Infanticide and the Evolution of Pair Bonds in Nonhuman Primates

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Social relationships between adult males and females vary widely among mammals. In general, interactions between the sexes, particularly those of an affiliative nature, are associated with and, indeed, often limited to the period of copulation or female estrus.[1] Nevertheless, cohesive male-female bonds persist beyond estrus in some species, particularly nonhuman primates,[2] for reasons that remain largely obscure. Protection from male infanticide has been offered as a potential benefit to females of bonds with males in a variety of primates, including mountain gorillas and gibbons. Here I evaluate this hypothesis within a comparative framework that considers alternative costs and benefits of social relationships between the sexes.

PAIR BONDS AND INFANTICIDE IN HISTORICAL PERSPECTIVE

Explanations for the evolution of male-female bonds originally emphasized the apparent importance of reproductive context, or mating system. Durable "pair bonds" were regarded as typical, or even diagnostic of monogamous species[3] such as Asian gibbons (*Hylobates* spp.)[4] and neotropical titi monkeys (*Callicebus* spp.).[5] On the other hand, polygynous monkeys such as guenons (*Cercopithecus* spp.)[6] and squirrel monkeys (*Saimiri* spp.)[7] exemplified relatively undifferentiated or weak heterosexual relationships. The theoretical rationale for this distinction derived from the fundamentally divergent reproductive interests of the sexes, as articulated by Trivers[8]: Males are more likely to increase reproductive success by acquiring multiple mates, whereas females enhance fitness by discriminative choice of individual mates. Consequently, to the extent that an enduring bond with an anestrous female limits a male's sexual access to additional estrus females, this social arrangement should be relatively rare in polygynous systems. Conversely, when, for whatever reason, a male restricts his mating to a single female, strong heterosexual bonds are not only less costly to males, but may also offer fitness advantages to both participants. The proposed benefit to the female of this arrangement is the parental care her offspring receive from a male that is certain of paternity.[9] Thus, cohesive male-female relationships were originally viewed as part of a co-evolved suite of behaviors including monogamy, biparental care, and, in gregarious animals, "nuclear families" of parents and offspring.[3] Essentially the same argument has been offered in some models of hominid evolution.[10–12]

This argument has been challenged from at least two directions. First, avian studies reveal that mating exclusivity and certainty of paternity are not natural corollaries of "social monogamy"[13,14] and that males may,[15] but more commonly do not, adjust their parental effort accordingly.[16] Furthermore, recent modeling and computer simulations suggest that substantial parental care by monogamous males does not invariably result from a high certainty of paternity combined with a male's ability to increase offspring survival through such care.[17] Thus, in some birds,[18] as well as in nonhuman primates,[19] it is not always clear whether male care of infants constitutes parental effort or mating effort. Second, it is now clear that variation in male-female social relationships is not meaningfully differentiated by mating system.[20,21] Not only may monogamy entail weak heterosexual attachment,[22] but strong bonds between males and anestrous females occur in a number of polygynous primates, including ring-tailed lemurs (*Lemur catta*),[23] rufous lemurs (*Eulemur fulvus*),[24] capuchin monkeys (*Cebus* spp.),[25–27] rhesus and Japanese macaques (*Macaca* spp.),[28–31] mountain gorillas (*Gorilla gorilla*),[32–34] and savanna baboons (*Papio cynocephalus*).[35–38] Because paternal care in polygynous primates is typically, though not uniformly, less direct and extensive than it is in monogamous species, recognition of these patterns has directed analytical attention to other potential adaptive causes of male-female bonds. One of these is infanticide by adult males.

Infanticide, the killing of unweaned young by conspecifics, is widespread among animals.[39–41] Hrdy[42] hypothesized that infanticide creates breeding opportunities for males that, as a consequence of intrasexual competition, have limited sexual access to fertile females. With some possible exceptions, such as the chimpanzee,

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Pan troglodytes,[43] this hypothesis accounts for patterns of infant-killing among nonhuman primates better than do alternative explanations. One of the most notable implications of the hypothesis is that some aspects of female biology may be best understood as adaptations to reduce the risk of male infanticide. Possible female "counter-strategies" include a variety of behavioral and physiological phenomena,[39] but one clear option is for females to form close bonds with conspecifics that will help protect young. These allies could be other females, as is the case among lions,[44,45] but, for reasons not entirely understood, female primates generally fail to form effective coalitions against infanticidal males. (Hanuman langurs,[46] red colobus monkeys,[47] chacma baboons, [R.A. Palombit, unpublished data], and mountain gorillas[48]). Thus, as Hrdy[39] and Wrangham[49] proposed, an adult male, especially one that has some probability of paternity of an infant, may represent a critical defensive ally for a female whose offspring are at risk of infanticide.

Male infanticide, then, is a potential selective agent for the evolution of bonds between the sexes. It has been offered to explain male-female relationships in several polygynous taxa, such as Malagasy lemurs,[24] capuchin monkeys,[26] mountain gorillas,[32] and savanna baboons.[37] Armed with this insight, van Schaik and Dunbar[50] applied the model to pair-bonded, monogamous gibbons. By employing the Mitani-Rodman[51] index of territorial defendability "in reverse," they argued that individual male gibbons are capable of maintaining home ranges large enough to encompass multiple females, but do not do so because such a polygynous strategy would leave females vulnerable to infanticide by other males. Given the spacing of female gibbons, male protection of infants requires cohesive pair bonds and, ultimately, monogamy.

The infanticide-protection hypothesis has not yet been tested for hylobatids. There are, unfortunately, few directly relevant data for gibbons. Anecdotal observations of gibbon behavior and vocal playback experiments on their own have yielded equivocal conclusions. Therefore, I adopt here a comparative perspective with the goal of evaluating whether patterns of gibbon behavior and ecology are consistent with those observed in animals among which sexually selected infanticide and pair bonds not only co-occur, but appear to be functionally related. Two taxa offer good starting points for such an analysis: birds and savanna baboons.

The socially monogamous birds provide a logical comparison to gibbons, especially tropical populations such as house wrens (*Troglodytes aedon*), which, like gibbons, maintain permanent territories and pair bonds and breed throughout most of the year but, unlike gibbons, are known to commit infanticide. Birds thus offer a valu-

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able opportunity to identify the ecological and demographic conditions that intensify intrasexual selection among socially monogamous males and, ultimately, promote infanticide. Indeed, the hypothesis that sexually selected infanticide maintains pair-bonded monogamy was originally proposed to explain avian behavior.[52]

The lack of direct evidence of infanticide among wild monogamous primates dictates that we turn to polygynous species to examine the nature of primate male-female relationships in known infanticidal systems. Patterns of heterosexual association in two primates, the chacma baboon (*Papio cynocephalus ursinus*) and the mountain gorillas, among which male infanticide is relatively frequent, shed light on how this selective pressure influences the evolution of pair bonds.

Because of my focus on two taxa, this analysis constitutes a preliminary comparison, not a comprehensive review. I hope, however, that this evaluation will highlight the relative strengths and weaknesses of the infanticide protection hypothesis as well indicate possible directions for future research.

PAIR BONDS AS A DEFENSE AGAINST INFANTICIDE IN NONHUMAN PRIMATES

As Birkhead and Møller[13] have argued (see also Hrdy[39]), the infanticide-protection hypothesis for the evolution of pair bonds predicts that a female will invest substantially in a social relationship with a male willing to assume the costs of defending her offspring against attacking infanticidal males. This may be reflected by females contributing as much, if not more than, their male partners to maintaining the bond between them.

Although the mountain gorilla is probably the best-documented example of a primate that has evolved male-female bonds as an anti-infanticide strategy, savanna baboons are particularly relevant for two reasons. First, a close, affiliative bond typically exists between a lactating female and an unrelated adult male with which she is likely to have previously copulated. Because females are not all attracted to the same dominant male of the group (as female mountain gorillas are), a baboon group at a given time includes several *dyadic* pair bonds, or "friendships," which collectively involve multiple males of all dominance ranks. Second, Smuts[37] proposed that baboon friendships might have evolved as a female counter-strategy to male infanticide, but emphasized the difficulty in rejecting, on the basis of only observational data, alternative hypotheses. Two examples of these alternate hypotheses are that males protect female friends and their infants from harassment from higher-ranking females[36,53–55] and that friendships confer no immediate protection-related benefits to females but, instead, constitute a female tactic to promote the development of an attachment between an infant and a particular male, which later benefits the young juvenile by virtue of the care and attention it receives from this male.[56,57] A crucial question is whether the special relationship that develops between a lactating female and a particular male actually enhances his predisposition to intercede on her behalf when she is the victim of aggression, as Smuts originally proposed.

There is recent evidence that risk of

infanticide may be a primary adaptive cause of these bonds in at least one subspecies, the chacma baboon, where infant killing occurs relatively frequently.[58] During a two-year study of a northern Botswanan population, infanticide accounted for at least 38% of infant mortality and conformed to patterns predicted by Hrdy's sexual selection hypothesis in that all observed killings were committed by newly immigrant adult males that had attained the alpha position in the hierarchy and later copulated with the mothers when, after the death of their infants, they resumed cycling.[59] Among chacma baboons, the formation and termination of friendships is tightly linked to the presence of neonates: Before an infant's birth and soon after its death, there is no overt sign of the special relationship that exists between a particular male and female during her lactation. Playback experiments recently conducted by Palombit, Seyfarth, and Cheney[59] suggest that male "friends" are more predisposed than are control males of similar rank and friendship status to come to the aid of females under attack, but primarily do so when the aggressor is an established infanticidal male rather than a high-ranking female or a noninfanticidal male. If a female's infant dies, however, males show significantly less interest in the distress of their former female friends than do control males. These findings, in light of observational data showing that lactating females do not avoid interacting with higher-ranking, unrelated females, suggest that friendships confer protection-related benefits to females, and that this protection is more likely to operate in the infanticidal rather than the female-harassment context.

Thus, the chacma baboon presents a system in which sexually selected infanticide accounts for a significant portion of infant mortality and in which pairs of males and females with dependent infants share close bonds that appear to be related directly to reducing the risk of infanticide.

We now turn to the prediction that a female should invest significantly in a social relationship with a male that provides an important service to her, in this case, infanticide protection. This prediction is strongly supported by the behavioral data (see Box).

First, females are more responsible than males for the maintenance of close proximity between friends. Second, friendships involve extensive allogrooming between the sexes, but almost 90% of that grooming is done by females. Males rarely reciprocate grooming by females. In short, female chacma baboons invest more heavily than males do in the behaviors responsible for generating and maintaining the bond between them. Further support for the prediction comes from field studies of mountain gorillas,

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among which infanticide accounts for at least 37% of infant mortality.[48] Patterns of close proximity, movement ("follows"), and grooming in gorillas indicate that, again, females generally contribute disproportionately more than does the resident dominant male to maintaining the relationship between them.[32,60]

If male-female bonds in gibbons are an infanticide counter-strategy, do female gibbons invest in pair bonds in a manner similar to that of female chacma baboons and mountain gorillas? Field studies have generated few *detailed* data on gibbon pair bonds, but my study of sympatric white-handed gibbons (*Hylobates lar*) and siamang (*H. syndactylus*) in northern Sumatra, Indonesia, provides a basis for comparison partly because it uses many of the previously described behavioral measures used for chacma baboons and mountain gorillas (see Box).[61]

Patterns of pair-bond maintenance in hylobatids contrast with those of chacma baboons and mountain gorillas. In all five of the pairs of hylobatids studied, males had primary responsibility for the maintenance of close proximity. The striking similarity in the absolute values of the Hinde indices for hylobatids and chacma baboons, −23 and +26, respectively (see Box) suggests that these primates are roughly *equivalent* in the degree to which one sex is more responsible for the maintenance of proximity. The important point is that the identity of that sex is different in the two taxa.

Male and female gibbons also groom one another differently than chacma baboons and mountain gorillas do. Among white-handed gibbons, allogrooming is distributed between the sexes in essentially the opposite pattern of chacma baboon friends, with male grooming accounting for approximately 85% of all grooming exchanged between pair mates. This is partly because a female white-handed gibbon rarely initiates grooming with the male, actively solicits grooming from him at a higher rate than he does from her, and rejects many more of his "presents" for grooming than he rejects of hers.[61] In siamang pairs, grooming exchanges are more often equivalent and reciprocal, but where an asymmetry exists, it is, again, the male that contributes more. Solicitation of grooming by either sex is rare among siamang and rejection of "presents" is exceptional.

These behavioral measures provide a means of assessing the investment of individuals in their relationships and, ultimately, the "value" ascribed to the bond by the participants.[62,63] The data suggest that among hylobatids, particularly white-handed gibbons, the contributions of the sexes to maintaining pair bonds are contrary to those predicted by the infanticide-protection hypothesis. They are also contrary to the patterns exhibited by chacma baboons and mountain gorillas, in which infanticide is functionally implicated in male-female associations. These differences are most manifest in the white-handed gibbon, where females invest little in maintaining the pair bond. A comparative perspective suggests that some other selective factor besides male infanticide maintains pair bonds in hylobatids.

Maintenance of Male-Female Relationships in Chacma Baboons and Hylobatids

Description of social relationships in nonhuman primates relies on numerous behavioral measures.[116] Spatial proximity and allogrooming are considered fundamental mechanisms of social affiliation.[117–119] The patterns summarized here were observed in field studies of chacma baboons,[59] sympatric white-handed gibbons, and siamang.[61] Hinde[120] provided a quantitative index for identifying the responsibility for maintenance of close proximity between members of a dyad. The index is simply the percentage of approaches due to one member divided by the percentage of withdrawals due to the other member; approaches and withdrawals are defined as movements that bring individuals into or out of close proximity. The Hinde Index thus provides a quantitative basis for comparing the relative contribution of the sexes to the maintenance of proximity in chacma baboon "friendships" and hylobatid "pair bonds." Strongly negative values signify a greater male responsibility for the maintenance of close proximity; strongly positive values indicate a greater female contribution. As shown, the Hinde index was positive for 16 of the 17 baboon friendships measured (involving 12 females and 7 males), which suggested a greater female responsibility for the maintenance of close proximity. Among two white-handed gibbons and three siamang mated pairs studied, Hinde indices were negative, suggesting a greater male role.

The distribution of grooming between pair mates also reveals different contributions of the sexes. Shown is the percentage of all grooming observed that was performed by the male and female in chacma baboon friendships. In all friendships, female grooming accounted for the majority (approximately 88%) of allogrooming exchanged between friends. Also shown is the mean percentage of grooming performed per grooming session by the male and female in mated pairs of hylobatids. In both white-handed gibbon pairs and in one siamang pair, males groomed females significantly more than females reciprocated. In the other two siamang pairs, there was no statistical difference between the average contributions of the sexes to grooming sessions.

Responsibility for Close Proximity Maintenance Between Male and Female

■ Chacma Baboon Dyad   □ Hylobatid Dyad

Mean (±SD) Hinde Index for Hylobatids = −22.5 ± −12.3

Mean (±SD) Hinde Index for Chacma Baboons = +26.0 ± 16.4
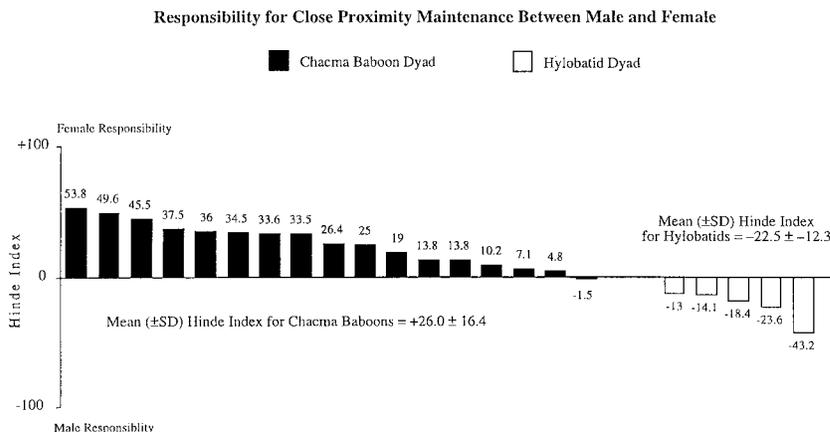
Male and Female Contribution to Grooming Exchanges

□ % Male Groom Female   ■ % Female Groom Male

Chacma Baboon Friendships

Female-Male

Hylobatid Pair Bonds

Heterosexual Pair
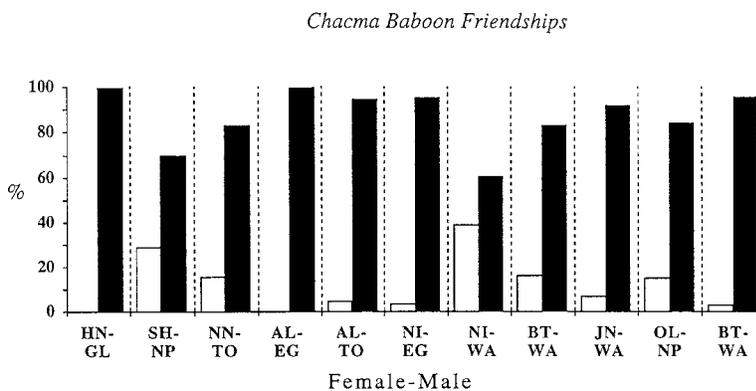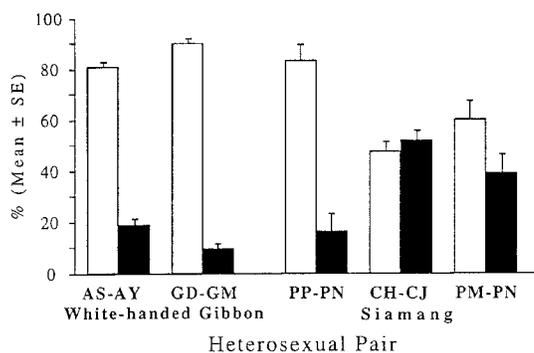
Two caveats must be recognized. First, the same selective pressure (in this case, sexually selected infanticide) may generate different evolutionary outcomes in different taxa.[64] The apparent convergence of a hominoid and cercopithecoid on disproportionately greater female investment in social relationships with male protectors argues against this proposition, but the infanticide-protection hypothesis may nevertheless benefit from more explicit attention to this issue. For example, how may the number of females in a group, and any resulting female-female competition for access to male protectors, affect the nature of pair bonds that evolve as anti-infanticide strategies? Second, there is a great need for detailed data on more hylobatid pair bonds, so that we may identify consistent social patterns in light of intraspecific variation.[61]

INFANTICIDE AND MONOGAMY IN BIRDS

At one time, the paucity of reports of infanticide by male birds suggested that reproductive competition among socially monogamous males is generally too weak for infanticide to evolve as a male reproductive strategy.[65] Darwin,[66] however, went to some trouble to elaborate conditions that generate mate competition among monogamous animals as do, for example, an early mating advantage or skewed sex ratios. In addition, recent research confirms that monogamy does not preclude significant intrasexual selection.[67] Indeed, observational and experimental studies of birds have documented destruction of eggs, nestlings, and fledglings by males (and often by females as well).[52,68–74] Several ornithologists have argued that infanticide has been largely neglected as a possible selective agent for the evolution of behaviors such as monogamy, male-female relationships, nest guarding, dispersal after nest failure, and responses to extra-pair conspecifics. Avian studies provide the best data for understanding the general conditions that select for infanticide by socially monogamous males, partly because ornithologists are able to perform male-removal experiments, which are barred to most field primatologists for practical or conservation

reasons. There is no comparable data set for monogamous mammals.

The conditions selecting for infanticide operate at three distinct but independent levels, which I will consider separately. They are features of female reproduction that establish a potential for infanticide; conditions that reduce the costs of infanticide to males and, therefore, increase the opportunity for infanticide; and factors that enhance the benefits of infanticide to males, usually by limiting breeding opportunities and increasing intrasexual mate competition.

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Female Reproductive Physiology and Potential for Infanticide

For infanticide to evolve via sexual selection, males must have access to a female reproductive system that is organized to provide breeding opportunities soon after the loss of offspring. Typically, this means that females breed relatively asynchronously and nonseasonally, or at least over long breeding seasons. This is the case in many populations of birds in which male infanticide occurs, and is in contrast to the strictly seasonal reproduction of other birds. It is particularly the case for tropical birds, among which infanticide may occur throughout the breeding cycle. Reproductively, gibbons also demonstrate a clear potential for sexually selected infanticide. This condition is necessary but insufficient for the evolution

of sexually selected infanticide. In addition, male breeding opportunities must be limited in some way so that the benefits of infanticide in mate competition exceed the costs.

Costs of Infanticide

The costs of infanticide for male birds are mitigated by diverse factors (Table 1). Not all the factors listed in Table 1 necessarily apply to any single avian population, but all have been identified as probable causes of infanticide by male birds. These include a weak pair bond or demanding nest provisioning so that vulnerable young are left unattended for extended periods; dependence of female reproduction on experience so that infanticidal males have access to a relatively large number of vulnerable young females, particularly first-time breeders; low relatedness among neighbors so that potential victims are not likely to be related to infanticidal males; reduced potential for effective maternal aggression so that energy expenditure and risk of injury in attacking solitary females are low; and coloniality. Birds breeding in colonies are more vulnerable to infanticide than those breeding as dispersed pairs. For example, temporary removal of males significantly reduced nest guarding by both colonially and solitarily nesting swallows, but only colonial nests were subsequently visited by unmated males and, in some cases, nestlings in them fell victim to infanticide; solitary nests remained unharmed.[71] The greater proximity of reproductive competitors in colonies may account for this pattern. In summary, monogamy and infanticide in bird populations co-occur with specific conditions that reduce the potential costs of this strategy to males (relative to other populations) and thereby provide greater opportunity for its successful execution.

Previous analyses of gibbons have focused on the potential benefits of infanticide to males more than they have on the costs that must be overcome for this reproductive strategy to evolve. Admittedly, consideration of costs is seriously hampered by the lack of information on the conditions under which monogamous male primates do and do not kill infants. The regular, conspicuous vocal duets of

TABLE 1. Conditions Favoring Sexually Selected Infanticide Among Socially Monogamous Birds, With Implications for Gibbons

	Condition Favoring Infanticide in Avian Populations	Does Condition Apply to Hylobatid Populations?
Features of Female Reproduction That Create Potential for Infanticide: Factors That Reduce the Costs of Infanticide:	Asynchronous breeding	Yes
	Long breeding season	Yes (aseasonal breeding)
	Offspring often left unattended due to weak pair bond or demand for nest provisioning	No
	Coloniality, gregariousness	No
	Limited opportunity or effectiveness of maternal aggression	No
	First-time female breeders abundant	Unknown
	High mortality among mated adults	No
	Low relatedness among (colony) neighbors	Unknown
Factors That Increase the Benefits of Infanticide to Males by Limiting Breeding Opportunities):	Large adult male floater population	No
	Skewed sex ratio	No
	High mortality among unmated adults	Yes (promotes takeover infanticide)
	Low adult mortality	Yes (promotes takeover infanticide)
	Low opportunity for extra-pair copulation	Unknown
	High competition for nests sites (e.g., secondary cavity nesters)	Yes (gibbons lack nest sites, but competition for territories is probably intense)
	Females cannot mate with males other than the infanticidal male	Unknown

many mated hylobatid pairs may reduce costs by providing male competitors with a means of quickly locating recently widowed and presumably vulnerable females. This hypothesis has not been tested and as Møller[71] pointed out, localizing a solitary female may not be the primary cost a monogamous male faces when pursuing an infanticidal strategy.

Sexual monomorphism may require greater expenditure of energy and risk of injury in overcoming maternal defense, as well as male protection, under some conditions. Observations of infanticide in species such as Milne-Edward's sifaka[75,76] and colobines[77] have established that low sexual dimorphism does not preclude infanticide in primates. Given the opportunistic nature of many infanticidal attacks, this is to be expected. On the other hand, sexual dimorphism in primates enhances male ability to "coerce" females in many contexts, including infant-killing,[78] and, among mountain gorillas[48] and chacma baboons, appears to account for the apparent ineffectiveness of maternal defense against infanticidal males. Thus, equality of body size and weaponry such as canine teeth may enhance maternal defense, as reflected in reports of individual females thwarting potential or actual infanticidal attacks of males in species such as ring-tailed lemurs,[79]

monogamous birds,[73] and some rodents.[80] The fact that the majority of successful infanticides in monomorphic birds are committed when nests are completely unattended implicates costs relating to aggression from mothers as well as males. This probably is not because maternal aggression serves

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simply to postpone infanticide long enough for the male protector to arrive. Widowed female tree swallows, for example, may vigorously fight potential replacement males for days, permanently ousting even males that manage to kill a nestling and raising

the rest of the brood successfully.[70,73] Widowed, nonlactating female gibbons are capable of aggressively frustrating the attempts of solitary as well as multiple males to establish pair bonds with them for up to two years.[81,82] The carrying of infants by primate females might physically encumber maternal aggression in a way that does not occur for avian females, but it may also decrease opportunities for infanticide by facilitating continuous mother-infant proximity, the lack of which apparently makes bird nestlings particularly vulnerable. Resolution of this issue awaits a comprehensive examination of how the frequency and effectiveness of maternal defense vary with the degree of sexual dimorphism, the energetic demands of lactation, and the developmental state of offspring. In general, the factors that reduce the costs of infanticide for male birds fail to operate in gibbons, but a comparative analysis is hindered by the paucity of relevant hylobatid data. The importance of these data is underscored by recognition of two variants of infanticide practiced under social monogamy that are likely to differ in their relative costs and benefits.

Benefits of Infanticide

In birds, infanticide may enhance male fitness in two ways that consti-

tute related but distinct reproductive strategies. First, infanticide may disrupt an existing pair bond and subsequently allow the male to acquire the female as a mate ("takeover" infanticide). Second, infanticide may accelerate the resumption of female receptivity after a male has acquired a breeding position left vacant by a male that left his mate or died ("passive replacement" infanticide). It is likely that the first of these strategies is more costly to males but, in either case, potential benefits increase as breeding opportunities for males become more limited. It is partly for this reason that sexually selected infanticide has generally been attributed to polygynous systems. However, breeding opportunities are also restricted among socially monogamous birds among which male infanticide occurs (Table 1). Reproductive competition may be increased by: a large population of unmated "floater" males, a male-biased sex ratio, low opportunity for extra-pair copulation (as an alternative reproductive tactic), and intense competition for nest sites.

The first of these, the density of floaters, deserves special attention for two reasons. First, unmated male birds are relatively abundant and generally constitute a large proportion of the floater population.[69,71] The option of mating with mated females is typically closed to these males because females as a rule preferentially pursue extra-pair copulations with mated males.[83] Second, male infanticide in birds is committed primarily by *unmated* individuals. Sometimes these are males that have lost their mates, but more often they are single floaters and first-time breeders.[52,70,71] Indeed, using both observational data and male "detention" experiments, Møller[71] found that the proportion of unmated males in the population was the single most important factor accounting for variation in the frequency of male infanticide and defensive behaviors such as nest guarding. The higher rates of infanticide observed in breeding colonies turns out to be a result of the aggregation of unmated males in densities that vary positively with colony size. In summary, unmated males appear to constitute a significantly greater threat to females than do

breeding males in populations of socially monogamous birds.

This conclusion is consistent with sexual selection theory. For a currently mated male bird, infanticide is associated with an *attempt* to switch mates, which involves its own potentially high costs,[84] not with the opportunity to acquire additional mates. An unmated male that kills, however, may alter his breeding status entirely. Avian data suggest that the cost-benefit ratio of infanticide for a monogamous male that already has a mate and breeding territory is rarely as favorable as it is for a male that has neither or only one of these prerequisites for reproduc-

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tion. If male gibbons commit infanticide, this "less to gain, more to lose" perspective of already mated males seems likely to operate as well. Indeed, the principle may be quite general. Even in a species such as the mountain gorilla, where a harem-holding male can potentially acquire additional females by killing an infant in another group and inducing maternal transfer,[50,85] solitary, physically mature silverback males may nevertheless pose more of a threat in this respect than do long-established males in neighboring groups (D.P. Watts, per-

sonal communication). This is reflected in the persistent "tracking" of groups by lone silverbacks[48] and by the higher intensity and duration of intergroup encounters involving lone silverbacks than those involving established harem-holders.[86]

What is the relevance of this finding for evaluating the infanticide protection hypothesis in monogamous gibbons? The hypothesis argues that females are "vulnerable to infanticide by males attempting a takeover or by neighboring males attempting to expand their territories, but also by transient males."[50] Given the lack of documented cases of gibbon infanticide, we cannot directly test the hypothesis that unmated males constitute a greater infanticidal threat than do mated neighboring males possessing territories. Indirect support for the hypothesis comes, however, from a series of field experiments in which Mitani simulated the presence of mated pairs, solitary females, and solitary males by playing back their respective songs to conspecific gibbons. Van Schaik and Dunbar argued that the responses of agile gibbons (*H. agilis*)[87] to these three types of song indicated that mothers with dependent infants were less willing than nonlactating females to participate in territorial interactions, a finding they attributed to the attendant risks of male infanticide.

This argument, however, overlooks a more general result emerging from both this study and Mitani's previous experiments on allopatric Mueller's gibbons (*H. muelleri*).[88,89] Mitani found a "clear and striking similarity" in the responses of gibbons to the duets of mated pairs and to the songs of solitary females. Among his agile gibbon subjects, this was true for females with and without infants. If reducing the risk of infanticide is the primary motivator of female response under playback conditions,[50] then Mitani's result suggests that mated males pose a relatively low risk of infanticide, one roughly equivalent to that presented by solitary, unmated females. If this were not the case, we would expect contrasting female responses to the duet versus female-solo playbacks. Also, Mitani's playback results suggest that female agile gibbons with infants are just as wary of strange, solitary

males as they are of strange, solitary females. This is contrary to the predictions of the infanticide-protection hypothesis, although the small sample used in this playback study prevents resolution of this issue. A possible alternative explanation for both patterns is, of course, that *females* also pose an infanticidal threat.[52,90] However, I will not explore this possibility here because it is not a component of the infanticide-protection hypothesis in its current form.

There is an important implication of the proposed difference in infanticidal predisposition between unmated and mated males. Currently available data suggest that gibbon populations differ from birds with respect to a fundamental cause of avian male infanticide, the abundance of unmated, fully adult floater males. With few exceptions,[82] adult floaters of either sex are generally rare in hylobatid populations. Few sightings of floaters have been recorded in studies exceeding three years of agile gibbons in western Borneo[91]; white-handed gibbons in Thailand,[92] Malaysia,[93] and northern Sumatra[94]; and siamang in Malaysia[93] and northern Sumatra.[94] Although direct corroborative data are lacking, Chivers and Raemaekers,[93] Leighton,[4] and Mitani[91] have therefore argued that dispersing young adults suffer high mortality rates.

Alternatively, Brockelman and coworkers[92] suggest that the rarity of floaters may occur because subadults are retained in their natal groups. This is probable, but only a negligible number of hylobatid groups have been found to contain more than one adult of each sex (except, possibly, *H. concolor*[95]). Hence there clearly is a limit on the efficacy of such a strategy. Subadults can postpone dispersal and any incumbent mortality risks by remaining in their natal groups, but only for so long. They cannot stay beyond their achievement of physical maturity.

Further evidence of the rarity of floaters is suggested by the fact that numerous breeding vacancies that occurred over six years in hylobatid groups in Sumatra were all filled by known residents of neighboring groups, not floaters.[94] Finally, a "natural experiment" transpired at the Ketambe Research Area when two con-

tiguous siamang territories became available for colonization after all residents had died or dispersed following contraction of disease by adults.[96] The total area of more than 80 ha of productive lowland rainforest was not reoccupied by siamang in the ensuing five years or more, even though sympatric primates such as long-tailed macaques and orangutans, as well as closely related white-handed gibbons, continued to live and breed there successfully. In many bird populations, analogous provisioning of nest boxes rapidly reveals the presence of unmated floaters that seize such rare breeding opportunities.[71] In total, these observations accord with the views of

> Currently available data suggest that gibbon populations differ from birds with respect to a fundamental cause of avian male infanticide, the abundance of unmated, fully adult floater males.

Mitani[91] and Brockelman and coworkers[92] that physically mature, unmated adult males are exceptionally rare, or at least rarer than in many birds. If future demographic data from gibbons confirm this pattern, then the potential threat of sexually selected infanticide to mated or widowed females may be lower than it is in the socially monogamous birds in which infanticide is known to occur.

Both low and high adult mortality have been suggested to promote infanticide by male birds (Table 1), but this apparent contradiction is resolved when the two forms of infanticide are kept distinct. All else being equal, low adult mortality will tend to discourage infanticide by monogamous males that already are in possession of a territory and mate, even a newly acquired mate, through long reproductive tenure, as has been argued for noninfanticidal alpha male savanna baboons in East Africa relative to infanticidal chacma

baboons.[58] On the other hand, for males that lack a mate, low adult mortality means fewer breeding opportunities over time and therefore promotes "takeover" infanticide. High mortality among unmated floaters similarly increases their potential benefits from "takeover" infanticide because it diminishes the option of postponing breeding. Conversely, high mortality among mated, territorial adults promotes "passive replacement" infanticide by providing frequent breeding vacancies for males to fill, and without the additional costs of takeover infanticide. Breeding vacancies may be more common in gibbon populations than has previously been appreciated,[94] but the much higher mortality of unmated than mated males reinforces the expectation that the unmated ones represent a significantly greater infanticidal threat than do the mated males.

PAIR BONDS AND INFANTICIDE RECONSIDERED

Field studies of chacma baboons, mountain gorillas, and birds confirm that 1) sexually selected infanticide may be a potent selective force even in socially monogamous animals and that strong heterosexual bonds may evolve in response to this pressure. Thus, it is entirely feasible that pair-bonded monogamy in gibbons has evolved as a counter-strategy to infanticide, especially in light of the high saturation of breeding habitat by gibbons[4] and the low reproductive output of females.[97] The lack of reports of infanticide in gibbons should not necessarily bias us against the hypothesis. Even among organisms for which infanticide appears to be a general feature of the mating system and accounts for much infant mortality, it is not necessarily frequently observed.[98]

On the other hand, there is no *a priori* reason why indirect evidence, such as the disappearances of infants, need be lacking in populations with significant rates of male infanticide. Leighton[4] and Mitani[91] have argued persuasively, however, that infant gibbons experience exceptionally low rates of mortality relative to that among other catarrhines. For example, only 1 infant out of 19 disappeared during the six years that Mitani[91] moni-

tored ten groups of agile gibbons in West Kalimantan, Borneo. Among white-handed gibbons monitored for longer periods in northern Thailand, only 1 of 30 infants born in more than eight groups disappeared before weaning, which Brockelman (personal communication) has argued represents only one loss out of a total of 42.7 infant-years. Given the probable action of other causes of infant death, such as disease,[97] infanticide can potentially account only for some unspecified portion of this already low infant mortality.

Depending on competing selective pressures, a low rate of mortality can certainly wield important evolutionary consequences over long periods, but extremely low infant mortality contrasts with the demography of confirmed infanticidal populations, both polygynous and monogamous. As with predation, infanticide will exert greater evolutionary influences on populations when it occurs at higher rates.[99] Moreover, much higher rates of mortality among adolescent and, presumably, subadult gibbons raise the possibility that other selective forces besides male infanticide have operated on male and female social behavior. For example, how does the presence of the male influence survival in these age groups?

It might be argued that infanticide is infrequent in hylobatid populations simply because the conditions for it do not arise often. For example, virtually all females have mates that might shield their young from infanticide. However, comparative data weaken this argument in two ways. First, among primates and birds in which males seem to deter infanticide it is clear that although the risk of infanticide increases substantially with widowhood,[43] it is not uniformly negligible during periods when a male accompanies a female. The offspring of the accompanied females still disappear, sometimes relatively frequently, or are even killed by other males.[48,52,59,85] If the infanticide-protection hypothesis is correct, we expect that adult male gibbons, like their catarrhine and avian counterparts, will vary in their ability and propensity[100] to protect young from attack, and that this will translate directly into a *variable* risk of death for the young.[71]

Indeed, such variation may provide a basis for female mate choice[48,71] or female-female competition for access to protector males.

Second, the argument that observations of infanticidal attacks are rare because widowhood is infrequent overlooks the fact that if infanticide occurs at all in gibbons it is more likely to assume a takeover than a passive replacement form. The high mortality of unmated males, combined with low mortality among mated, territorial

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It is these three patterns *taken together*—the rarity of physically as well as sexually mature unmated males, which are the most likely to commit infanticide, the rarity of observations of actual or even attempted takeover infanticidal attacks under widespread conditions favoring it, and the low infant mortality of gibbons—that raise doubts as to whether male infanticide constitutes the overriding selective force maintaining hylobatid pair bonds.

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males, should select forcefully for takeover infanticide. Indeed, low mortality among mated males is, by itself, sufficient to promote frequent takeover infanticide by both males and females among tropical birds living in permanent pair bonds and territories. The fact that subadult hylobatids, unlike cooperatively breeding birds, apparently cannot (or do not) routinely postpone dispersal in favor of remaining

in the group as adults and helping parents to raise offspring should further augment selection for takeover infanticide. We cannot easily predict the rate of takeover infanticide in hylobatids, but opportunities for it should be more common than for passive replacement infanticide, which requires widowhood by death or emigration of the male. Nevertheless, takeover infanticide probably is rare because an important causal agent suggested by avian studies is lacking. That agent is a relatively large population of fully adult, reproductively disenfranchised floater males with severely constrained reproductive options. Young adults still residing in their putative natal groups are relatively abundant and might functionally constitute a floater population, but their invariable physical immaturity makes them less likely perpetrators of takeover infanticide than fully adult male floaters would be.

It is these three patterns *taken together*—the rarity of physically as well as sexually mature unmated males, which are the most likely to commit infanticide, the rarity of observations of actual or even attempted takeover infanticidal attacks under widespread conditions favoring it, and the low infant mortality of gibbons—that raise doubts as to whether male infanticide constitutes the overriding selective force maintaining hylobatid pair bonds. The operation of some other selection pressure is further suggested by the convergence of chacma baboons and mountain gorillas, under the apparent selective influence of male infanticide, on male-female bonds that protect infants and are maintained by females, but differ significantly from those of hylobatids. What other selective agent might operate in gibbons?

An important lesson of avian studies in the last 20 years is that the close spatial proximity of mated male and female birds, which was always assumed to reflect a "pair bond" necessary for effective breeding (as in gibbons), often functions instead as a paternity guard.[13] I have argued previously that mate guarding is a likely adaptive reason for hylobatid pair bonds.[61] The same argument has been offered for monogamous ungulates.[101] Indeed, male responsibility for the maintenance of close proximity in both white-handed gibbons and siamang is

consistent with observations of mate-guarding in many socially monogamous birds that engage in extra-pair copulations. Recent observations of extra-pair copulations in two hylobatid species suggest the possibility that mate-guarding influences male reproductive success.[102,103]

Although the function of mate guarding is to discourage extra-pair copulations by the female, it is important to recognize that females do not necessarily restrict such behavior to their fertile periods. Recent research has highlighted the potentially important nongenetic benefits of extra-pair copulations to females, including appraisal of the receptivity, availability, and quality of potential extra-pair mates.[104,105] Thus, some male birds may guard mates not so much to deter an immediate threat of extra-pair insemination, but rather to prevent the female from obtaining useful information about potential extra-pair mates.[106] In permanently bonded animals such as gibbons, this information may pertain to future *bonded* mates as well, for extra-pair copulations might facilitate the establishment of a new pair bond with a neighbor if mate-switching were to become possible later through the death or desertion of the male or his eviction by the female.[97] Thus, mate guarding will persist beyond the period of female fertility. Relatively frequent turnover in gibbon pair bonds[94] suggests an important potential for mate guarding to function in the long-term retention of a male's pair-mate or breeding status. This argument is consistent with the suggestion that mammalian monogamy is generally a "risk aversion" strategy of males whereby staying with one female minimizes variability in mating success. Thus, even if a male mammal is capable of maintaining a home range encompassing two females' territories, restriction of ranging to one female may still be selected for *if* mate guarding effectively prevents loss of mate, loss of pair-bonded status, and extra-pair fertilizations.[107] One challenge for future analyses is to evaluate the cost-benefit ratio of guarding a single female with respect to the cost-benefit ratio of attempting to obtain polygynous matings.

A second possible selective agent has been suggested for passerines, in which, despite the fact that paternal care, if any, is nonessential to the survival of offspring, males remain closely bonded to females. This scenario is strikingly reminiscent of that among most hylobatids. These males may stay with their socially monogamous partners because females seeking extra-pair copulations can locate them more efficiently.[108] Thus, a male that stays near his female mate increases his chances of extra-pair fertilizations.

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These two hypotheses do not propose immediate benefits of the pair bond to the female, which studies of chacma baboons, siamang, and white-handed gibbons suggest is a highly relevant issue. Where females of these species appear to benefit from a cohesive relationship because the male provides some service, they invest more than males do in the relationship (infanticide protection among chacma baboons) or at least invest as much as males do (direct paternal care among siamang). It may not be a coincidence that pair bonds among white-handed gibbons offer no conspicuous benefit to females and are maintained predominantly by males. The white-handed gibbon may be an example of what Gowaty[109] calls pair bondage. The male makes no substantive contribution to his partner's fitness, but it is simply less costly for the female to tolerate his presence than to attempt to expel him from the territory. Indeed, monogamy in mammals may revolve primarily around male ability to monopolize a solitary female, with any accompanying benefits to females constituting evolutionary side effects.[107] That conclusion is reinforced by the theoretical models of Hawkes, Rogers, and Charnov,[17] which suggest that a relatively high certainty of paternity and a potential for males to increase offspring survival will often be insufficient to select for monogamy and parenting over greater mating effort by males. Thus, monogamy may often be enforced by mating competition. These models suggest that mate guarding via pair bonding may evolve as a mating tactic and that it does not promote increased allocation to care in the ways expected.

Thus, a possible evolutionary scenario for hylobatids is that mate guarding or facilitation of extra-pair copulation (or both) is the primary selective force behind the origin and maintenance of pair bonds. Where males then provide direct care of infants, which is not necessarily an inevitable consequence of certainty of paternity and the fitness-enhancing effects of paternal care,[17] females increase their investment in the those bonds. Ecological differences generating lower intra-group feeding competition may have been the factor that facilitated the evolution of paternal care (limited infant-carrying) in siamang but not in white-handed gibbons, among which males provide no direct, substantive parental care.[61] If males vary in their propensity to provide care, then female investment in pair bonds should vary accordingly, and this has been observed in siamang[62] and other primates.[110]

In summary, this preliminary comparative analysis suggests that the infanticide-protection hypothesis is a likely explanation of the evolution of male-female bonds in chacma baboons and mountain gorillas. The hypothesis in its current form receives little or, at best, equivocal support for gibbons because several aspects of gibbon biology are inconsistent with predictions based on comparative data. There is clearly a great need for more data on gibbon behavior, reproduction, and demography, and for refinement and clarification of the hypothesis. One specific area of potentially fruitful research concerns my suggestion that, assuming infanticide occurs,

unmated male gibbons, like their avian counterparts, constitute a greater risk of to infants than do mated males. Recognition of the possibly contrasting infanticidal risk presented by unmated and mated males may beneficially inform analyses of gibbon behavior as well as the design of field playback experiments.

Playback experiments offer a powerful methodology for testing among these hypotheses. Although Mitani's experiments are suggestive, they were not designed to test these hypotheses, and so critical field experiments controlling for the possible effects of familiarity have not yet been conducted. One goal of such experiments is to differentiate between the infanticide hypothesis and Mitani's[87] alternative hypothesis that lactation and the *general* vulnerability of dependent infants impose costs and constrain female involvement in intergroup interactions. The theoretical framework developed here will also benefit from explicit treatment of alternative strategies, such as adoption. Rohwer[72] has argued persuasively that conditions may arise whereby replacement male birds enhance fitness more by adopting or at least tolerating[111] a female's current offspring than by killing them and subsequently mating with her. The costs and benefits of this strategy for socially monogamous primates have received little analytical attention (but see Dunbar[112] for consideration of similar processes in "helper-at-the-nest" callitrichids).

Finally, the comparative analysis will be much improved by a greater quantity and quality of descriptive data on male-female relationships among primates in general, which historically have been studied less than within-sex social relationships.[113] Study of lemurs may be especially fruitful in this respect, given that strong male-female bonds characterize several species,[114] infant mortality is generally high, and infanticide has been documented. Overdorff,[115] for example, has recently argued that protection against infanticide is an unlikely adaptive reason for male-female bonds in *Eulemur fulvus,* as originally proposed by van Schaik and Kappeler,[24] although she additionally questions whether these heterosexual relationships should be considered "pair bonds" in the first place.

Because infanticide protection can be viewed as a form of paternal care,[50] future studies of socially monogamous neotropical cebids will also help clarify the more general problem of the evolution of pair bonds in contexts where single males provide substantial, direct care of infants. Theoretical models suggest that even with high certainty of paternity, pair-bonded males may often still be selected to invest heavily in mating effort and little in parental effort.[17] And yet nonhuman primates such as titi monkeys

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(*Callicebus* spp.) appear to exemplify this constellation of traits: social monogamy, pair bonds, and extensive paternal care. Such studies will place us in a better position to examine how male infanticide has acted as a selective force in the evolution of primate behavior.

ACKNOWLEDGMENTS

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