Social monogamy and the threat of infanticide in larger mammals

Carola Borries · Tommaso Savini · Andreas Koenig

Abstract The evolution of social monogamy in larger mammals is difficult to explain because males usually do not invest much in direct offspring care and might achieve greater fitness by deserting a pregnant female to reproduce with additional females elsewhere. It has been hypothesized that socially monogamous males remain with the female year-round to protect their offspring from infanticide by new immigrant males. We investigated this idea by analyzing all cases of infant loss in a wild population of white-handed gibbons (*Hylobates lar*; Primates), in which most groups were socially monogamous and some polyandrous (137.5 group years). We examined the influence of (a) male intruder pressure on male immigration rates and (b) the presence of a new male in the group on infant loss. We found no relation between intruder pressure and male immigration rates. Infant loss was lowest (4.5%) for stable monogamy (probable father stayed from conception through infancy) and intermediate (25.0%; $p=0.166$) for stable polyandry. If a new male immigrated after conception, however, the infant was lost in all cases ($p<0.01$) independent of the presumed father's presence. Overall, 83.3% of infant losses were associated with the presence of a presumably unrelated male. Although the sample size is small, our results provide the first true support for the idea that the risk of infanticide is an important factor in the evolution of social monogamy in larger mammals.

Keywords Infant loss · Intruder pressure · Male immigration · Polyandry · Take-over · White-handed gibbon

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Introduction

Social monogamy (i.e., living in pairs) is rare in mammals (approximately 5% of the species) and its evolution difficult to explain (Clutton-Brock 1989; Kleiman 1977; Rutberg 1983) in light of the very similar variances in reproductive success for the sexes (Shuster and Wade 2003). This is in contrast to sexual selection theory, which suggests that a male would benefit from reproductive access to as many females as possible (Bateman 1948; Trivers 1972), in order to sire additional offspring. This begs the question as to what prevents a monogamous male from deserting an impregnated female to breed with other females elsewhere (Dunbar 1995). In birds, where social monogamy is the norm (Wittenberger and Tilson 1980), one driving factor seems to be paternal investment, which may improve the reproductive output of the pair (see Gowaty 1996a, b; for an alternative explanation). However, this does not hold true for most mammals, in which females generally invest more heavily in offspring than males (due to internal gestation and long lactation, Trivers 1972) and, in most cases, do not depend on paternal care either (van Schaik and Dunbar 1990). More generally, the evolution of social monogamy in mammals seems to have preceded the emergence of paternal care (Komers and Brotherton 1997).

Gubernick (1994) summarized 17 hypotheses for the evolution of monogamy in mammals, assigning them to three dimensions: mating exclusivity, pair bonding/association, and male care. The best predictor for monogamy in mammals, however, seems to be the spatial distribution of females (Komers and Brotherton 1997): If females are intolerant of each other and live in small, exclusive ranges (presumably related to strong feeding competition), we often find only a single adult male with them. In some of these monogamous species, a male may stay with a single female for decades, even though he could potentially cover the ranges of additional females (Dunbar 1995; Reichard 2003; van Schaik and Dunbar 1990). Such an association will only be beneficial, and should only evolve, if permanent pair living significantly increases male reproductive success, e.g., via essential services the male renders to the female and her offspring as direct paternal care or more indirectly via resource defense or predator avoidance (Dunbar 1995). However, because larger mammals rarely provide paternal care, these benefits alone are unlikely to explain why males stay on after fertilization or even form year-round associations, which are so common in nonhuman primates (van Schaik and Dunbar 1990; van Schaik and Kappeler 1997).

To better explain this conundrum, it has been hypothesized that the threat of infanticide by males plays a major role in the evolution and maintenance of sociality (van Schaik and Janson 2000; van Schaik and Kappeler 1997). Following fertilization, males stay on to protect their offspring from other males (Borries et al. 1999b; Palombit et al. 2000) for whom it might be advantageous to kill an unrelated infant so that they themselves can reproduce faster with the mother (Hrdy 1979). Slowly reproducing species with a long lactation period relative to gestation (van Schaik 2000b) are particularly vulnerable to infanticide by males because more time can be gained. This is one of the main reasons for why sexually selected infanticide is common in mammals (Ebensperber 1998; Hrdy 1979), especially primates with their even slower life histories (van Schaik 2000b). For additional explanations for infanticide by males, see e.g., Hrdy (1979) or van Schaik (2000a).

Infanticide has frequently been reported to occur if a new male had immigrated into a group after an infant had already been conceived or born (Hrdy 1979). This sequence of events makes it unlikely that the new males could be targeting their own offspring (Borries et al. 1999a; Soltis et al. 2000). The proximate mechanism might be a simple discrimination based on mating history: if a male has not mated with a female prior to conception, he might attack the infant (Hrdy 1979; van Schaik 2000a). Other resident males who remain in the group may defend their putative offspring against the new male (Borries et al. 1999b; Palombit et al. 2000; Soltis et al. 2000). When a male stays on in monogamous species, the group becomes polyandrous, an option rarely observed in mammals (Hrdy 2000). In most cases, the new immigrant male ousts the current resident male (Hrdy 1974) so that no male defender remains.

Under social monogamy, infanticide by males seems to be rare in larger mammals (Palombit 2000; van Schaik and Janson 2000) perhaps because male tenures tend to be long (Brotherton and Komers 2003). Thus, during the course of a typical study period, few infants are ever exposed to new, unrelated males. Therefore, while the threat of infanticide has been repeatedly cited as leading to and maintaining monogamy in larger mammals, the fact that direct observations are so infrequent has meant that the actual role of infanticide remains unclear (Palombit 1999; van Schaik and Dunbar 1990; van Schaik and Kappeler 2003).

Here, we investigate the circumstances of infant loss in a wild population of white-handed gibbons (Hylobates lar). With their slow reproductive rates, their very stable groups, and their long life spans (Brockelman et al. 1998; Leighton 1987; Reichard and Barelli 2008; Savini et al. 2009), white-handed gibbons are not necessarily the ideal study subjects for mammalian monogamy. However, the family of Hylobatidae has repeatedly been scrutinized in the context of monogamy and infanticide:

Firstly, all species of the family predominantly live in socially monogamous groups defined as a pair of adults (one adult male and one adult female) plus immatures/offspring (Bartlett 2007). However, long-term research has revealed some variation in this pattern with polyandrous groups (two, rarely more, adult males unrelated to the adult female) constituting more than 20% of the groups in a population (Lappan 2007b; Savini et al. 2009). This variation allows for studying the possible effect of polyandry on the likelihood of infant loss. We note that polygynous groups (more than one adult female residing with a single male) are always rare and unstable (see Fuentes 1998). This also holds true for situations when a male alternately stays with two females occupying adjacent territories (as e.g., in lions in which male coalitions may reside in two prides; Pusey and Packer 1987). Only one such case is reported for white-handed gibbons on Sumatra where, for 10 months, the male changed daily between a nulliparous and a pluriparous female (neither had an infant at the time) until finally remaining with the pluriparous female (Palombit 1994a).

Secondly, gibbons maintain territories of which large portions are used exclusively by a single group (Bartlett 2007). Behavior during intergroup encounters seems to further emphasize the important role of the male in mate defense and prevention of infanticide as opposed to food defense (more general considerations in Brockelman 2009; Reichard and Sommer 1997). At least in small mammals,

territoriality has been interpreted as a counter-strategy to infanticide by males (Wolff 1993).

Thirdly, gibbon males usually do not provide direct infant care (Reichard 2003; but see Lappan 2008 for the exceptional siamang), which should make their long-term associations with females all the more unlikely. Furthermore, based on energetic calculations, males seem able to cover the range of more than one adult female and, therefore, could theoretically live polygynously (Reichard 2003; van Schaik and Dunbar 1990). Thus, infanticide has repeatedly been proposed as the primary cause for the observed long-term male–female associations in the taxon (Palombit 1999; van Schaik and Dunbar 1990). However, infanticide has only been witnessed once so far in gibbons (wild hoolock gibbons, Alfred and Sati 1991): on the day of birth, the adult male took the screaming infant from the subadult male of the group, handled it roughly, bit, and finally dropped it. It died from its wounds the same day. Although background information is scant, the adult male was the presumed father. He had been present in the group and was observed to mate around the time when the female must have conceived. In a second case, involving wild white-handed gibbons, infanticide was suspected (Reichard 2003): A one-year old, otherwise healthy infant died 7 weeks after a male take-over while the former group male was not around. The new male had been a resident in a different group at the time when the infant was conceived and, thus, is very unlikely to be the father. Unfortunately, neither the actual cause of death nor details about the new male's behavior prior to the event were provided. A third case refers to a captive male silvery gibbon killing and partly consuming an infant capped langur (Zuckerman 1981). While this cross-species event confirms that gibbons are capable of killing other mammals, it does not add to our understanding of infanticide by males.

One of the main explanations for the presumed absence of infanticide in gibbons has been the low male intruder pressure measured as the number of unpaired, so-called floater males in a population (Palombit 1999). More recently, however, there is evidence that floaters might be rare because natal males may delay dispersal (sometimes years into adulthood) to later immigrate directly into an often nearby group (Lappan 2007a; Savini et al. 2009). This would reduce the number of floater males but not the presence of non-breeding adult males in the population (as suggested also by, e.g., Brockelman et al. 1998; Koenig 1981). Instead of the number of floater males, it seems therefore more appropriate to describe intruder pressure by the mean number of adult males per group (including natal adult males).

In the following, we investigated all cases of infant loss in relation to male intruder pressure and male immigration events in a wild population of white-handed gibbons

(Brockelman et al. 1998; Savini et al. 2009). If infant losses were largely due to infanticide by new immigrant males, we expect infant loss to be:

1. More likely after immigration of a new male (who was absent when the infant was conceived and is likely not related to the infant), with male immigrations more frequent when male intruder pressure (the mean number of adult males per group, including natal adults) is high;
2. Lowest under stable monogamy (i.e., no male immigration, no infanticide);
3. Highest after a male take-over (i.e., the former resident male as defender is not available); and
4. Intermediate in polyandrous groups (i.e., either the former resident male might defend the infant or paternity confusion in stable polyandrous groups reduces the likelihood of infanticide).

As such, our analysis focuses on the associations of infant survival with certain demographic patterns. We are not directly testing hypotheses for infanticide nor are we trying to investigate why males would commit infanticide. Instead, we seek explanations for the evolution of monogamy. As such, the core question of this analysis asks whether the presence of the presumed father increases infant survival in gibbons following immigration of a new male and hence whether monogamy likely evolved or is maintained through the threat of infanticide.

Methods

We used published, demographic data spanning 29 years (1978–2006; 137.5 group years, 9 groups; sample sizes are summarized as Online Resource 1) for the wild population of white-handed gibbons (*Hylobates lar*) living at the Khao Yai National Park, Thailand [data derived from Fig. 1 in Brockelman et al. (1998) and Fig. S1 in Savini et al. (2009)]. For details on the study site, see e.g., Brockelman (1998), Raemaekers and Raemaekers (1985), Reichard (2009), or Savini et al. (2008). Presence–absence was recorded for individually known group members at a resolution of 3 months. We identified all infants present during the immigration of a new male any time between their conception [gestation in this population lasts about 6 months (Barelli et al. 2007)] and the end of infancy at 2 years of age (Reichard and Barelli 2008). Infants who disappeared without their mothers were assumed to have died. Note that paternity data are not available for the study population, and we took the male residing in the group when the infant was conceived as the presumed father.

Immigration of a new male resulted in either (a) *take-over monogamy*, when the older resident male from a
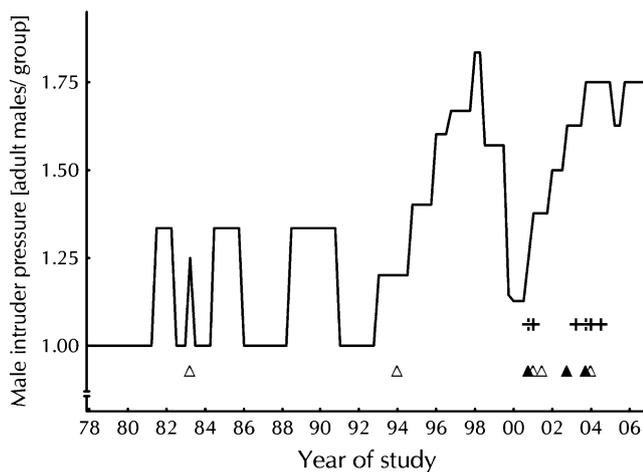
Fig. 1 Timing of infant losses (*crosses*) and male immigration events (*triangles*) in relation to male intruder pressure (*solid line*, i.e., mean number of adult males per group, including natal adults); *open triangle* no infant present in the group; *closed triangle* infant present and subsequent infant loss (data source: Brockelman et al. 1998; Savini et al. 2009)

monogamous group was ousted and replaced by the new male, or (b) *new-male polyandry*, when the new male immigrated after the infant had been conceived and the older resident male stayed on (note that no adult male immigrated into an already polyandrous group). These two scenarios were distinguished from (c) *stable monogamy*, i.e., the infant stayed with its mother and the presumed father from conception until 2 years of age, and (d) *stable polyandry*, i.e., the same two males, one of which was likely the presumed father, resided in the group from conception through infancy. In these scenarios, adult natal males were not considered. The difference between new-male polyandry and stable polyandry lies with paternity probability. A new immigrant male (new-male polyandry) should have a low probability of paternity, whereas under stable polyandry, both males should have some probability of paternity because females in polyandrous groups reportedly mate with both males, even though mating is skewed (Barelli et al. 2008). In most cases, details on mating preferences or male dominance relationships within groups were not available. Thus, these factors could not be considered.

We adopted the age classifications for adulthood provided in the original sources (Brockelman et al. 1998; Savini et al. 2009): 8 years in both datasets. To estimate population-wide male intruder pressure, all adult males in the study groups were considered (including adult natal sons). However, when distinguishing monogamous from polyandrous groups, we considered only those adult males presumably unrelated to the resident female (based on known birth and past dispersal records, Savini et al. 2009), thereby excluding adult natal sons unlikely to breed with

their mothers or to attack a younger sibling. The sampling effort was assessed as the mean number of study groups per year. The study began in 1978 with a single group. Thereafter, the sampling effort increased steadily until it reached (and maintained) eight groups from 2000 onward (Online Resource 2). We used this measure for sampling effort instead of, e.g., observation hours, because unlike for instance a rate of behavior, the presence or absence of individuals should be relatively independent of observation hours (which fluctuated between groups and years).

Statistical testing was conducted using STATISTICA 6.1 (© StatSoft Inc. 1984–2003). To avoid pseudo-replication, we compared means and 95% confidence limits for male intruder pressure, mean number of adult females per group, as well as sampling effort. We also ran that analysis using the adult sex ratio and the number of adult females per group (results not shown). Adult sex ratio revealed almost identical results to those of the number of adult males per group. The number of adult females (including natal adult females; mean, 1.1; range, 1.0–1.3; Online Resource 2) itself was not associated with male immigration events nor infant loss. Neither the adult sex ratio nor the number of adult females was considered further.

Results

Overall, six infants were lost during the study period accounting for 18.2% of all infants born [six of 33 infants; Table 1; further details on infant mortality in (Reichard and Barelli 2008)]. The lost infants ranged in age from about 3 to 21 months (Table 1). All losses occurred during just 5 years of the 29-year study period (from 2000 to 2004). During the same 5 years, most of the male immigration events took place (75%, 6 of 8; Table 2). If an infant was

Table 1 Gibbon infants lost at Khao Yai National Park between 1978 and 2006 (during 137.5 group years) in chronological order and the subsequent group composition (data source: Brockelman et al. 1998; Savini et al. 2009)

Infant's Name	Sex	Age (months)[a]	Group	Year of loss	Subsequent group composition
Rio[b]	m	15	R	2000	Take-over monogamy
Tarzan	m	9	T	2001	Stable monogamy
Dingo	?	3	D	2003	Stable polyandry
Juub	?	21	J	2003	New-male polyandry
Chumphon	m	18	C	2004	Take-over monogamy
Jai	?	9	J	2004	Stable polyandry

[a] Maximum age (data in 3 months increments)

[b] Infant's body was found and infanticide by a new male suspected (details in Reichard 2003:205)

Table 2 Immigration events by adult males

Take-over monogamy				
New male	Group	Older resident male (left)	Year	Infant present?
Fearless	A	Achilles	1983	No
Elias	R	Frodo	2000	Rio, died[a]
Christopher	A	Fearless	2001	No
Chana	C	Cassius II	2003	Chumpon, disappeared
New-male polyandry				
New male	Group	Older resident male (stayed)	Year	Infant present?
Chet	B	Bard	1994	No
Fearless	T	Amadaeus	2001	No
Joe	J	Actionbaby	2002	Juub, disappeared
Cassius II	A	Christopher	2004	No

Take-over monogamy (older resident male replaced by a new male) was as common as new-male polyandry (new male joined and the older resident male stayed on). All three infants present when a new male immigrated were subsequently lost (data source: Brockelman et al. 1998; Savini et al. 2009)

[a] Infant's body was found and infanticide by a new male suspected (cf. Reichard 2003:205)

present in a group at the time a new male immigrated ($n=$ 3), it was subsequently lost in all cases (Fig. 1), suggesting a direct link with male immigration. Prior to immigration, at least one infant was documented as having been healthy ($n=1$, Reichard 2003) and, when health data were not available ($n=2$), the infants were known to have co-resided with the new male for at least 3 months. No infant was present in the other five male immigration events (Fig. 1).

For the first 17 years of the study, male intruder pressure seemed comparatively low, ranging from 1.0 to 1.3 adult males per group (Fig. 1). From late 1994 onward, it increased (maximum, 1.8 adult males per group), although it continued to fluctuate. During the 5 years when infants were lost and most male immigrations occurred (2000–2004), male intruder pressure was relatively high; however, it was similar to the five preceding years when no male immigrated and was within the confidence limits of that period (mean$_{2000–2004}$=1.50 males, 95% confidence limits= 1.39–1.59; mean$_{1995–1999}$=1.57 males, 95% confidence limits=1.49–1.64). This indicates no simple, direct connection between male intruder pressure (as measured here) and the chance of a male immigration.

The sampling effort, which increased steadily over the course of the study, was at its highest from year 2000 onward when infants began to disappear. It remained at this high level through the end of the study period (Online Resource 2).

Of all 33 infants born, three (9.1%) were present during the immigration of a new male. All three were subsequently lost regardless of the group composition following immigration (take-over monogamy or new-male polyandry,

Fig. 2). Of the three other infants lost, one disappeared during stable monogamy and two during stable polyandry. Overall, infant loss during stable monogamy (4.5%, 1 of 22) was significantly lower compared to all other scenarios combined (45.5%, 5 of 11, Fig. 2, three columns on the right, Fisher exact test $p<0.01$) but did not differ from stable polyandry (25.0% or 2 of 8; Fisher exact test, $p=0.166$). In the absence of male immigration, infant loss was 10.0% (3 of 30). If there was a new male in the group, however, infant loss was 100% (3 out of 3), which holds true for both take-over monogamy (2 of 2) and new-male polyandry (1 of 1), a significant difference (Fig. 2, left two columns (3 of 30) versus right two columns (3 of 3); Fisher exact test $p<0.01$). Overall, 83.3% of the infants (5 of 6) were lost, while there was either a new male (take-over monogamy) or a second, supposedly unrelated male (new-male polyandry or stable polyandry) in the group. In all cases of infant loss, male membership in the group subsequently remained stable at least until the next infant was conceived.

Discussion

Infanticide and social monogamy

While still indirect, our results suggest infant loss is strongly associated with the presence of a new and likely unrelated male. The exact same scenario is reported for other primate mating systems, in which immigrant males commit infanticide (van Schaik 2000a). These similarities suggest infanticide by males as a cause of infant loss. Among the gibbons in the study population, infanticide might explain between 50.0% (i.e., if a new male
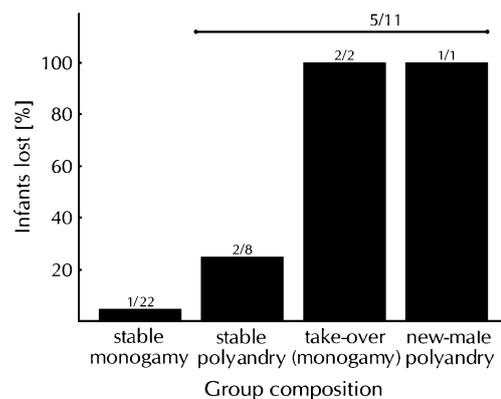

Fig. 2 Percentage of infants lost in relation to group composition and group stability. Infant loss was lowest (4.5%) under stable monogamy (*left column*). In stable polyandrous groups, 25.0% of the infants were lost (*second column from the left*). If a new male immigrated after the infant had been conceived (*last two columns on the right*), all infants were subsequently lost whether the immigration resulted in take-over monogamy or new-male polyandry (data source: Brockelman et al. 1998; Savini et al. 2009)

immigrated) and 83.3% (i.e., if infants were with a second male whether he was new or not) of infant loss. Thus, similar to non-monogamous primate males defending their offspring against attacks from other males (Borries et al. 1999b; Palombit et al. 2000), it seems that gibbon males must stay on throughout an offspring's infancy to prevent other males from joining and to ensure offspring survival. The key issue could be the prevention of male immigration because once a new male successfully joined a group, the infant invariably disappeared. The presence or absence of the older resident male (new-male polyandry or take-over monogamy, Fig. 2) had no influence. Defense by the probable father, if it occurred, was ultimately ineffective.

Our findings are consistent with the idea that year-round social monogamy might have evolved due to the threat of infanticide (van Schaik and Dunbar 1990; van Schaik and Kappeler 2003; see also below). In all cases of infant loss, male membership subsequently remained stable at least until the next infant was conceived so that an infanticidal male would have had the chance to sire the next infant and thus benefit from the infanticide. Furthermore, killing an unrelated infant would save time because premature loss significantly shortens the next birth interval of the mother (Reichard and Barelli 2008) allowing an infanticidal male to reproduce sooner. This matches the conditions expected under the sexual selection hypothesis for infanticide (Hrdy 1979; van Schaik 2000a). We would like to re-emphasize, however, that the present analysis did not directly address this topic. A detailed test of the sexual selection hypothesis or other potential explanations (Hrdy 1979; van Schaik 2000a) for the occurrence of infanticide in the study population still needs to be performed.

With only six cases of infant loss, the sample size is small, and tests have low statistical power. However, the small numbers are mainly due to the generally low infant mortality in the population. In fact, with 33 infants and 137.5 group years, the underlying sample size is comparatively large. Low infant mortality seems to be common in other gibbon species as well (Mitani 1990). Likewise, male immigration rates seem to be very low and tenures consequently long such that <10% of the infants born were lost under circumstances resembling those of infanticide. Longer tenures are typically found in territorial species (Agrell et al. 1998). At present, it is not clear whether the threat of infanticide could also help to explain why gibbons are territorial as has been suspected for smaller mammals (Wolff 1993) and, based on an extensive analysis of intergroup encounters, for the study population as well (Reichard and Sommer 1997).

Infanticide, immigrations, and intruder pressure

The clear link found between the presence of new males and infant loss suggests that immigration of a male into an existing group indeed poses a threat to the infant. This result could also explain extra-pair copulations with males from neighboring groups (Palombit 1994b; Reichard 1995), which have been interpreted as preventative paternity confusion in case these males were to later immigrate into the female's group. Indeed, males seem to have greater chances of gaining residence in a territory close to their natal group (Brockelman et al. 1998; Sommer and Reichard 2000). Furthermore, even ousted, former resident males may immigrate into a neighboring group, as in the case of male "Fearless" of the Khao Yai study population. Likely a native of group F, Fearless immigrated as an adult into neighboring group A where he stayed as the only adult male for 18.3 years (Brockelman et al. 1998). When Fearless was ousted, he then immigrated into neighboring group T where he joined his presumed adult son "Amadaeus", making the group polyandrous for 3.8+ years until the end of the study period (position of home ranges from Brockelman et al. 1998; Savini et al. 2009). A similar case occurred in 2003 when "Cassius II," after a 21-year-long tenure in group C, was replaced by "Chana" (whose prior residence is unknown). Cassius II subsequently joined his presumed adult son "Christopher," making the group polyandrous for at least 3 years until the end of the study period. In both of these reunions between father and presumed son, no infant was present in the group. These two examples highlight the need for a detailed analysis of male dispersal in the study population.

With four to five groups/square kilometer, group density in the study population is relatively high (Brockelman et al. 1998; Reichard 2009), but does not seem to have changed much during the course of the study. However, the number of adult males per group (our measure of intruder pressure) increased in the second half of the study, which indicates an increase in population density (as opposed to group density). Such an increase might be due to a decline in predation pressure. For instance, tigers locally went extinct at the beginning of this century, and other felids are reportedly rare (Lynam et al. 2006). Furthermore, sports hunting had dropped to a very low level by the 1980s, at around the onset of the data collection on gibbons. Surprisingly, however, male intruder pressure, as measured here, was not directly associated with male immigration events as one might expect. As it turns out, the best fit for male immigration events in our sample was sampling effort, which was highest when new males immigrated most frequently (Fig. 1 and Online Resource 2). However, while there could be a causal link between male intruder pressure and male immigration rates, this is not the case for sampling effort. The latter will increase the statistical likelihood of *any event* not just male immigrations. The unexpected lack of fit suggests that we might have to revisit our definition of intruder pressure. Ideally, one would combine all sexually

mature individuals, floaters, and those remaining on their natal territory (Koenig 1981), which was not possible here. Even more importantly, *successful* male immigrations, which pose the actual threat to infants, will depend on additional factors such as the occurrence of reproductive vacancies (Koenig and Stacey 1990) and the relative resource holding potential of the opponents (Parker 1974).

In this regard, it is puzzling that most male immigrations were clustered within a few years between 2000 and 2004. Although not directly tested, it is unlikely that this clustering is the result of a vacancy chain (e.g., Chase 1991), in which a sudden vacancy due to mate desertion or disappearance of a breeding individual could have induced a series of changes or immigrations. During the period analyzed here, there were no vacant breeding positions and immigrant males either joined a pair or replaced a male. However, as the description of the two events above (males Fearless and Cassius II) has shown, dispersal events may not always be independent of each other, which has also been reported for monogamous owl monkeys (Fernandez-Duque 2009). The two father–son reunions in the study population certainly contributed, to some degree, to the clustering of events.

In addition, it is possible that some of the resident males were of a very similar age, such that they lost strength at about the same time and new males were able to immigrate. However, this remains a mere assumption as the age of most resident males is unknown. A detailed study of male resource holding potential would be required to elucidate individual differences in ranging behavior, together with the frequency and performance during between group encounters. The calling behavior in relation to tenure length might also convey information, as has been shown for Thomas' langurs (Wich et al. 2003, 2004).

In sum, while male immigrations and infant loss seemed to be associated, it remains unclear as to why intruder pressure did not predict immigrations and why immigrations were clustered in time. Determining reliable predictors for the combination of these two events—immigration followed by infanticide—may seem to be challenging perhaps because of the stochastic nature of immigrations in addition to the fact that infanticides are so rare.

Perspectives

The results presented in this study provide the first true support for the idea that the risk of infanticide is an important factor in the evolution of social monogamy in larger mammals. However, we need to emphasize that more direct testing is still crucial for two reasons: Firstly, while we found a close association between the presence of a new male and infant disappearance, actual infanticide has not been observed. Assuming that the infants lost were indeed victims of infanticide, the results indicate that the male—

whether alone or together with the female—is unable to prevent infanticide once a new male resides in the group. The defense patterns, as well as the behavior of new males towards infants, have not yet been closely observed (as e.g., in Borries et al. 1999b). In particular, the role of stable polyandry in preventing infanticide could not be determined satisfactorily, although infant loss was intermediate as predicted. While there was no statistical difference in the percentage of infant loss between stable monogamy and stable polyandry, the value was, nevertheless, 5.5 times higher during stable polyandry (4.5% versus 25.0%). If these infants were killed by one of the group's males as assumed, then prior polyandrous mating failed to confuse paternity. This could be due to a strong skew in mating (reported for polyandrous groups of the study population, Barelli et al. 2008), which might provide males with clues about paternity, thereby reducing their risk of killing own offspring. Furthermore, it remains unclear at what point, in relation to age of their offspring and other breeding opportunities, a resident male will or should desert the female and his offspring (e.g., Pusey and Packer 1987), i.e., understanding which factors drive male take-over and dispersal in this population. Such data are essential for understanding whether male dispersal decisions are governed by the risk of infanticide as predicted by the infanticide avoidance hypothesis.

Secondly, although the association of new male immigration and infant disappearance is consistent with infanticide avoidance, additional (or alternative) explanations for the evolution of monogamy cannot yet be ruled out. For example, males might not remain with a partner solely to prevent infanticide; by staying, they may also improve their chances of extra-pair fertilizations as suggested for passerine birds (Gowaty 1996b). Under both scenarios (i.e., infanticide avoidance and extra-pair fertilizations), females should also seek extra-pair matings. It would be important to find ways to distinguish between the two hypotheses and to test their relative importance. The latter could be done via paternity analysis, which would also allow for testing the ultimate causes of infanticide in this species by determining the reproductive outcome of male and female strategies.

Perhaps, it might be necessary to collect yet another 29 years of data for multiple gibbon groups in order to improve statistical power and test the ideas mentioned above. At present, our results support the notion that "At one level, monogamy is a compromise offering something for everyone—especially immatures." (Hrdy 1999:232).

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