPTER FOUR

SIAMANG TAKEOVERS: INSIGHTS ON SMALL APE COMMUNICATION, INFANTICIDE RISK, FEMALE CHOICE

Abstract

The aggressive takeover of a hylobatid group is a rare event that has massive impact on the fitness of the individuals involved. Data on takeovers can help us to understand many aspects of gibbon sociality, such as group formation, dispersal, and the relative roles of female choice and male-male competition. Nevertheless, although several researchers describe takeovers or the consequent demographic changes, few systematic data are available to date. I present data on three takeovers, occurring during a 21-month study of a population of wild siamangs in Sumatra (Indonesia), and test four hypotheses: 1. Variation in siamang daily calling is associated with periods of social instability (such as a takeover attempt); 2. A change of the resident male in a siamang group represents a threat to vulnerable infants; 3. Female 'preferential' behavior toward one of the contenders can influence the outcome of a takeover; 4. A secondary adult male in the group contributes to the defense of the territory/mate (or serves as a deterrent against prospective challengers).

1. Compared to stable periods, duets performed during socially unstable periods were not significantly longer or more frequent, but started significantly later in the day, and contained more great calls and fewer vocal responses by the resident male than

usual. After the arrival of the first challenger, three more contenders appeared, and I argue that the changed calling pattern alerted these males of the takeover opportunity. 2. Three infants disappeared from the groups involved in the takeovers, and mother and infant behaviors suggest 'forced weaning' is used as an anti-infanticide tactic: the takeover coincided with a sudden and sharp drop in carrying and suckling rates, and an increase in the mother-infant distance. 3. Data on aggressive and affiliative interactions, sexual behavior, and singing suggest that takeovers succeeded after the resident female stopped supporting her mate and 'accepted' the challenger. 4. In all three takeovers, older males in one-male groups were ousted, which supports the hypothesis that additional males may be tolerated in a social group because they contribute to territorial defense.

These findings underline the importance of systematically collecting data on rare, important social changes, to improve our understanding of the gibbon social system.

Introduction

Gibbons are small, arboreal, territorial apes living across Southeast Asia (Leighton, 1987). Males and females form long-lasting associations, and predominantly live in one-male or two-male groups (Fuentes, 1999; Lappan, 2007a; Reichard, 2009). While inter-group encounters are an almost daily occurrence for gibbons, the successful aggressive ousting of a resident male is a rare event (Chivers, 1974; Tenaza, 1975; Ellefson 1974; Tilson, 1981; Palombit, 1994a, Brockelman et al., 1998). These episodes, although rare, can greatly affect the reproductive success

of the individuals involved and are thus critical for a full understanding of gibbon

sociality. Many open questions surround the proximate causes and the consequences

of a takeover. How does a "floater" (or a male delaying dispersal) "select" a territory

holder to challenge? Can he obtain relevant information, such as number of adult

males in the group and the strength of the holder(s), from that group's calls? Is the

number of adult males in that group a factor in his decision? How do females affect

the outcome of the challenge? Under what conditions do immigration attempts result

in a stable polyandrous group? Is there a risk of infanticide for the resident

offspring? Are there counter measures against this risk?

Many researchers have described takeovers they have witnessed, although more

often only the outcome is reported (Tilson, 1981; Treesucon and Raemaekers, 1984;

Brockelman et al., 1998; Palombit, 1994a; 1996). The rarity of these events, the lack

of systematic data on them, and the chronically small sample size of gibbon field

studies all conspire against a quantitative approach to the questions listed above.

In this paper I present data on takeovers that occurred over a two-year period in a

population of wild siamangs in Indonesia. In particular I focus on a three-month-long

period of instability involving one focal group and a series of 'challengers', as

several characteristics make this event particularly informative: with one exception,

all the individuals involved were known and well habituated; a high-intensity

observation schedule produced reliable data throughout the various stages of the

challenge; finally, data from the instability period could be compared to 'baseline'

data collected during more than a year prior to it.

I use these data to test hypotheses addressing four main aspects of a takeover.

1. <u>Function of duets</u>. Most gibbon species exhibit complex calling behavior, including 'duets' with sex-specific components and a fixed structure (Haimoff, 1981; Geissmann, 2000). A siamang duet can be divided into distinct phases, and moving from one phase to the next requires vocal and positional coordination between the singing individuals (Haimoff, 1981). One of the most complex phases is the 'great call' sequence, during which the female produces a stereotyped, rhythmic, accelerating sequence of barks and booms. At its climax, the male gives a loud 'bitonal scream', which is not uttered in any other circumstance (Haimoff, 1981). Gibbon songs have been hypothesized to broadcast to neighboring groups information on the location, number, identity, 'fighting ability', and strength of the 'pairbond' of the singers (Chivers, 1974; Mitani, 1985; Raemaekers et al., 1984; Raemaekers and Raemaekers , 1985; Cowlishaw, 1992; Geissmann and Orgeldinger, 2000). Several researchers report more frequent, less coordinated, or structurally different – e.g. lacking the great call sequence – calling for lone individuals and recently paired individuals (Chivers, 1974; Tenaza, 1975; Haimoff, 1981; Tilson, 1981; Geissmann, 1986; Palombit, 1994a; Brockelman et al., 1998). Thus, acoustical features of these calls (e.g. reflecting physical weakness in the caller or disruption in the group) could reveal periods of social instability (e.g. a takeover attempt) and could thus conceivably influence the 'decision' of a listening individual to challenge a certain territory holder.

I tested the following predictions:

Compared to the calling pattern in a stable period, during a takeover attempt there will be:

1a. More calling bouts/day, and longer bouts: if calling is a territorial/"pairbonding"

display, its rate and duration should increase when the group/male is challenged.

This would also be predicted if calling is a way to test or compare potential mates.

1b. A larger proportion of bouts starting later in the day: gibbons typically sing in the

early morning (Chivers, 1974, Leighton, 1987), although singing activity is often

triggered by intergroup conflict (e.g. Ellefson, 1974). The presence of a

challenger could disrupt the habitual singing schedule, eliciting duets irrespective

of the time of day.

1c. More great calls/bout: in a siamang duet, the great call sequence requires sex-

specific vocalizations and accurate timing, thus it seems an ideal measure of

coordination within a gibbon pair. When a pairbond is challenged, a duet is

expected to contain more of these sequences.

1d. A lower proportion of resident male responses to female great calls: during

intergroup encounters, duets are often disturbed by the opposing group (Morino,

pers. obs.). Thus, during a takeover, the challenger calls with the group,

responding to the female's great calls and potentially disrupting the resident

male's response.

Some differences should also be evident between the 'double responses' produced by

the two males in stable two-male groups and those given by two males engaged in a

takeover attempt. Compared to the calls of a stable two-male group, calls given

during a takeover attempt will have:

1e. A lower proportion of secondary male (either the long-term resident subordinate
   male or the challenger) responses to female great calls (for the same reasons of
   prediction 1d).

1f. A higher proportion of non-simultaneous replies from the secondary male: if
   coordination is correlated with the stability of a 'bond' (as it is supposed to be for
   the female and male parts of the great call sequence), then it is expected that two
   males living rather peacefully together (Chapter 2; Lappan, 2007a) sing in more
   coordinated fashion than two males that have never sung together (and are
   ferociously fighting each other).

2. <u>Infanticide</u>. Infanticide is an important selective force in many primate species
(Palombit, in press), and it has been suggested to play a role in shaping the gibbon
monogamous social systems (van Schaik and Dunbar, 1990; but see Palombit, 1999,
2000). According to this hypothesis, adult male gibbons remain in their group to
protect their offspring from other males, who would kill them so that their mother
came into estrous more rapidly (van Schaik and Dunbar, 1990). Some recent data on
Hylobates lar lends some support to this hypothesis, suggesting that "infant loss is
strongly associated with the presence of a new and likely unrelated male" (Borries et
al., 2010: 12). Thus, infanticidal behaviors and countermeasures could be expected
during and after the takeover of a group with a vulnerable infant.

   I tested the following predictions:

2a. The resident female should support her offspring's presumed father against an
   immigrating male (not an exclusive prediction, as males and females could fight

intruding males for different reasons). This may entail initiating or participating in chases and other aggressive behaviors against the challenger (as long as this does not put her offspring in peril), as well as directing affiliative behaviors toward the defender (e.g. grooming or tending to wounds, Ellefson, 1974: 113).

2b. The immigrating male should attempt to kill the infant, during the takeover (to reduce the female's reason to fight him and/or to undermine defending male's anti-infanticide credentials) or after successfully ousting the defending male.

2c. If the infant is at an advanced stage (about to be weaned, around 15-24 months old, Lappan, 2005; Morino, pers. obs.), the resident female could accelerate the weaning, thus removing the cause for infanticide. She could reduce (or stop) carrying or nursing the infant, and keep it at a distance (as measured by the Hinde index, see methods below). This female counterstrategy has been recently reported for wild ursine colobus monkey (Teichroeb and Sicotte, 2008), white-headed leaf monkey (Zhao et al., 2011) and others (reviewed by Palombit, in press).

2d. The female could produce a swelling and copulate with the immigrating male to signal her receptivity and fertility.

2e. If the infant is already able to move independently, it will (try to) avoid the immigrating male.

3. <u>Female choice</u>. The importance of female choice in shaping primate social systems is difficult to quantify, and probably underestimated (Small, 1989; Manson, 1994; Paul, 2002). There is evidence that females may choose their mating partners

in multimale-multifemale groups (Paul, 2002), and they can influence male rank

acquisition (Raleigh and McGuire, 1989), rank reversals (Parga, 2009), and whether

the current male partner will be challenged (Bachmann and Kummer, 1980). Female

gibbons are about the same size as males (Leighton, 1987), have similarly sized,

dangerous canines, are sometimes dominant over their male partners (Ellefson,

1974), and have been shown to play a role in coordinating group activity (Barelli et

al., 2008). Palombit (1994a) reviewed field and captive data suggesting that female

hylobatids can exert significant control over their pair bonded status. For example,

he suggested that one case of a siamang male deserting his mate could have been

caused by the frequent aggression and low levels of affiliative behaviors he received

from her. Similarly, Kawakami and Kollias (1984) wrote that captive lar females

often used overt aggression to reject a mate they had previously mated with (and

readily accepted a new one). It is thus plausible that siamang females could strongly

influence the outcome of a takeover attempt, by supporting either their current

partner or the new suitor. A testable, non exclusive, predictions is that that the male

remaining with a female after a takeover is the one who received support from the

female (measured as grooming and affiliative behaviors, maintenance of proximity,

and absence of overt aggression).

4. <u>Benefits of polyandry</u>. A number of two-male groups have been observed in some

gibbon populations (Lappan, 2007a; Bartlett, 2007; Reichard, 2009). Several

evolutionary benefits have been hypothesized to explain the acceptance of an extra

adult male in the group, but few data are currently available to evaluate them

(Lappan, 2007a). One possibility is that the additional male is tolerated because he helps with territorial or mate defense (Chivers and Raemaekers, 1980; Brockelmann et al., 1998; Lappan, 2007a). If this were true, takeover attempts should be expected to occur more often against monandrous males than polyandrous ones.

Methods

The observations described here are part of a study of siamang behavioral endocrinology, which took place at the Way Canguk Field Station, in southern Sumatra (Indonesia) between August 2007 and April 2009 (for a total of ~4,100 hours of focal follows). The area is a primary lowland rain forest that supports a wide variety of fauna and flora, including two hylobatid species, the siamang and agile gibbon (*Hylobates agilis*) (O'Brien and Kinnaird, 1996). Way Canguk comprises 900 ha of largely undisturbed rainforest, apart from a 165-ha area in the southeast corner which was damaged by forest fires in 1997 (Kinnaird and O'Brien, 1998).See Chapter 1 for more details on the study site and population.

The data presented here were primarily collected on the study group B during three time periods. During the first period (September 2007 to July 2008), two adult males (Bram and Bimbim) were resident in the group. The second period began after Bimbim dispersed in August 2008, leaving Bram as the only group male, and ended at the beginning of January 2009, when the first challenger started following group B regularly. During this third, unstable period, a total of four potential contenders appeared at different times within group B's home range. Two of them (a neighboring male and an unknown individual) only briefly appeared in the area,

countercalled, and were involved in a few chases, whereas the other two (a strange

male, Buster, and the former group member Bimbim) mounted a prolonged

challenge to the resident male. The third period ended when a new stable social

group was formed (more than 15 days with the same partner, Bimbim), in early April

2009. Other members of group B included an adult female, a juvenile female and an

still dependent female of age approximately two years (Table 3.1). The takeover of

group B is described in detail in Appendix A. I integrate these data with some

limited information on the replacement of the resident males in two additional study

groups (Appendices B and C).

Table 3.1 individuals involved in the takeover of group B. Age estimated on the basis of census data and physical appearance (wrinkles, scars, fur quality). Dominance rank was established on the basis of the direction of aggressive interactions and displacements.

Name	Age/sex	'Affiliation'
Bram	Adult male (>20 yrs)	Group B – (Dominant)
Bimbim	Adult male(~8-9 yrs)	Group B – (Subordinate)/ Bram's challenger
Bambina	Adult female (~15 yrs)	Group B
Bondri	Juvenile female (~6 years)	Group B
Bel	Infant female (~2 years)	Group B
Buster	Adult male (~11 yrs)	Bram's challenger
Gatot	Adult male (>20 yrs)	Group G
Garwo	Adult female (>20 yrs)	Group G
Garin	Subadult female (~8 yrs)	Group G
Gawi	Juvenile male (~6 yrs)	Group G
G	Infant	Group G
Combre	Adult male (~15 yrs)	Group C/Gatot's challenger

To analyze intra- and intergroup aggression, I recorded all behavior that could

be considered agonistic in nature: open-mouth threats, chases, lunges, bites, slaps,

(for operational definitions see Chapter 2) during continuous focal follows (Altmann, 1974). I recorded inter-individual distances during instantaneous scan observations (every 10 minutes – Altmann, 1974). Daily grooming data were summarized from continuous focal follows. From focal data on approaches and withdrawals between female and infant (entering or leaving a radius of 3m from the other individual), I evaluated responsibility for the maintenance of proximity (Hinde index), according to the formula: $A1/(A1+A2) – W1/(W1+W2)$, where A is an approach, W is a withdrawal and 1 and 2 are two individuals (Hinde and Atkinson, 1970). I compared Hinde indices during three periods: the month before the first take over (December 2008), the four days immediately after the first takeover (18-21 Jan 2009), and those immediately after the second takeover (18-21 Mar 2009). I did not calculate a Hinde index for the period immediately before the second takeover because two additional males were present at the same time, thus confusing the interpretation of those data (as it would not be clear who the infant was reacting to). These intervals allowed me to obtain a minimum number of interactions while being brief enough, and close in time, to reduce the influence of other factors affecting the mother/infant relationship (e.g. natural development of the infant, seasonal changes). At the end of each observation day during these three periods, I estimated the percentage of travel time (moving >10m and out of a tree) the infant was carried by the female, and recorded whether or not suckling was observed at least once during the day (*ad libitum* observation, Altmann, 1974). I defined Bel an 'infant' even though she was at the upper end of this age category. Lappan (pers. comm.) found weaning ages to be very variable, but some infant weaned as early as 15 months. At the time of my

observations, Bel was regularly nursing, and while she mostly moved independently within trees, she was consistently carried when traveling, thus I think it is warranted to consider her a dependent offspring.

I define an intergroup 'encounter' as a period of more than 10 minutes in which the study group was within 30m of one or more extra-group individuals. Encounters invariably included counter-singing, defined as a singing bout that started within 5 minutes of the opponent's bout, and/or agonistic interactions (Morino, pers. obs.).

Every time a group duetted, I recorded the following:

- Starting time and duration of the call. A singing bout started when an individual began calling, and ended when the group stopped calling for at least 5 minutes.

- Number of female great calls: complete, aborted (Haimoff, 1981), double – if given in unison with a non-adult female of the same social group.

- Number of resident male replies to the female's great calls. A reply is defined as Haimoff's (1981) "bitonal screams", delivered within 2 seconds of the end of the female's great call.

- Number of challenger male replies to the female's great calls.

- Timing of male replies: whether they were simultaneous or not (if there was a delay of more than 1 sec between them).

Results

Comparison among time periods

The instability period in group B comprised two attempts to oust the resident male, by different challengers. The takeover attempts followed a similar pattern: an initial period of fighting, then ≥2 days during which the resident male no longer ranged with the group and the challenger was the only male to range with the resident female, and then further conflict involving other, floater, males. At the end of the first attempt, the resident male returned to his original position, whereas in the second case, the challenger retained the position as resident male in group B (see Appendix A for more details).

Group B was involved in a significantly higher number of intergroup encounters (including those with the challenger) during the period of instability compared to the period before it, whether one or two males were in the group (Table 3.2). The frequency of male intrasexual aggression was likewise significantly higher during the period of instability than in stable phases (Table 3.2).

Table 3.2 Inter-group encounter rate (per day) and aggressive interactions for group B, during the three phases: (1) two resident males (Sep 2007- Jul 2008); (2) one resident male (Aug 2008-Dec 2008); (3) transition (Jan-Apr 2009).

	Phase 1	Phase 2	Phase 3
# observation days	45	24	40
# of encounter/observation day	0.15** (±0.36)	0.25* (±0.44)	0.57 (±0.5)
# of aggressive interactions/observation day	0.06** (±0.32)	-	1.52 (±2.75)
# of encounter/observation day (excluding challenger)	0.15 (±0.36)	0.25 (±0.44)	0.17 (±0.38)

*Independent samples T test comparing with Phase 0: p<0.05; **: p<0.01

During the period of instability (phase 3), there was no significant difference in number of encounters with neighboring groups when compared to the previous phases (Table 3.2). During the three months (Jan-Mar) of the takeover, however, there were 7 intergroup encounters in 38 observation days (a rate of one encounter every 5.4 days), while during the same period of the previous year no encounters were observed in 13 observation days.

Singing

The number of singing bouts per day was not significantly higher during the instability period compared to the preceding stable period (Table 3.3). Two factors contributed to a higher variability in the takeover period: during the takeover there were six days with 4 or more duets, a number never recorded in the stable period; but there were also three days when the adult female (Bambina) did not join the challenger in a duet. The average bout duration during the takeover period was not significantly different from that of the preceding stable period (Table 3.3). During the takeover, bouts started significantly later in the day, contained significantly more great calls, and significantly fewer responses to female great calls from the resident male. There were other peculiarities in the singing during this period. For example, in one instance (on March 16) Bambina started singing when the primary male was away from the group and gave 7 'solo' great calls. Within 10 minutes three adult males (Buster, a neighbor and an unknown individual) approached her and replied to her calls.

Table 3.3 Comparison of singing bouts during the three phases. Phase 1: two resident males (45 days, 37 bouts); phase 2: one resident male (24 days, 36 bouts); phase 3: transition (40 observation days, 66 bouts). Primary male is the resident (dominant). Secondary is the subordinate in Phase 1 and the challenger in Phase 3.

	Phase 1 ((Mean±SD)	Phase 2 (Mean±SD)	Phase 3 (Mean±SD)	t	df	P*
Bouts/day		1.5 (±1.1)	1.65 (±1.48)	-0.43	62	0.669
Bout duration (min)		14:15 (±7:43)	13:48 (±5:36)	0.34	100	0.738
Singing time (min/day)		24:54 (±16:19)	27:10 (±21:39)	-0.41	51	0.687
Bout initiation time (hh:mm)		8:42 (±1:28)	9:40 (±2:23)	-2.57	96.40	**0.012**
# Female Great Calls/Bout		4.78 (±1.55)	5.91 (±3.16)	-2.42	99.17	**0.017**
Primary male reply/GC		0.98 (±0.05)	0.88 (±0.29)	2.77	72.43	**0.007**
Secondary male reply/GC	0.56 (±0.41)		0.50 (±0.44)	0.63	101	0.529
Secondary male reply/GC (simultaneous)	0.49 (±0.38)		0.26 (±0.33)	2.39	80	**.019**

*Independent samples T test comparing to Phase 0

When comparing the 'challenger' with the resident subordinate male, I found no significant difference in the proportion of great calls they responded to. There was a significant difference, however, in the timing of the reply: when the secondary male was a stable resident in the group, nearly half of his replies were simultaneous to those of the primary male, whereas when he was a challenger, only 26% of his replies were simultaneous (Table 3.3). To control for a possible confounding effect of seasonality, I ran the same analysis on three other groups who remained stable

throughout the study, and found no significant variation in the secondary male singing between the two time periods.

Infanticide

The first prediction of an 'anti-infanticide' tactic on the female's part is that she would support the resident male against the challenger. In the first three days of the takeover of group B, all of the aggression was directed by the resident male (Bram) toward the challenger Buster (N=15). On the fourth day, Bram seemed impaired by the wounds he had received during conflict with Buster, e.g. he moved slowly, reacted less often to Buster's approaches, fell out of a tree during a chase. On this same day, Bambina was seen for the first time participating, with Bram, in two chases of Buster. Throughout the takeover period, whenever Bram was present she groomed and tended to his wounds (while only agonistic behaviors were directed toward Buster). When Bram stopped fighting Buster, trying to avoid him instead, Bambina stopped supporting Bram and accepted Buster (by allowing him to approach her without lunging at him).

Fewer data are available on the takeover of group G, but the resident adult female Garwo was seen siding with the challenger and chasing the resident male. It is unclear whether this happened from the beginning or, as in the case of group B, only after it had become clear that her mate was not able to repel the challenger. According to the infanticide avoidance hypothesis, both the females of groups B and G should have supported the male defender (assuming it was their infant's father) against the challenger.

No infanticidal attempts were observed from Buster, Bimbim or Combre. Nonetheless, an analysis of the pattern of proximity between Buster and the females of group B suggests that the infant of group B, Bel, avoided Buster (Fig. 3.1A): while Buster's distance from Bambina and the juvenile Bondri significantly decreased on the third day they spent together (1/21/2009 on Fig. 3.1A), the distance from Bel remained relatively large (ANOVA, $F=8.18$, $p=0.001$; Contrasts: Bel-Bambina: $t=-4.04$, $p<0.001$, Bel-Bondri: $t=-2.11$, $p=0.041$; Fig. 3.1A). Figure 1A also suggests that the average distance between Bel and Bambina varied inversely to that between Bambina and Buster. Bel also avoided passing close to Buster, moved in a peculiar way, with frequent brief stops (in contrast to the usual fluid, uninterrupted movements), when near him and never participated in grooming bouts involving him. Buster was never seen moving directly toward Bel, whereas he did approach and groom Bondri. Bel's behavior toward Bimbim seemed more relaxed: she moved less jerkily around him, did not flee when approached, and did not avoid him. The distance between Bel and Bimbim was not significantly different from that between him and the other females, but this might be due to him being relatively far from the rest of the group (Fig. 3.1B).

Figure 3.1 Average distance (± S.E. bars) between the challenger and the females of group B (Bambina: adult female; Bondri: large juvenile; Bel: infant) and between Bambina and Bel during the takeover period. On parenthesis the number of scans. A) Buster; B) Bimbim.
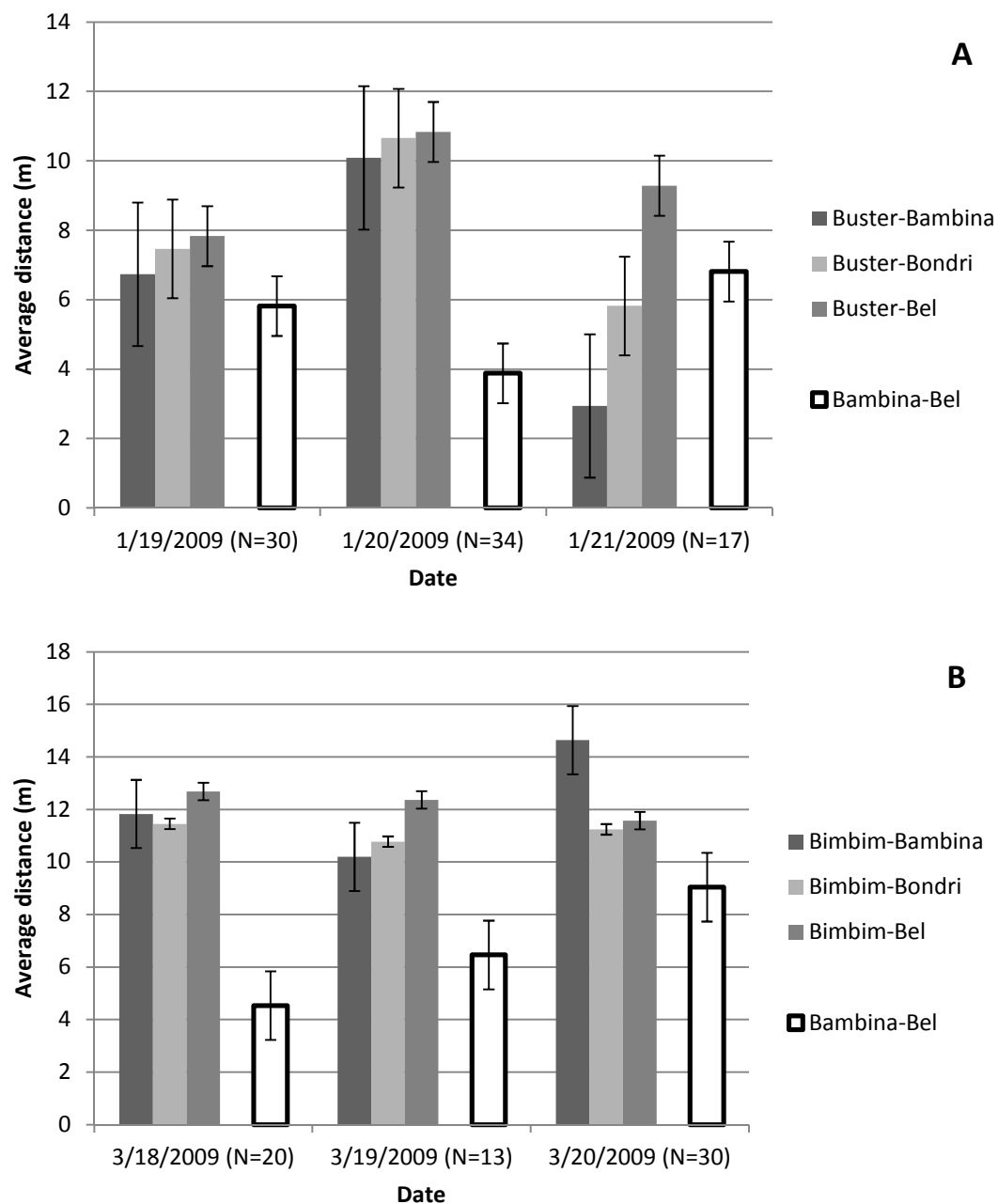
During the takeover periods, focal animals were out of sight more often than usual, thus limiting the number of maternal behaviors I could analyze quantitatively. At the time, the infant female Bel was already moving independently within trees, but she was regularly carried by her mother when traveling, and she regularly suckled. During the first four days of the takeover, I estimated Bel to be carried by Bambina around 90% of her traveling time, and I observed her suckling several times each day (N=41 focal follows on Bambina). From the first day that Bram was not in the group, however, both carrying and nursing suddenly and sharply dropped, and never returned to the previous levels: my estimates of carrying time were 4-8% (18-21 January, N=81 focal follows on Bambina), and Bel was never observed nursing until more than a month later. Bambina rejected Bel's attempts at suckling or being carried (open-mouth threat, Palombit, 1992, Liebal et al., 2004), Bel struggled to keep up with the group, often cried (but muted her cries if Buster was nearby), fell to the ground a few times, and suffered a small superficial wound behind the left ischial callosity. In the same period, the average distance between Bel and Bambina increased inversely to that between Bambina and Buster (Fig.1). The Hinde index showed a minimal decrease, going from -0.36 (N=60) during the month preceding the takeover to -0.31 (N=38) in the four days afterwards (a Hinde index of 1 would indicate complete responsibility of Bambina). During the time Bimbim was the sole male in the group, the Hinde index between mother and infant was -0.5 (N=24). The sudden drop in carrying and nursing time, and the distancing from Bel suggest that Bambina might have anticipated the weaning of her daughter. The fact that this occurred in correspondence to the arrival of a new male suggests infanticide

avoidance as a possible explanation for it. While these results are partly based on estimates of carrying and nursing, the difference between before and after the takeover are so sharp that they are unlikely to be due to sampling error. It is possible that Bambina nursed her infant when the group was not observed (e.g. after entering the sleeping tree), but this would be consistent with the hypothesis if the purpose was signaling to the new male a change in reproductive status.

In terms of sexual behavior, Bambina mated with Buster at least twice after Bram ceased fighting him and left the group. Interestingly, at the time of Buster's takeover Bondri and Bel also started developing what looked like a sexual swelling (turgid, light-pink labia), which noticeably enlarged during the following month. This was the first time such swelling was observed in Bel, while Bondri showed some swelling for the first time in mid-December 2008. This is the first time that such swellings are reported in wild juvenile siamangs. A peculiar behavior that all three females in group B performed toward the invading males was 'branch shaking': holding two branches with the two extended hands, and rhythmically shaking them, at intervals of 1-2 seconds. The behavior seems to be a sexual solicitation, as it was often followed by the female taking a copulatory position (Palombit, 1992, 1994a; Morino, pers. obs.), but it may also have a threatening component (cf. branch-jerk – Ellefson, 1974: 130). In the same period, Bel sometimes participated, for the first time, in a group calling bout, and Bondri started giving regular great calls, synchronized with Bambina's (as is typical for juvenile siamangs).

Bel disappeared from the group within four months of the end of this study (A. Elder, pers. comm.). Similarly, the two-year old infant of group G disappeared within a month of Combre's taking over the group. Additionally, the infant in group C, who had been carried by Combre, also disappeared within a month of Combre's emigration. Unfortunately, no data are available on how that happened and whether or not the other adults in group C carried this infant. Prior to Combre's emigration, the other adult male Congo was seen carrying the infant only once in 20 observation days.

Female preference

As mentioned above, Bambina attacked and chased Buster when Bram received wounds that impaired his ability to fend off the challenger, and tolerated Buster's proximity only after Bram completely stopped fighting, avoided Buster and eventually left the group. Bimbim's challenge followed a similar pattern. On the last day of conflict, a wounded Bram was unable to defeat the younger, faster, healthier male, and after the last chase moved slowly away. Bambina, who had previously followed Bram, supporting and defending him from Bimbim, waited 20 minutes, and then moved in the opposite direction, followed by Bimbim and her offspring. In contrast, Garwo, the resident female of group G, was seen directing affiliative behavior toward the challenger and attacking her own mate. It is unknown for how long that takeover had been occurring at the time of the first observation. Soon after the female changed her allegiance, all three takeover attempts ended with the displacement of the resident male.

Some differences were evident in Bambina's behavior toward the two challengers, Buster and Bimbim. Although her average distance from them did not differ (independent t test: t=-1.41, p=0.16, N= 50 scans - Buster, 159 scans - Bimbim; Fig. 3.1A and B), and she copulated with both males, she reciprocated Bimbim's grooming three days after his reappearance, versus the six it took before she groomed Buster. Bambina also sang with Bimbim from the first day they spent together (without Bram), whereas she did not sing with Buster during the first two days they spent alone, and only sang one duet in all subsequent days, in spite of his repeated attempts at starting duets (group B sang on 77% of a total of 104 observation days, and on 92% of 36 observation days during the transition phase). Finally, Bambina directed aggressive behaviors toward Buster 19 times, across 6 observation days, as compared to only 4 aggressive behaviors against Bimbim, all of which occurred in a single day. The different behavior of resident females toward resident or challenger males seems to confirm the important role they play in determining the outcome of a takeover.

Benefits of polyandry

In 21 months of data collection on 11 siamang groups (5 two-male groups, 4 one-male groups, 2 groups changed composition during the study), all three male replacements I witnessed involved a monandrous male, whereas no dominant male in two-male groups lost his breeding position. Bram was challenged after he had become the single resident male in group B. This suggests that the presence of a

second resident male in a group might reduce the risk of aggressive takeovers from floater or neighboring males.

Discussion

Singing

There is disagreement about the function of the complex gibbon duets. One hypothesis is that they advertise the strength of the bond between the adults in a group (Cowlishaw, 1992). A male looking for a territory (e.g. a floater or "helper in the nest"), after listening to neighboring calls may decide not to challenge a male if his duetting is well coordinated with his pair mate, whereas flaws in their song may indicate poor coordination in a pair or a moment of social instability that could be tested.

In this study, significant changes in a group's duetting patterns were associated with a period of increased intergroup confrontations and agonistic interactions (Table 3.2, Table 3.3). The direction of causation could go both ways: a potential challenger could be attracted by changes in the singing pattern, and its arrival may affect the singing pattern in turn. One can only speculate whether the first challenge to Bram was triggered by signs of weakness apparent in his calling, but the subsequent arrival of two additional suitors seems quite likely to be related to the change in group B's singing pattern. These changes included: frequent duets at unusual afternoon hours (once well after sunset), more great calls than usual, and fewer responses by the resident male. This situation recalls a report on a group of Kloss' gibbons: after an adult male disappeared and was replaced by the group's subadult male, many

'suitors' appeared in the territory; it is possible that these suitors were attracted by the subadult's 'inexperienced' calling (Tilson, 1981).

Some changes in siamang duetting are evident (such as the number of males responding to female great calls), while others (such as the lack of coordination between these males) are more subtle. More data are needed to confirm that a listener is able to distinguish between a secondary male integrated in the group and an extra-group challenger based on this variation in calling. On the other hand, it is very likely that siamangs possess a much more sophisticated auditory processing ability allowing them to directly identify different callers, as suggested for Javan gibbons (Dallmann and Geissmann, 2001).

Two predictions were not confirmed by the data. First, in spite of the fact that the highest daily duet rates were recorded during the takeover, average duet rate did not significantly increase in this period. The intense duetting of some days was probably offset by the days with no singing, when Bambina did not respond to her new and potentially unwanted partner's calling. Second, duets were also slightly shorter (rather than longer) during the takeover period compared to the preceding stable period. One possible explanation of this result is that during the takeover period, many duets were cut short by the escalation of the great call sequence – which is typically accompanied by a vigorous visual display (Chivers, 1974) – into a chase of the challenger.

Duets during a takeover contained significantly more great calls than during stable periods. This is not simply a side-effect of elevated arousal, as alarm calls, elicited by potential predators, entirely lack great call sequences. The exact meaning

of these great calls requires more data to be elucidated. One possibility is that they are used to attract potential suitors and test their quality or compatibility, possibly shown by the timing and strength of their replies, the length and quality of the male-specific parts. The fact that a 10-min female solo calling elicited the vocal response of three surrounding males, and fighting that went on throughout the day, confirms the importance of this aspect. Another possibility is that these great calls are a female's demonstration of support of her partner. Ellefson (1974) describes how some male lar gibbons involved in intergroup confrontations 'received reassurance' from their mates in the form of calling and grooming.

Bambina's failure to duet with Buster after the ousting of Bram could be interpreted in this light. Newly formed pairs typically sing less coordinated duets, and fail to produce complete great call sequences (Haimoff, 1981; Geissmann, 1986; Palombit, 1994a; Maples et al., 1989), but also sing more frequently, possibly to quickly learn to coordinate singing (Geissmann, 1986). The fact that the new pair Bambina-Buster spent three days without singing could mean that Bambina accepted Buster's grooming and copulated with him (activities that are not broadcasted outside the group), but did not 'announce' Buster's position as her new mate by singing with him. Two facts are consistent with this idea: Bambina rushed to and duetted with the recovered Bram, and she readily sang with Bimbim – two individuals whom she might have preferred (see below).

Unexpectedly, the duets Bambina sang with both challengers were reasonably well coordinated from the start. This could be due to the facts that a) Buster had sung with the group for at least a month before remaining Bambina's lone partner (and

indeed his mis-timed replies during that period showed that he was learning); and b) Bimbim was a former member of group B, and therefore already accustomed to singing with them. Further data and analysis are needed to assess the importance of the various behaviors surrounding the establishment of a new pair (e.g. approaching, grooming, copulating, singing).

Infanticide

No infanticide or infanticidal attempts were witnessed during these transitions. Several aspects of group B's takeover, however, were consistent with an anti-infanticide strategy. Bambina supported her offspring's putative father, up until it was clear that he could not defeat the challenger. It is unclear whether the female of group G did the same. Active participation in chases is uncommon in female gibbons, and, in fact, Bambina had never been seen participating in a physical confrontation prior to the takeover period. Her support of Bram, however, could have other explanations than infanticide prevention (see below).

After Buster's takeover, Bambina abruptly stopped nursing and carrying her infant, making threat-faces to dissuade her approaches. As Bambina spent more time close to Buster, mother and daughter also spent less time in close proximity to one another. In sum, within a few days Bel's place in the group changed radically: before the takeover she was still considerably dependent on her mother, while after Buster took over she would have looked to a naïve observer as at a much more advanced developmental stage. These data must be interpreted with caution: first, they come from a single takeover attempt; second, by the time the abrupt change in behavior

occurred, the challenger had had time to assess the infant's developmental stage; third, although Bel was definitely heavily dependent on her mother at the time of these observations, she was already old for an 'infant'. The picture these data suggest, however, seems consistent with an anti-infanticide strategy: if Bel was seen by the immigrating male as already independent from Bambina, it would not be necessary to kill her in order to accelerate Bambina's return to cycling. This countertactic has also been documented in white-headed leaf monkeys: in a recent study, all 17 females that had older infants at the time of a takeover successfully force-weaned them (Zhao et al., 2011). Other anti-infanticide options exist, for example defending the infant from the infanticidal male, or emigrating from the group/following the ousted male, but they seem ineffective for female gibbons: defending a vulnerable infant is not sustainable in the long term, especially with no help from other individuals (and this was found to be an unsuccessful strategy in other taxa, e.g. Teichroeb and Sicotte, 2008). Likewise, loss of a territory would have far worse fitness consequences than losing a baby for a species in which reproduction is so strictly connected with successfully defending a breeding territory.

A rather puzzling circumstance, possibly related to an anti-infanticidal strategy, is the appearance of a sexual swelling in Bel, a two-year-old, unweaned female. I could not find a comparable report in the literature. Sexual maturation in gibbon females occurs at around 6-8 years of age (Palombit, 1995; Barelli et al., 2007). The appearance of sexual swellings in both immatures, their proceptive behavior, and their participation in group calling suggest that a takeover may act as a catalyst for the sexual maturation (or external signs thereof) of opposite sex individuals.

Within four months of the end of my study, Bel had disappeared. The same happened, under very similar circumstances, to the infant of group G: a change in resident male, the infant not carried, struggling and falling to the ground in an attempt to keep up with the group, and eventually disappearing. A third infant, that was usually carried by the male who immigrated into group G, also disappeared from his group C. The fate of these young siamangs is unknown, but it is unlikely that they survived on their own, given their young age. The 1-year old infant in group U, on the contrary, survived the disappearance of his putative father and his replacement by the subadult of the same group, who cared and carried him throughout the study (Appendix C). These data strongly suggest that while these infants' disappearances cannot be directly linked to an infanticidal attack by an immigrating male, they were undeniably caused by periods of social instability, thus supporting the pattern proposed by Borries et al. (2010) for *H. lar*.

Female preference

Both challenges to Bram succeeded after a shift in Bambina's support. After Bram received a disabling wound, he was able to fend off Buster with Bambina's aid, but then it became clear that he could not be able to evict Buster. At that turning point, Bambina copulated with Buster, who subsequently started to actively attack Bram, and rapidly ousted him from the group. A similar pattern occurred during Bimbim's challenge. Fewer data are available on the takeover of group G, but the challenger rapidly won the conflict when the resident female of that group took his side against her previous mate. Another suggestion of the female's influence on a

male's social position could be seen in the different behavior of Bambina toward Buster and Bimbim. Data on aggression, singing and grooming suggest that she 'preferred' Bimbim over Buster. It may thus not be accidental that Buster lasted only a week as her partner, whereas Bimbim remained as her stable mate. While the small sample size and some qualitative assessments limit the conclusions of this study, the data seem to indicate that female preference for one of the contenders can strongly influence the outcome of a takeover in this species, as also noted by Palombit (1994a, 1996).

Data on female choice are now available for a good number of wild primate populations, but most of them refer to the choice of a mating partner, often in the context of sneak copulations, and only few studies address a female's influence on a male's acquisition and maintenance of social status (e.g. Bachmann and Kummer, 1980). Determining who is the partner of a single mating event can have direct fitness consequences, but influencing the social position/rank of a male (assuming that it correlates with reproductive success) will have a considerable long-term impact on both the chosen male's and the choosing female's fitness. This is especially true for the monogamous gibbons, where a mating pair can be together for several years, and the mating success of unmated adults is uncertain, but probably much lower than territory holders.

More data are needed to determine what attributes a female gibbon selects for in a male. She could favor a male who is capable of defending the group's resources, or one with a good knowledge of the territory, or a time-tested mate with whom she is well coordinated. In the case of siamangs, where some males are involved in infant

care (Lappan, 2008), females could prefer a helping male. Both of the males ousted during this study were never seen carrying an infant, and Palombit (1994a) reports another case of possible eviction of a non-helping male.

 Infanticide avoidance and preference for her present mate both predict that a female gibbon with vulnerable offspring will support her mate against an outsider. More data on takeovers in groups with or without vulnerable infants will help disentangle these competing hypotheses.

Benefit of polyandry

The three takeovers that were witnessed during the study period occurred at the expense of resident males in monogamous groups, in both cases males past their prime, thus suggesting that a secondary male may indeed help to deter such attacks. Their low frequency and the chosen targets support the idea that takeovers are dangerous for a challenger, and thus attempted only when the odds are favorable. In a saturated habitat, this creates a feedback loop: young adult males delay dispersal because immigrating into an established group or living as a floater are risky strategies; thus, they remain in their natal groups and help in territorial defense, consequently making dispersal harder.

If multi-male groups have a competitive advantage in territorial fights, they could also be expected to sustain fewer inter-group encounters. Preliminary data on this siamang population show that the number of resident males in a group does not affect the amount of inter-group encounters that group is involved in. Single resident males, however, are involved in a significantly higher number of inter-group

agonistic interactions than males living in two-male groups (Chapter 2). This supports the idea that takeovers are more commonly attempted against one-male groups.

Dispersal and group formation

Several authors have suggested that male gibbons emigrate into neighboring territories (Brockelmann et al., 1998; Lappan, 2007b). The two successful takeovers I report confirm this hypothesis: Combre ousted his neighbor; Bimbim spent five months away from the group he belonged to, then returned and took over its contested breeding position. It is not known where he spent those five months, but it is possible that he had remained 'in hearing range' given that he returned when his former group was undergoing a period of instability (presumably detected by changes in its singing pattern). Several analogous cases are reported in the literature (Tilson, 1981; Palombit, 1994a). The fact that Combre stayed in his original group as a subordinate male until he was able to obtain a breeding position supports the notion that some of these subordinate males are allowed to delay dispersal in their group. It is unknown if his putative father Congo helped Combre taking over group G, as was reported in a Kloss' gibbon group (Tenaza, 1975). Finally, in the male replacement in group U, it is likely that the very old resident male died or left the group, and the resident subadult inherited it, another known way to obtain a territory for a gibbon (Palombit, 1994a; Brockelman et al., 1998).

Conclusions, limitations, perspectives

This account of takeovers of two well-habituated groups supports some current hypotheses about gibbon socioecology and suggests new ones. Variation in singing reflects periods of social instability in a siamang group. Some behavioral and physiological changes observed during takeovers are consistent with anti-infanticide tactics. Female choice may influence the outcome of male-male competition for breeding positions. The value of these observations, however, is limited by the small sample size, and the difficulty of following and correctly interpreting behaviors that often develop and change very fast. To expand our knowledge of gibbon sociality, thus, it is necessary to systematically collect and compile data on takeovers and other rare but pivotal behaviors and events across field sites.

CHAPTER FIVE

CONCLUSIONS

The three components of this study contribute to our understanding of the gibbon social system, the interplay between hormones and behavior, and in general to mechanisms of mate selection and retention, dispersal, and intraspecific communication. In this section, I briefly summarize the major findings of this study, try to draw general conclusions and suggest future directions.

The hormonal analysis accomplishes several major goals. It provides the first data on the androgen profiles of any wild male hylobatid. The sample size (19 individuals) is remarkably large for this taxon, and the fact that these samples were collected under natural conditions makes them even more significant. Studying wild arboreal primates, and gibbons in particular, poses many difficulties: subjects are highly mobile, making it hard to follow them; they spend most of the time high in the canopy, making it difficult to observe their behavior in detail and collect fecal samples; they and their environment are threatened, making it difficult to find healthy and large populations to study. I could achieve such large sample size by investing a long time in habituating the study groups (and thanks to the work of previous researchers), in training and employing qualified and motivated field assistants, and thanks to the high density of siamang groups in the Way Canguk area. The results of the testosterone analysis represent a valuable test of the Challenge Hypothesis: the vast majority of the work on this subject has been conducted on birds, and among the studies focusing on mammals, this is one of the very few that

tested predictions in a species somehow resembling birds, with its monogamous/polyandrous, biparental mating system. Therefore, the correlations I found linking testosterone levels with social challenges and male parenting behavior support and expand the validity of the model, thus significantly improving our understanding of the complex interactions between hormones and behavior. Finally, given that humans and siamangs are the only two catarrhine primate species forming long-term pair bonds and exhibiting paternal care, these results confirm a continuum between the endocrine responses of our own species and those of other mammals/vertebrates. Besides, research on hylobatids could benefit from studies on various human populations, which can suggest interesting new directions: in fact, besides the fact that fathers have lower T than non-fathers (Gray et al., 2002; 2006), it has been shown that single males have higher T than males in long-term relationships (Booth and Dabbs, 1993; Gray et al., 2002); and that polygynous men have higher T levels than monogamous or single males, possibly due to mate guarding (Gray, 2003).

The other major contribution of this project is the study of polyandrous groups. Many questions surround the origin and maintenance of such configuration in gibbon populations, and this study provides solid answers to some, and good indications for others. This research revealed a mechanism allowing adult males to coexist peacefully in close proximity to one another, making this social organization possible. Furthermore, it provides the first evidence for a benefit for a resident (dominant) male that might offset the potential costs of tolerating an additional adult male in the group: males in two-male groups were exposed to significantly less

physical aggression, and were less likely to suffer a takeover. Finally, from the perspective of the subordinate individual, this study shows that while his reproductive success as a secondary male is likely to be very low, he is suffering very limited aggression (especially compared to the fate of the few floaters I and others have seen), and, importantly, he could still be able to monitor potential dispersal opportunities, by listening to neighboring duets and directly testing neighbors through encounters.

On a broader perspective, results of this study can also contribute to the conservation of this (and other) species. The high frequency of polyandrous groups in Way Canguk may be due to an increase in demographic pressure, brought by natural forest fires (Morino, Lappan, O'Brien, Kinnaird, in prep.). Given the rate at which forests are disappearing, it is likely that most gibbon communities will face the same issues, and the endocrinological and behavioral data provided by this study can help and direct conservation effort, for example in assessing the potential effect of the ecological features of a certain forest patch on the siamang groups inhabiting it, or in showing the socio-ecological conditions under which it is possible to socialize or reintroduce groups with more than one male.

These results also open up new avenues of research. Three components will greatly enrich the current analyses. Genetic data would allow a better understanding of the relationships between adult males, of the true effectiveness of different male reproductive strategies, and of additional services subordinate males may provide (e.g. infant carrying). Data on female reproductive profiles would help interpret male aggressive behavior and possibly female behaviors reflecting her preferences.

Finally, data on cortisol levels would allow the measurement of stress levels associated with different social groupings and dominance ranks, and the possible detection of non-agonistic forms of competition regulating the interaction between males (e.g. physiological suppression of sexual function).

APPENDIXA – TRANSITION IN GROUP B

Group B:
Bram: dominant adult male (AM1). At least 20 year old, based on census data, amount of wrinkles and scars on face and body and fur gloss.
Bimbim: subordinate adult male, ~8-9 years old.
Bambina: adult female (AF), at least 15 years old.
Bondri: large juvenile (BJ), about 6 years old.
Bel: infant (SJ), about 2 years old. Only carried by Bambina

Challengers:
Buster (AM2): younger than Bram, estimated to be 10-11 years old (based on wrinkles, scars and fur).
Lony: resident male of the neighboring gr. L (composed of adult male and adult female). Estimated to be 17 years old (based on physical appearance and census data).
AM4: unknown male, estimated to be ~10 years old (based on physical appearance).
Bimbim. See above.

Timeline
December 18, 2008: an unknown male, called Buster, appeared near group B. He remained within 50m of them for most of the day, countercalling and responding to the female's great calls. When he approached too close, he was chased away from Bram, once for over 200m. Also the sole adult male of group L, Lony, came in contact with group B, for the first time since the beginning of the study.
December 20: another encounter with gr. L. No sign of Buster.
December 21: another encounter with gr.L. Only Lony participates to these encounters. I did not observe any physical aggression.

January 13, 2009: there are calls from gr. B's home range at 18:00 and later at 21:57, with three great calls, responded to by two males.

January 14: I transcribe my notes to give an example of the group dynamics. I will then summarize the happenings of the following days.
6.01 – Gr. B calls
6.38 – Gr. B calls again
7.33 – Gr. B calls. Both males reply and give many ululating calls. Most replies (to female great calls) are synchronized.
8.13 – AM2 is still 3m above AM1, AF and SJ, who rest and groom. BJ is 4m from either, resting.
8.24 – SJ ventured about 1m far from AM1+AF
8.33 – AM2 sings, then they all sing (BJ approaches AM1 and AF).
9.56 – AF moves 2m toward AM2, AM1 quickly moves 2m as well, and they groom (4m from AM2).

10.06 – Long (20m) medium intensity chase (AM1 on AM2). AF follows AM1 with SJ. Then gr. B changes direction, and AM1 feeds (first time I see them feeding today). AM2 is >20m far, but then approaches them again.
10.25 – Now gr. B is slowly "following" AM2, who emits low uhs. Then they sing again.
AM1 received a large (~4cm long) wound at the base of the right big toe.
10.27 – They sing again.
11.55 – They had another long rest. Then AM1 moves fast, seems a display because AM2 had come closer. AM2 comes even closer, then runs away.
Then gr. B moves 20m, AM2 again closer, AM1 chases him fast 80m! He is followed by AF carrying SJ, and BJ.
12.12 – Regrouped again, all within 1m, AM2 about 10m far. BJ briefly checks AM1's wound. He doesn't show much pain, nor does he seem impaired when moving (he grabs branches with that foot). Overall they don't seem particularly concerned, they tend to leave him alone.
12.42 – Gr. B sings again.
13.50 – AM2 is relentless. Now re-enters a fruiting tree where gr. B is resting and feeding. He feeds 4m from AF, who seems relaxed.
14.04 – AM1 chases AM2, fast, they drop 7m to a different tree, AM2 flees slowly, then loops and follows them again.

January 15: the same pattern repeats: Buster approaching gr. B until Bram snapped and chased him away fast. Then Buster would slowly return and the same happened. When gr. B sang, Buster disrupted the call and responded to the female's great calls. After a chase, Buster showed a large (~4cm), heavy-bleeding wound at his lower lip. He seemed to have reduced the number of challenges after the injury.

January 16: same pattern, many chases, Buster seemed to have recovered from the wound. Bram received two more wounds, one on the back (4cm) and one on top of his head (3cm). The chases became shorter, Bram seemed impaired by the foot injury.

January 17: Bram fell at the first chase attempt I witnessed. Buster seemed more daring: he was very active around gr. B, coming closer, and often higher than them. When chased by Bram, he fled to shorter distances, and returned quickly back. For the first time, Bambina supported Bram by leading two chases against Buster. Bambina also 'shook branches' often (see text for details).

January 18: Bram was not in the group. He was observed slowly wandering alone, feeding and tending to his wounds. Buster followed closely Bambina the whole day, for the most part ignoring the youngs. He groomed Bondri, and two hours later he groomed Bambina for one minute, then solicited grooming from her, but she moved away. Bambina shook branches often, unclear if threat or sexual solicitation. Once she chased him very fast out of a fruiting tree, down to 4m high, with screams and a lunge, which he parried. They never called. The youngs looked tense. After 7.30 Bel traveled alone all day; she was forced to take alternative routes to access difficult

trees, and to avoid passing near Buster when her path to Bambina was cut off. When Bel tried to suckle, Bambina bit her (delicately) on the nape, and made a threat face (open mouth).

January 19: Bram not with the group the whole day. In the morning, Bambina traveled around the home range, fast and jerky movements, at times followed by Buster, at others without him. Bondri and especially Bel struggled to keep up. In a prolonged grooming bout, Bambina groomed Buster for the first time. No copulation and no singing.

January 20: No Bram in the morning. Suddenly, Bambina moved fast more than 100m and started duetting with the partially recovered Bram, the first time she sang since his disappearance. Then a very long grooming bout. Bambina and Bondri groomed Bram and licked his wounds. Then the fighting resumed. Bambina actively chased Buster, alone or with Bram, once driving Buster to the ground. Bram moved rather slowly, unable to compete with the healthier, stronger Buster, who for the first time took the initiative and attacked Bram several times. Lony, from group L, approached, moving around very excitedly, but did not participate in the action.

January 21: Bram seemed unable to attack or defend himself (he never chased Buster, moved away when Buster approached him). Bambina stopped shielding him from Buster, once she even chased him slowly away. A few hours later, Bambina copulated with Buster: she was slowly following Bram, 7m far, when Buster approached her and they copulated for 6s. Bram attempted to go back toward them but renounced after 2m, and Bambina followed him. One hour later, upon yet another approach from Buster, Bram moved away (and lower) and Bambina moved 1m to Buster and initiated a long grooming bout with him (later joined by Bondri – Bel was not in sight). After that, there was an escalation in Buster's attacks toward Bram, who was relentlessly pushed low and toward the ground. Buster always occupied a higher position than him in the canopy, and did not allow him to climb back up, by quickly moving to the tree Bram was trying to reach on the ground. Interestingly, however, Buster never seemed to seek physical contact, just chased and pushed Bram down.

January 22: Bram was gone from the group, I followed him wandering slowly about, eating and self grooming. Later in the day, Bambina briefly sang with Buster for the first time, during an encounter with a neighboring group. When gr. B moved away, Bel struggled to keep up, 40m far from the others.

January 23: Bram alone.

January 24: Bram alone. Bondri and Bel shook branches to Buster. While gr. L was calling, there were few barks, about 200m from gr. B. Bambina, followed by Bondri and Bel, darted off in that direction, met Bram and they immediately started calling (cf. Jan 20). Few minutes later Buster arrived and countercalled. Bel seemed elated,

she groomed Bram and even sang with the group (first time I hear her). Bondri for the first time gives a great call with Bambina.

January 29: Buster was not with the group.

January 31: Same. Bambina seen carrying Bel.

February 1: Buster was seen countercalling, and approaching the group.

February 2-3: Back to the beginning. Gr. B huddled together and Buster moving around them, defiant. Bram looked healthier, his wounded foot looked healed and could bear weight. Bram and Bambina chased several times Buster away, a few times quite aggressively (with screams and lunging), and Bambina lashed at Buster when he lunged at Bram. But she also kept branch-shaking at Buster, and allowed him to approach her often, although there was never physical contact between them.

February 7: Bram not with the group. Buster seemed integrated within the group, was groomed, led group traveling.

February 17: I heard gr. B calling, two males replying to the female's great calls.

February 18: Buster not with the group, all day. Bram looked healthier, although two toes on the injured foot were still swollen and stiff. He was with the group when I checked them on Feb 20, 22, 24 and Mar 1.

March 7: Bimbim, the secondary male who had left the group in August of the previous year, returned. Physical fights and chases ensued between him and Bram (similar to those with Buster). Bambina shook branches at Bimbim once. Twice Bram moved first away, Bambina lingered closer to Bimbim, and Bram came back and gave a vigorous display, moving about putting all his weight on branches.

Mar 8: Same situation, several chases, some quite aggressive (screaming and grappling), countercalling. On one occasion Bambina attacked Bimbim when he lunged at Bram from a higher branch. Bambina protractedly licked and tended to a spot in Bram's right lower back, probably a wound.

Mar 10: Same situation, but after a long chase at 9:00, Bimbim was the one that returned, and groomed and fed with the group. After two hours Bambina (followed by the group) moved where Bram turned out to be, and they sang. Then a grooming bout and a brief copulation between Bambina and Bram (5 sec). Bambina kept a presenting position immediately afterward, but Bram groomed her instead. Then more hard chases against Bimbim, who today turned and counterattacked Bram (with chasing, biting and grappling). Bambina and Bondri licked Bram's wounds. Bram also has a half-closed eye.
After the last fight, Bram remained low for a while, self-grooming and looking, while Bambina "waited" 15m far, with Bimbim 4m above her. Then Bram moved

away, Bambina waited 20min more, then she left in the opposite direction, followed by the others (except Bram). Bimbim didn't try to get closer, even when she was grooming with Bondri. Instead he waited and then moved back in the direction taken by Bram. The others followed him after a while.

Mar 13-15: Bram was not with the group. Bimbim had a large (2-3cm) V-shaped wound on his lower lip. Bambina and the youngs do not seem afraid of Bimbim as they were with Buster (they move smoothly, do not look in his direction much, do not keep a distance from him). Bambina solicited copulation 5 times, but I did not observe any.

Mar 16: Bram feeding alone, far from the group. I heard Bambina calling alone (no male responded to her seven great calls). Gr. L countercalled from about 40m far. Then Bambina approached a vocalizing male and a singing bout ensued, with two males on opposite sides of Bambina. One of them, 50m far, was Buster, with a large (5cm), fresh wound on his left foot and a scarred lip. After singing, he slowly moved away. The other male, 20m from Bambina, was a new suitor (AM4), unhabituated, remained high up in the canopy, probably afraid of me. No signs of Bram or Bimbim. Later Bambina and her offspring left, and AM4 followed, not daring to approach. There was a long, fast chase, not clear who chased whom, probably Bambina chasing AM4. At some point, I lost Bambina and AM4, as did Bondri and Bel. Bondri moved around the area vocalizing softly, laboriously followed by Bel. After 40min Bambina returned, and they traveled along together.

Mar 17: Gr. B followed by AM4. They did not respond to nearby calls (only low vocalizations). As on the previous day, Bambina and AM4 disappeared for about 20min, while the youngs searched for them, vocalizing. Bambina 'reappeared' about 30m from them, feeding. Five minutes later there was a long chase, involving AM4 and Bimbim. It took them >200m far, it was fast and intense. Bambina followed them fast, the young much slower. Bimbim returned toward the group while vocalizing, and when he reached it they all started singing (at 14:36, a rather late time to sing – average is around 9 a.m.).

Mar 18: Gr. B with Bimbim, countercalling with gr. L, and then feeding together. Bram appeared on the same large fruiting tree, but left it after displays from Bimbim and Bambina. When the group reached the area where AM4 had appeared originally, Bimbim disappeared for 20 min. The rest of the group sat and groomed. Twice Bimbim reappeared, participated briefly in the grooming and left again. I later saw AM4, assumed they were displaying, but I could not hear them. After two hours Bambina started moving slowly away, without Bimbim.

Mar 19: Bambina's first calls were not answered, then Bimbim vocalized from a short distance, Bambina moved in that direction and they sang together. A later singing bout was disturbed by male countercalling from 300m (I am almost sure it was Buster, but only had a glimpse before he left). Bimbim approached quickly, inspected the area (looked in many directions, rested in the same tree the other male

had been), then went back. Later, Lony displaced gr. B from a fruiting tree. Bambina and Bondri solicited copulation several times throughout the day, Bimbim generally did not respond. Once he briefly took a copulating position with Bambina, not clear what they did, but Bel went over and slapped them and ran away (they separated, ignored her).

Mar 20: Bambina and Bimbim called together, then copulated (8sec). Bambina solicited more, Bondri too. When foraging, Bimbim did not seem concerned about the direction taken by Bambina. Later in the day, he left them and wondered alone deep in a neighbor's territory, having a brief encounter with them.

Mar 22: Another copulation (25sec) between Bambina and Bimbim. Twice he displaced Bondri from a small fruiting tree. Bel did not seem afraid of him, often came very close to him, who ignored her, also when she shook branches.

Mar 23: Countercalling with a lone male 150m far. He moved away while still singing, as I approached. He might have been AM4.

For the two weeks until I left the study area Bimbim was the sole male of gr. B, singing, grooming and copulating with Bambina.

APPENDIX B – TRANSITION IN GROUPS G/C

The second male ousting I witnessed involved neighboring groups C and G. The level of detail is much lower than in B's case, but the players are well known.

Gr. G:
Gatot: adult male, more than 20 years old, long-established.
Garwo: adult female, more than 20 years old.
Garin: subadult female, 7 years old.
Gawi: large juvenile male, 4.5 years.
G: infant, about 18 months old, only carried by Garwo.

Gr. C:
Congo: adult male, more than 20 years old, long-established.
Combre: secondary adult male, about 12 years old.
Connie: adult female.
Chelsea: subadult female, 6 years old.
C: infant, about 2 years old. Mostly carried by Combre, occasionally by Connie, very seldom by Congo.

Timeline
In Jan 2008, Combre was observed hovering around gr. G., much like Buster in gr. B. He was often chased away by Gatot, but persisted for 3 observation days. Gatot

received a wound on his inner right leg, near his groin, 4cm long. Combre received a small wound on his right wrist. From the beginning of the observations, Garwo did not seem to support her mate Gatot. On the contrary, she and the subadult Garin were twice seen attacking him (chasing, slapping and lunging).

G's infant, normally carried by Garwo, was not carried except to cross large gaps in the canopy, and was seen falling three times while attempting to keep up (and possibly, once, when his attempt at being carried was rejected).

The next time the group was followed, after about a month, both Gatot and the infant G had disappeared, and Combre was established as the new resident male. About a month after Combre's emigration, the infant of group C also disappeared.

Combre was seen copulating multiple times with both the adult and subadult female, and he sang complete duets with them from the start. He also experienced (and delivered) a large number of aggressive interactions throughout the study period.

At the end of the study, Combre was still the (sole) resident male in group G, and Congo the sole resident of group C.

APPENDIX C – TRANSITION IN GROUP U

This is a case of a young male (almost subadult) replacing the disappeared older male of the group. At the onset of the study, an illegal road was being cut across group U's home-range, virtually segregating them into a smaller than average territory and potentially disrupting their activity.

Gr. U:
Una: adult male, more than 20 years old, long-established, looking old (many wrinkles, opaque fur).
Upam: secondary male, ~7-8 years old, slightly smaller than Una.
Uni: adult female, more than 20 years old.
U: infant, about 1 year old. Carried by the female at the time of the replacement, and later mostly by the subadult male.

Timeline
In Mar 2008, the older male of group U disappeared. Upam, the younger male, remained as the sole male in the group.
No aggressive interaction was witnessed before the transition, and very few afterward (8 interactions in 12 study months).
The new pair started singing complete duets from the start (Upam had regularly participated in duets before the replacement, replying to female's great calls).
They were observed participating in very few intergroup encounters (4 in 12 months).
Three months after the replacement (Jun 2008), Upam was regularly carrying the infant.
The new pair was seen copulating in Jul 2008 and then in Feb and Mar 2009.
At the end of the study, the pair was still together.

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