
Infanticide and the evolution of male–female bonds in animals

Introduction

Sexual selection theory suggests that divergent reproductive interests of the sexes impede the evolution of enduring social bonds between males and females. Males are more likely to increase reproductive success by acquiring multiple mates whereas females enhance fitness more by discriminative choice of individual mate(s) (Darwin 1871; Trivers 1972). Consequently, insofar as postcopulatory bonds limit a male's sexual access to additional fertile females and are irrelevant to antecedent female mate choice, such bonds should be relatively rare. The mostly polygynous mammals, for example, fulfill this expectation: male mating effort generally exceeds paternal effort, and affiliative interactions between the sexes center on the period of copulation or female fertility (Clutton-Brock 1989b).

And yet, males and non-fertile or anestrus females maintain stable relationships with one another in some species. The same theoretical framework that predicts the rarity of persistent heterosexual bonds also highlights a primary context for their evolution: when a male restricts his mating to a single female, a postcopulatory relationship with her is not only less costly to him, but may also offer fitness advantages to both parties. The proposed benefit to the female is the extensive parental care she receives from a male that is now certain of paternity. Thus durable male–female relationships were originally viewed as part of a coevolved suite of behaviors including monogamy, biparental care, and, in gregarious animals, “nuclear families” of parents and offspring (Morris 1967; Wittenberger & Tilson 1980; Gubernick 1994). The primarily monogamous, biparental birds have long served as vivid examples of this system (Lack 1968).

In spite of the rigor of its evolutionary precepts, this version of the "mating system" perspective fails to fully explain variation in male-female bonds. First, avian studies reveal that mating exclusivity and certainty of paternity are not natural corollaries of social monogamy (Birkhead & Møller 1992; Avise 1996), and that the impressive parental efforts of "caring" monogamous males fail to benefit their female mates as uniformly as originally assumed (Bart & Tornes 1989). Second, male-female social relationships vary independently of mating system (Kleiman & Malcolm 1981; Wickler & Seibt 1983): not only may monogamy entail weak heterosexual attachment and negligible paternal care, but strong bonds between males and anestrus females occur in polygynous mammals in which "classic" forms of direct male care, such as feeding and social thermoregulation, are absent (Palombit 1999). These data direct our attention toward alternative adaptive benefits of male-female bonds.

One of these is male protection against infanticide. A growing body of evidence (Hausfater & Hrdy 1984; Parmigiani *et al.* 1994) indicates that sexually selected infanticide often accompanies a change in breeding males, either (1) as part of a takeover strategy in which a male physically ousts another male from a breeding position; or (2) following "passive replacement" of a male that has disappeared, died, or deserted his female(s). The infanticide protection hypothesis suggests that females form bonds with males who will deter infanticide (Hrdy 1979).

Male defense and male-female social relationships

A male's protection of an infant does not *a priori* imply a social bond with its mother. In some teleost fish and amphibians, for example, males care for and defend young without the help of females, who leave males in possession of broods to seek additional mates and/or tend a second clutch (Sargent & Gross 1993). Such uniparental care by males is rare in birds, and essentially non-existent in mammals (Clutton-Brock 1991). Prolonged postnatal maternal investment in these taxa often means that a male guardian will necessarily associate at least spatially with the mother, especially when females carry their young rather than cache them in burrows or nests (van Schaik & Kappeler 1997). Propinquity may or may not, however, promote social affiliation between the sexes (Wickler 1976). If the primary cause of their association remains simply the spatiotemporal conjunction of their independent parental efforts, then males may share weak relationships with females, and be socially more attracted to their young.

There are several reasons why a cohesive social relationship between male and female may accompany infanticidal defense. First, if paternity improves male defense of an infant, then a prior association extending into prenatal periods may be selected for. Second, affiliation between mother and protector may facilitate infant protection. In mice, even modest postcopulatory cohabitation with a female markedly enhances the chances that a male will care for her offspring (Elwood 1989) rather than kill them (Soroker & Terkel 1988; Gubernick *et al.* 1994). Third, ongoing social relationships may be critical for maintaining male defense at maximally effective levels. In non-human primate aggression, individuals preferentially aid those with whom they have interacted affinitively in the *recent* past (Harcourt 1992). Dunbar (1980) invoked the generality of this principle in organizing primate social behavior by arguing that strong social bonds between cercopithecine mothers and daughters are the reason for the elevated frequency of coalitionary support between them. Thus, among gregarious animals maintaining dynamic, differentiated social relationships with one another, a female's ability to garner infanticide protection will often vary with her current social relationships with prospective male defenders. Females will therefore invest in social relationships with these males (Hrdy 1979; Birkhead & Møller 1992).

The economics of pair bonds and infanticide defense: benefits to females and males

I assume that male-female bonds will evolve as an anti-infanticide strategy when the benefits of the constituent behaviors exceed their costs. Limitations of space preclude consideration of costs, but attention to alternative benefits generates the competing functional hypotheses against which the infanticide protection hypothesis is tested.

Alternative potential benefits to females

The infanticide protection hypothesis identifies deterrence of infant-killing as the adaptive advantage that anestrus females gain from associating with males. Competing benefits to females derive from two sources: other forms of infant care or services provided directly to mothers (Table 11.1).

Paternal care with an immediate, physical impact on young provides examples of infant-specific benefits. These include male thermoregulatory incubation or huddling, provisioning and food sharing, carrying,

Table 11.1. *Hypothetical benefits of male-female bonds to females*

Hypotheses based on protection	
Infanticide protection hypothesis	Male protection of young from infanticide
Predation protection hypothesis	Male protection of young and/or females from predation
Female harassment hypothesis	Male protection of young and/or females from harassment by female competitors
Sexual coercion hypothesis	Male protection of females from harassment from adult or subadult males
Other hypotheses based on infant care	
Alternative male care hypothesis	Direct, extensive male care of infant (e.g., provisioning)
Male-infant bonding hypothesis	Male-female bonds facilitate development of male-infant social bonds, which generates post-weaning benefits for juveniles

retrieving, socialization, and cleaning or grooming (Kleiman & Malcolm 1981; Woodroffe & Vincent 1994). This "alternative male care" hypothesis typically emphasizes these forms of extensive, direct male care, partly because indirect contributions (such as resource defense, territoriality, maintenance of nests or burrows, and "vigilance" behavior) may benefit mothers and the males themselves, besides infants.

A variant of this hypothesis applies to gregarious animals with a prolonged period of male-young interaction: females (and infants) initially derive no substantive benefits – defensive or otherwise – from male companions. Rather, the "male-infant bonding" hypothesis argues that a female associates with a male to promote the development of social attachment between him and her infant, which later benefits the juvenile through post-weaning male attention, e.g., intervention in competition with peers, protection from predators, etc. (Ransom & Ransom 1971; Seyfarth 1978; Nicolson & Demment 1982; Stein 1984b; Smuts 1985; Collins 1986; Strum 1987).

A second group of hypotheses posits male protection against contingencies other than infanticide (Table 11.1). Protective vigilance against predation has been advanced as the primary benefit that females derive from associating with males in some birds (Hannon 1984; Dahlgren 1990), non-human primates (van Schaik & van Noordwijk 1989; Baldellou & Henzi 1992; Rose 1994; Rose & Fedigan 1995), and other mammals (Burger & Gochfeld 1994). Alternatively, male associates may shield mothers from elevated rates of agonistic interaction with

(high-ranking) female competitors (Altmann 1980) while simultaneously guarding infants from rough handling and kidnapping by these dominant females (Silk 1980; Collins *et al.* 1984; Rhine *et al.* 1988; Brain 1992; Maestripieri 1994). Finally, her bond with a male may buffer a female from harassment from adult males (Smuts & Smuts 1993). Gowaty & Buschhaus (1998) argued that pair-bonded monogamy may be an adaptive female response to the "dangerous environment" created by male aggressiveness toward them, particularly in sexual contexts. It is important to differentiate between infanticide and male sexual coercion of females, the latter of which is aggression directed explicitly at females to increase the probability of copulating with them (Clutton-Brock & Parker 1995).

Insofar as benefits apply exclusively to females, they may become crucial for mothers with dependent young for two reasons. First, females may become increasingly frequent targets of harassment or predation at this time. Second, the rate and intensity of attack may remain unaltered, but these interactions become effectively costlier to females in the context of energetically demanding lactation (Gittleman & Thompson 1988; Rogowitz 1996).

Alternative potential benefits to males

Parental or mating benefits are likely to account for male defense against infanticide (Table 11.2). The "paternal investment" hypothesis states that males increase the survival of offspring they have sired by protecting them from infanticidal attack (Palombit *et al.* 1997). The "female choice" hypothesis suggests that male care of an infant is a mating strategy that increases his chances of copulating with the mother in future reproductive cycles (Smuts & Gubernick 1992; van Schaik & Paul 1996–7; Freeman-Gallant 1997) or with additional females that observe his behavior (Gori *et al.* 1996). Females preferentially mate with these males to procure this care or because it signals a male's high genetic quality as mate (Freeman-Gallant 1996). Explanations emphasizing "parental effort" versus "mating effort" are not mutually exclusive, but the latter is obviously relevant in situations where males enhance their fitness through care of unrelated infants.

This dichotomy subsumes several other alternative hypotheses for postcopulatory association between a male and female with dependent offspring (Table 11.2). An alternative paternal investment model simply replaces infanticide defense in the above hypothesis with some other

Table 11.2. *Hypothetical benefits of male-female bonds to males*

Hypotheses based on parental effort	
Paternal investment hypothesis	Male invests in caring for and/or protecting offspring he has sired
Hypotheses based on mating effort	
Sperm contribution hypothesis	Male continues mating with female and thereby fertilizes replacement clutches in current reproductive cycle
Female choice hypothesis	Male attracts current female companion and/or additional females as mates in future reproductive cycles
Paternity guard hypothesis	Male guards his breeding and/or mated status
Pursuit of extra-pair copulation hypothesis	Male is locatable for (extra-pair) copulations with other females
Hypotheses based on non-reproductive social benefits	
Social tool hypothesis	Male exploits females and infants as social tools in agonistic interactions with other males
Immigration hypothesis	Immigrant male acquires stable residency in group through relationships with female(s)
Female allies hypothesis	Male obtains coalitionary support from female in agonistic interactions

form of paternal investment, e.g., provisioning of young, protection against predation or conspecific harassment, etc.

Likewise, males may derive several other mating benefits, besides female choice, through extended association with females. A distinctive feature of the following hypotheses is that they do not necessarily assume that females also benefit in any way from social relationships with males. Indeed, they allow for the possible *reduction* of female fitness from post-copulatory association with a male.

The "sperm contribution" hypothesis suggests that a male continues associating with a female mate in order to increase paternity of replacement clutch(es) should her first one fail. Repetitive copulation with the female achieves this goal by increasing his relative contribution to the sperm that she stores.

Avian studies reveal that the conspicuous proximity of socially monogamous males and females is frequently a paternity guard (Birkhead & Møller 1992). This hypothesis suggests that guarding by males may function genetically during fertile periods to prevent extra-pair fertilizations, or socially during both fertile and non-fertile periods to preserve mating status (Slagsvold & Lifjeld 1997).

The "pursuit of extra-pair copulation" hypothesis argues that a male maintains a postcopulatory bond with his partner because other females seeking extra-pair copulations can locate him more easily (Gowaty 1996a,b).

A final group of hypotheses focuses on potential social benefits of non-reproductive bonds with females (Table 11.2). Males may derive long-term strategic benefits in male-male competition through: (1) exploitation of female associates and/or their infants in triadic interactions; (2) coalitionary support from females; or (3) facilitation of immigration into new groups (Smuts 1983; Strum 1983).

Empirical studies: infanticide as a cause for male-female bonds

Below I focus on research examining the predictions of the Infanticide Protection hypothesis and alternative hypotheses in a number of relatively well-studied taxa.

Insects

The mating and social system of the burying beetle (Coleoptera: Silphidae, *Necrophorus* spp.) is exceptional among insects in combining prolonged postcopulatory association of the sexes, social monogamy, extensive biparental care of young, and sexually selected infanticide (Eggert & Müller 1997). A male and female jointly prepare a small vertebrate carcass that constitutes the sole food source for developing larvae. Both sexes generally remain with the brood for the 1-4 weeks of larval development (Scott & Traniello 1990; Trumbo 1991), feeding them by regurgitation of pre-digested food, and helping them access the interior of the "carrion ball" (Eggert *et al.* 1998). Adults also actively defend the carcass, which is vulnerable to takeover by conspecifics of either sex (Scott 1990; Trumbo 1990a). If a takeover occurs, the intruding conspecific replaces the former resident of the same sex, kills larvae that are present in the nest, and pairs with the remaining adult to produce a new clutch.

Studies of the burying beetle illustrate how multiple lines of observational and experimental evidence can be marshaled to support the infanticide protection hypothesis and reject other possibilities. First, carcasses defended by a single female are significantly more vulnerable to takeover infanticide than those defended by a pair of adults (Trumbo 1990a,b, 1991; Robertson 1993) (Table 11.3). Second, although parental investment in the

Table 11.3. Field removal experiments in species with sexually selected infanticide

Organism	Social/mating system	Experimental results	Source
Burying beetle (<i>Necrophorus orbicollis</i> , <i>N. vespilloides</i>)	Social monogamy/ biparental care	Single females were significantly more vulnerable to takeover infanticide than heterosexual pairs; experimentally widowed females produced fewer offspring than control females due to reduced initiation of replacement clutch	Trumbo 1990a; ^a Robertson 1993; ^a Sakaluk <i>et al.</i> 1998
Orange-tufted sunbird (<i>Nectarinia osea</i>)	Social monogamy/ biparental care	After a single territorial male was removed from his nest, an intruder male appearing the next day interfered with female attempts to feed chicks, and attacked fledglings that left the nest; the detained territorial male was released on this day, whereupon it chased the intruder male off in an aggressive fight	Goldstein <i>et al.</i> 1986
Orange-tufted sunbird (<i>Nectarinia osea</i>)	Social monogamy/ biparental care	Females made compensatory increases in provisioning, but not in nest defense; nests containing three chicks suffered greater mortality due to predation, not infanticide	Markman <i>et al.</i> 1996
Tree swallow (<i>Tachycineta bicolor</i>)	Social monogamy	Replacement males arriving during egg-laying period generally adopted chicks, but 79% of those arriving during incubation and 71% of those arriving during nestling period killed young	Robertson 1990; Robertson & Stutchbury 1988
Starling (<i>Sturnis vulgaris</i>)	Social monogamy	Males adopted eggs if replacement occurred before egg-laying period, but destroyed eggs if replacement occurred during female's egg-laying period; 4 out of 6 females affected by infanticide produced replacement clutches with replacement male	Smith <i>et al.</i> 1996
Barn swallow (<i>Hirundo rustica</i>)	Social monogamy / coloniality	Males detained for less than a day at onset of nestling period (cf. 20 controls). In colonial nests, infanticide occurred among those widowed females that did not show compensatory increase in nest guarding (i.e., 40% of experimental nests). No infanticide in any control nests or following male detention among relatively more dispersed, solitary breeding pairs. Solitary nests: no nestlings were killed (experimental or control nests); replacement males did not arrive	Møller 1988
House sparrow (<i>Passer domesticus</i>)	Facultative social monogamy/polygyny	Widows that obtained a new mate and remained socially monogamous suffered infanticide from replacement male; widows that became new mates of a polygynous male suffered infanticide from other females in the breeding unit	Veiga 1992
House wren (<i>Troglodytes aedon</i>)	Monogamy	Males removed 4–5 days post-hatching: no replacement males appeared, no infanticide	Bart & Tornes 1989
House wren (<i>Troglodytes aedon</i>)	Bigamy/monogamy	63% of replacement males in late incubation removed offspring from nests and most subsequently fledged offspring (remaining 37% failed to commit infanticide or to breed)	Kermott & Johnson 1990; Kermott <i>et al.</i> 1991
Wattled jacana (<i>Jacana jacana</i>)	Polyandry	Replacement females appeared on territories of "widower" males the day after female removal and aggressively attacked chicks; 7 of 9 of the chicks eliminated within 48 h of female removal	Emlen <i>et al.</i> 1989
Arctic ground squirrel (<i>Spermophilus parryii</i>)	Polygyny/coloniality	Following male removal at beginning of birth season, infanticide occurred when incoming intruder males were unlikely to have sired the young; overall reproductive success did not differ between experimental and control females	McLean 1983
Hanuman langur (<i>Presbytis entellus</i>)	Polygyny/one-male groups	After a single territorial male was removed, the male of adjacent group fatally attacked 4 infants, whose mothers "desert" them and did not defend; male attempted to integrate male-less group with his own group, but failed	Sugiyama 1967

Notes:

^a These studies did not involve experimental removal of an adult from established pairs; rather, single females and heterosexual pairs were established on carrion nests and monitored for takeover infanticide.

form of larval provisioning and carcass maintenance enhances offspring survival (Eggert *et al.* 1998), the male contribution is not critical. Broods cared for by a single female survive and grow as well as do those receiving biparental care (Bartlett 1988; Scott 1989; Reinking & Müller 1990; Trumbo 1991; Müller *et al.* 1998). Third, extended residency of a male is unlikely to significantly increase his copulatory success, partly because the resident female physically interferes with his attempts to pheromonally attract additional mates (Trumbo & Eggert 1994; Eggert & Sakaluk 1995). Moreover, extended residency does not improve male reproductive success through enhanced paternity of his own mate's replacement brood should her first clutch fail: males removed before the initiation of replacement clutches had the same high paternity of replacement broods as males permitted continued mating opportunities with their mates (Sakaluk *et al.* 1998). Finally, many experimentally widowed females fail to produce a replacement clutch at all. These females may curtail reproduction because the disappearance of the male reflects his low quality or vigor as a sire, but Sakaluk *et al.* (1998) argued that it is more likely that loss of the male signals an imminent takeover, prompting the female to postpone production of offspring likely to be killed in favor of conserving the carrion ball for a replacement clutch eventually fathered by the intruder male.

There are multiple adaptive reasons for the extended residency of male *Necrophorus* on carcasses, for populations vary considerably in rates of takeover and replacement brood production, as well as in the availability of carcasses and additional female mates (Scott 1990, 1994; Sakaluk *et al.* 1998). Nevertheless, there is compelling evidence that male-female association – and the consequent social monogamy – have evolved as an anti-infanticide strategy in at least some populations.

Birds

Contemporary research has confirmed Darwin's (1871) thesis that significant intrasexual breeding competition may occur under monogamy, due to factors such as an early mating advantage, skewed sex ratios, and (though not fully appreciated by Darwin), extra-pair paternity and exclusion of "floaters" from reproduction (Andersson 1994; Palombit 1999; Veiga, Chapter 9). The incidence of sexually selected infanticide hints at a largely unstudied potential to influence the evolution of avian behavior, e.g., nest guarding, dispersal, response to extra-pair conspecifics, and social monogamy itself. Arguments that pair-bonded monogamy predominates in birds because of a conspicuous avian poten-

tial for biparental care have traditionally emphasized "conventional" forms of care, such as incubation and provisioning (Mock & Fujioka 1990). Freed (1986) was the first to propose that infanticide defense is the crucial male contribution in some populations.

The potential deterrent value of males may be suggested by observations of their nest defense and by their absence preceding successful infanticides (e.g., in 11 of 14 attacks in barn swallows (*Hirundo rustica*); Møller, 1988). Controlled male removal or detention experiments measure more rigorously his effect on infanticide risk (Table 11.3). Typically, one or more intruder males (usually floaters) appear on the experimentally "widowed" female's territory within days or even hours after removal, but consequences for offspring depend upon the timing of replacement in the reproductive cycle. If replacement occurs before, and in some cases, during egg-laying, adoption of offspring is probable, but if replacement takes place during the incubation or nestling periods, infanticide becomes increasingly likely in some populations (Palombit 1999).

Study of the barn swallow underscores the importance of intervening variables – such as maternal defense and the spatial distribution of nests – in determining the value of male infanticide defense (Møller 1988). Among colonially nesting individuals, temporary detention of mated males at the onset of the nestling period precipitated immediate infanticide by unmated males, but only among those widowed females that failed to make compensatory increases in nest guarding. Among non-colonial females breeding in solitary heterosexual pairs, infanticide never followed male removal because replacement intruder males failed to settle subsequently on widowed females' territories. Thus males may help females to achieve a level of nest guarding that forestalls infanticide, without always being strictly necessary to do so.

The killing of young after experimental removal of the male strongly implicates reduced infanticidal risk as the adaptive benefit of social monogamy to females. Additional data are necessary to reject alternative hypotheses, however, as exemplified by numerous studies of the house wren (*Troglodytes aedon*). Individuals of this widely distributed passerine live in permanent socially monogamous pairs in tropical South America, and are facultatively bigamous and monogamous in northern populations. Infanticide is part of a common takeover strategy by unmated floater males (and females) in tropical latitudes (Freed 1986, 1987), and follows mate replacement in temperate populations (Kermott & Johnson 1990; Kermott *et al.* 1991; Table 11.3).

Freed (1986) argued that the need for infanticide defense by males

maintains social monogamy in tropical house wrens. Two likely other benefits that males provide to females are anti-predator protection and food provisioning of nestlings. Predator defense was unimportant in Freed's study, since avian predators were absent and since subjects' nest boxes were inaccessible to terrestrial predators. Johnson & Albrecht (1993) also rejected the predator protection hypothesis for temperate house wrens by demonstrating experimentally that, although bigamous males spent much less time near the nests of their secondary females than monogamous males did near their mates' nests, both types of males detected and defended against small diurnal predators equivalently. Johnson & Albrecht (1993) warned, however, that this result does not imply that monogamous and polygynous males are equally effective in detecting and ousting *conspecific* (potentially infanticidal) floater males, since "this aspect of male care is probably less 'shareable'" than anti-predator defense. Evidence against the alternative male care hypothesis comes from removal experiments conducted late in the nestling period. These demonstrated that male food deliveries enhance offspring survival only in poor years (Bart & Tornes 1989); under average conditions, the male's participation seems to make no difference (Mock & Fujioka 1990; but see Johnson *et al.* 1992). On the other hand, the higher fledging success of primary females whose provisioning of young is aided by bigamous males would seem to support the alternative male care hypothesis. Johnson & Kermott (1993), however, attributed the lower reproductive output of secondary females to the greater need for them to stay near nests and guard young against infanticide, which severely limits food deliveries. Finally, greater extra-pair paternity among the offspring of secondary females (compared with primary females) suggests that secondary females compensate for reduced infanticidal defense from the male by pursuing an alternative strategy based on confusing paternity among potentially infanticidal males (Soukup & Thompson 1997). Although these last two hypotheses await rigorous testing, the house wren provides another case in which several pieces of evidence oppose different hypotheses in favor of the conclusion that male-female bonds have evolved as an anti-infanticide strategy.

Rodents

Infanticide is widespread in rodents (Blumstein, Chapter 8), but evidence that it has selected for female association with male defenders is meager. Even in species where heterosexual relationships and infanticide

co-occur, an adaptive link between the two often remains vague. For example, deer mice (*Peromyscus maniculatus nubiterrae*) show greater pair-bond cohesion and male involvement with pups than do white-footed mice (*P. leucopus noveboracensis*), but the two species are similar in infanticidal behavior (Wolff & Cicirello 1991) as well as in the effectiveness of maternal aggression in successfully forestalling male infanticide (Wolff 1985). In these species, the data are more consistent with the alternative male care hypothesis than the infanticide protection hypothesis.

Nevertheless, infanticide has been offered as the adaptive reason for male-female bonds in a few species such as the Malagasy giant rat (*Hypogeomys antimena*) (Sommer 1997) and, more notably, the Arctic ground squirrel (*Spermophilus parryii*). In Arctic ground squirrels, immigrant males that establish residency at the end of the mating period commit infanticide. McLean (1983) presented four results to support his claim that infanticide has selected for the extended residency of male protectors: (1) resident males were territorial primarily when pups were most vulnerable to infanticide and when food was abundant, suggesting that male territoriality has not evolved to improve female access to limited resources; (2) males' greater amount of time devoted to alert postures and exploration compared to females suggested a "lookout" role; (3) infanticide was less common when a breeding male defended a territory during the ensuing period of pup vulnerability than when he did not; (4) male removal elicited infanticide, and mean litter size at emergence among experimental colonies was significantly lower than in control areas (Table 11.3) (though the specific causes of smaller litters were unknown, and replication a year later failed to generate similar results). Evidence against the potentially competing predator protection hypothesis is unavailable.

Numerous experimental studies in captivity have measured rates of infanticide by males introduced into cages with females and pups (Blumstein, Chapter 8). Parmigiani *et al.* (1994) speculated that the frequently observed failure of maternal aggression to deter infanticide among captive rodents such as *Mus domesticus* may be due partly to the artificial absence of the stud male. In the natural setting, he might be attracted to intervene by the female's conspicuous defensive behavior. Experiments systematically varying the availability of stud males are needed to test this hypothesis.

Non-human primates

Two aspects of their biology have made primates the most frequent subjects of tests of the infanticide protection hypothesis. First, permanent association between males and anestrus females is more common than in mammals generally, characterizing almost all anthropoids and many prosimians (van Hooff & van Schaik 1992; van Schaik 1996). Second, male infanticide occurs in many polygynous species, and is best understood as a sexually selective reproductive strategy in most, but not all cases (Hiraiwa-Hasegawa & Hasegawa 1994; Hrdy *et al.* 1995).

Socioecological models have traditionally viewed heterosexual relationships in primates simply as a secondary outcome of evolutionary forces shaping female–female and male–male social interactions (Smuts 1987b; van Schaik 1996). Largely in the last decade, however, infanticide has been offered as the adaptive reason for male–female bonds in diverse taxa such as capuchin monkeys (*Cebus olivaceus*) (O'Brien 1991), Malagasy lemurs (van Schaik & Kappeler 1993), humans (*Homo sapiens*) (Smuts 1992), mountain gorillas (*Gorilla gorilla berengei*) (Wrangham 1979), gibbons (*Hylobates* spp.) (van Schaik & Dunbar 1990), and chacma baboons (*Papio cynocephalus ursinus*) (Palombit *et al.* 1997), as well as in gregarious primates universally (van Schaik & Kappeler 1997).

Mountain gorillas

Infanticide defense has long been considered the adaptive reason for group living in polygynous mountain gorillas (Wrangham 1979). Several observations suggest a protective role of the resident male in one-male groups: (1) infanticide accounts for at least 38% of infant mortality and occurs primarily after this male dies or disappears (Fossey 1984; Watts 1989); (2) strong heterosexual bonds form the core of the group (Stewart & Harcourt 1987; Watts 1990, 1996); and (3) females transfer between groups when they are near one another, thereby apparently avoiding the dangers of being alone (Harcourt 1978). Indirect data appear to reject the other two likely hypotheses for mountain gorilla sociality. First, the relative abundance and even distribution of their folivorous food resources implies an absence of feeding-related benefits of grouping to females (Wrangham 1980), and, second, immense body size should largely eliminate predation risk (Wrangham 1979). Stewart & Harcourt (1987), however, favor renewed and rigorous testing of competing hypotheses by arguing that protection from predators (leopards) is just as important as infanticide defense in promoting male–female bonds.

Chacma baboons

The chacma baboon has provided an opportunity to test more directly the infanticide protection hypothesis against other possibilities. As in savanna baboons generally (Ransom & Ransom 1971; Altmann 1980; Anderson 1983; Strum 1982; Smuts 1985; Collins 1986; Bercovitch 1991), lactating females maintain close bonds with an unrelated adult male (or two) (Seyfarth 1978). Because a single dominant male does not attract all the females of the group (as in capuchin monkeys and mountain gorillas), a chacma baboon group at a given time includes several essentially dyadic pair bonds, or “friendships” (Strum 1974), based on pronounced spatial proximity and high rates of affiliative interactions, such as grooming and infant handling. Before birth and soon after an infant's death, there is no manifestation of the “special relationship” that exists between a particular male and female during lactation (Palombit *et al.* 1997). The strict temporal conjunction of these bonds with neonate presence suggests that the benefits of friendships to females involve infant viability and survival.

An especially clear possibility in the chacma baboon population of the Moremi Game Reserve, Botswana, is that males defend the offspring of their female friends from infanticide, which accounts for at least 37% of infant mortality and appears to be a sexually selected strategy of new immigrant alpha males (Palombit *et al.*, Chapter 6). Studies of East African conspecifics, among which infanticide is exceptional (Collins *et al.* 1984), provide the alternative protective benefits of male friends (Table 11.1). They may safeguard females from postpartum agonistic interaction or semi-abusive infant “handling” from higher-ranking females (the female harassment hypothesis) or from (non-infanticidal) aggression by adult and subadult males (the sexual coercion hypothesis). A final, fourth hypothesis is that friendships do not confer any protective benefits to infants (or females) at all, but instead function as a “maternally induced” mechanism facilitating male–infant affiliation that persists into the juvenile period (the male–infant bonding hypothesis).

A crucial question has always been whether the friendship that develops between a female and a male enhances his willingness to defend her when she is attacked, as predicted by the three protection-related hypotheses. Palombit *et al.* (1997) examined this question through naturalistic observations and field playback experiments that exploited the considerable variation in male chacma baboons' orienting responses to the screams females typically give when attacked. In these experiments, we played a female's scream to the male friend and, at another time under

similar conditions, to a control male who was of similar rank and also had a female friend in the group. Male friends responded significantly more strongly than control males (Figure 11.1a). Because the visual scanning elicited by a vocalization generally reflects the listener's investment in obtaining further information about the specific circumstances surrounding vocalizing (Marler *et al.* 1992), these results support the prediction that friendships predispose males to aid particular females under attack. This predisposition, however, depended upon the presence of infants. When the experiment was repeated in the period immediately following the death of a female's infant, male friends' responses were significantly weaker than control males (Figure 11.1b). A final series of experiments in which the threat calls of the simulated attacker accompanied the victim's screams suggested that male friends' responded more strongly than controls primarily when the aggressor was an infanticidal male, rather than a high-ranking female or a non-infanticidal male. In light of observational data showing that lactating females do not avoid interacting with higher-ranking, unrelated females, the combined results suggest that chacma baboon friendships confer protection-related benefits to females, and that this protection is more likely to operate in the infanticidal context rather than other harassment situations. Thus the chacma baboon provides a case where sexually selected infanticide accounts for a significant portion of infant mortality, males and females (with dependent infants) share close bonds with one another, and these friendships apparently function to reduce infanticide risk.

Gibbons

Infanticide defense has also been offered as the adaptive reason for social monogamy among gibbons. Van Schaik & Dunbar (1990) argued that individual male gibbons are capable of maintaining home ranges large enough to encompass 2–13 females, but decline to do so because a polygynous strategy would leave females vulnerable to infanticide by other males. Field studies of gibbons have generated few directly relevant data and no reports of infanticide with which to test the infanticide protection hypothesis. Comparative analysis, however, allows a preliminary test: are patterns of hylobatid behavior and ecology consistent with those observed in other primates as well as socially monogamous birds in which sexually selected infanticide and male–female bonds seem to be functionally interrelated?

Avian studies provide the comparative data base – currently lacking in

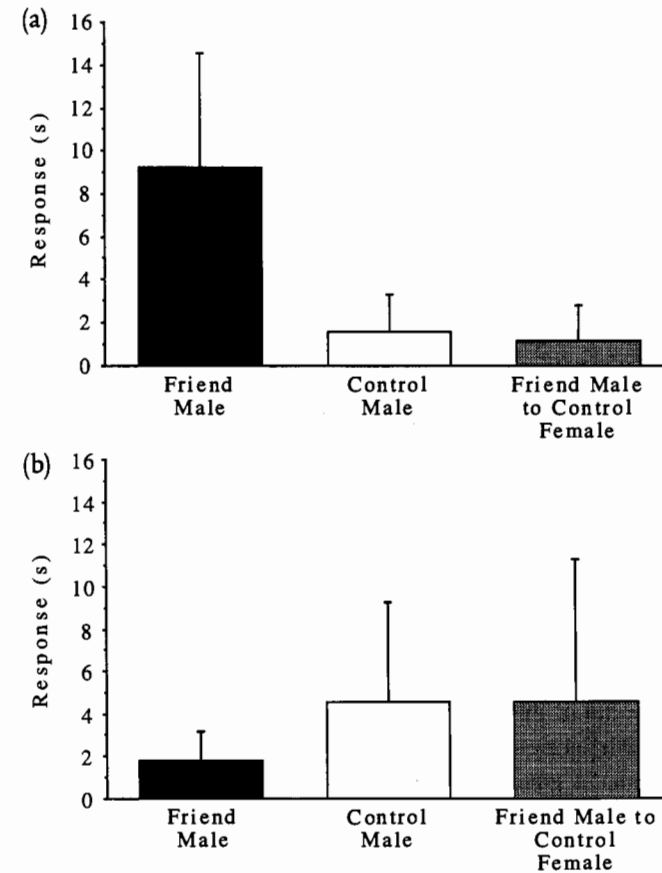


Figure 11.1. Results of playback experiments of female distress calls to males in chacma baboons. Black bars and white bars are the response of friend males and control males to playback of a particular female's scream. Gray bars indicate the friend male's response to the scream of a control (non-friend) female of similar rank and reproductive status. (a) Results during periods when female friends had infants. These indicate that male friends responded significantly more strongly than control males, and that males responded significantly more strongly to screams of female friends than to those of control females ($P < 0.01$, $N = 30$ experiments distributed equally across each condition). (b) Corresponding results but during the period immediately following the death of an infant. These indicate that male friends responded significantly less strongly than control males ($P < 0.05$), and that there was no difference in male response to the screams of female friends and control females ($N = 18$ experiments distributed equally across each condition). Response is measured as the duration of orienting toward the concealed playback speaker in the 20 s following the playback minus the duration of orienting in the same direction in the 20 s preceding the playback. Data are taken from Palombit *et al.* (1997).

mammalian research – that specifies the ecological and demographic conditions that intensify intrasexual selection among socially monogamous males and, ultimately, promote infanticide as well as anti-infanticide pair bonds (Table 11.4). Individuals of tropical populations such as house wrens are particularly relevant, for (like gibbons) they maintain permanent territories and pair bonds, breed throughout most of the year, and (unlike gibbons) they are known to commit infanticide.

Although aseasonal breeding and long interbirth intervals establish a clear reproductive potential for sexually selected infanticide (Palombit 1995), a fundamental demographic cause of avian infanticide appears to be lacking in gibbon populations: an abundance of unmated, fully adult “floater” males. In avian populations with sexually selected infanticide, unmated adult males, such as single floaters and/or first-time breeders, are relatively numerous (Crook & Shields 1985; Møller 1988; Veiga 1992) and account for most observed infanticides (Freed 1986; Goldstein *et al.* 1986; Møller 1988; Robertson 1990; Hotta 1994). This result is consistent with sexual selection theory. For already paired males, infanticide primarily offers an opportunity to *switch* mates. Even when bigamy is possible, as in temperate house wrens, mated males rarely use infanticide to acquire a second mate (Kermott *et al.* 1991). For unmated floaters, however, the potential value of infanticide is dramatically greater. These males have few reproductive options, not only because they lack pairmates, but also because females generally prefer mated males as extra-pair sexual partners (Birkhead *et al.* 1986). Thus infanticide as part of a takeover strategy may alter an unmated floater male’s breeding status entirely. In summary, high densities of adult floaters are responsible for intensifying intrasexual mating competition and thereby generating the potential reproductive benefits of infanticide for socially monogamous male birds (Table 11.4).

These avian data provide a general biological context for evaluating the hypothesis that female gibbons are “vulnerable to infanticide by males attempting a takeover or by neighboring males attempting to expand their territories, but also by transient males” (van Schaik & Dunbar 1990). If gibbons commit infanticide, then, like birds, the cost–benefit ratio of infant-killing should be less favorable for a monogamous male that already possesses a mate and breeding territory than for a male that lacks one or both these prerequisites for reproduction. The absence of observations of infanticide in gibbons precludes direct testing of this assumption, but corroborating data come from field experiments

Table 11.4. Conditions favoring sexually selected infanticide in socially monogamous birds, with implications for gibbons (from Palombit 1999)

	Condition favoring infanticide in avian populations	Does condition apply to hylobatid populations?
Features of female reproduction that create potential for infanticide	Asynchronous breeding	Yes
Factors that reduce the costs of infanticide	Long breeding season	Yes (aseasonal breeding)
	Offspring often left unattended due to weak pair bond or demanding nest provisioning	No
Factors that increase the benefits of infanticide to males (by limiting breeding opportunities)	Coloniality/gregariousness	No
	Limited opportunity or effectiveness of maternal aggression	No
	Inexperienced (“first-time”) female breeders abundant	Unknown
	High mortality among mated adults	No
	Low relatedness among (colony) neighbors	Unknown
	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 can not mate with males other than the infanticidal male	Unknown	

in which Mitani (1984, 1985, 1987) simulated the presence of mated pairs, solitary females, and solitary males by playing back their respective songs to conspecific agile (*Hylobates agilis*) or Mueller's gibbons (*H. muelleri*). Van Schaik & Dunbar (1990) maintained that these experiments reveal a decreased willingness of mothers with dependent infants to participate in territorial interactions (as compared with non-lactating females), which they attributed to the attendant risks of male infanticide. Mitani (1984), however, emphasized the "clear and striking similarity" of female responses 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 risk of infanticide motivates female response under these playback conditions, then Mitani's results suggest that mated males pose a relatively low risk of infanticide (i.e., roughly equivalent to that presented by solitary, unmated females). Also, Mitani's data suggest that female agile gibbons with infants are equally wary of interacting with unfamiliar, solitary adults of either sex, contrary to the predictions of the infanticide protection hypothesis in its current form. (A possible alternative explanation for both patterns is, of course, that *females* also pose an infanticidal threat.)

This difference in infanticidal behavior of unmated versus mated males is important because currently available data suggest that adult floaters of either sex are rare in most gibbon populations monitored for more than 3 years (Chivers & Raemaekers 1980; Mitani 1990; Palombit 1994a; Brockelman *et al.* 1998; but see Tilson 1981). Leighton (1987) and Mitani (1990) have consequently argued that dispersing young adults suffer high mortality. Observations that numerous breeding vacancies occurring over 6 years in hylobatid groups in Sumatra were all filled by known residents of neighboring groups, not by floaters, provide further evidence for the rarity of floaters (Palombit 1994a). Finally, a "natural experiment" transpired when two contiguous siamang territories became available for colonization after all residents died or dispersed following contraction of disease by adults (Palombit 1994a). Siamang (*Hylobates syndactylus*) did not re-occupy the total area of over 80 ha of productive lowland rainforest in the ensuing 5 years (or more), even though sympatric primates such as longtailed macaques, orang-utans and white-handed gibbons (*H. lar*) continued to live and reproduce successfully there. In most bird populations, analogous provisioning of nest boxes or removal of males rapidly exposes the presence of unmated floaters who seize the proffered reproductive opportunity. In sum, hylobatid data

suggest that physically mature, unmated adult males are extremely rare, or at least rarer than in many birds with infanticide. If future demographic data confirm this pattern, then the potential threat of sexually selected infanticide to females (mated or widowed) may be lower in gibbons than it is in those socially monogamous birds in which infanticide occurs.

Most gibbon populations reveal low or "near-zero" infant mortality (Leighton 1987; Mitani 1990; Reichard & Sommer 1997: 1135), suggesting a limited role of infanticide in maintaining pair-bonded monogamy relative to other potential sources of mortality. It is unlikely that infant mortality is low in hylobatid populations simply because male protectors accompany most females. 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/or propensity to protect young from attack, and that this will translate directly into *variable* risk of death for young. Moreover, 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 males should select forcefully for takeover infanticide (Table 11.4). The limited opportunity for subadult hylobatids to postpone dispersal by helping adults to raise offspring (as cooperatively breeding birds do) should intensify 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. Nevertheless, takeover infanticide is undocumented, probably because an important causal agent suggested by avian studies is lacking, i.e., a relatively large population of fully adult, reproductively disenfranchised floater males. 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.

Comparative social data from primates with infanticide and "anti-infanticide" male-female bonds additionally oppose the infanticide protection hypothesis for gibbons. Two well-studied primate systems support Hrdy's (1979) and Birkhead & Møller's (1992) prediction that a female will invest substantially in a social relationship with a male who will sustain the costs of defending her offspring against infanticide.

The male–female bonds constituting chacma baboon friendships (Palombit *et al.* 1997) and one- and multimale groups of mountain gorillas (Harcourt 1979b; Sicotte 1994; Watts 1996) rely upon a greater female contribution to two pivotal mechanisms used by primates to “service” their social relationships (*sensu* Hinde (1983) and Dunbar (1988)): close proximity and allogrooming. A lactating female is more responsible than the male for maintaining the close proximity they enjoy, and she grooms him more than he grooms her. It is not the case, however, that these patterns result from a general social indifference among males; they actively maintain social relationships with *estrous* females (Sicotte 1994; R. A. Palombit, unpublished data). Similar grooming patterns incidentally characterize howler monkeys, *Alouatta* spp., where infanticide and male–female association also co-occur (Crockett & Eisenberg 1987; Chiarello 1995). Independent support for the general prediction that females will invest heavily in bonds with males bestowing a fitness-enhancing service emerges from grooming data between paired titi monkeys (*Callicebus torquatus*), a socially monogamous species in which males extensively carry infants soon after birth (Figure 11.2).

Relevant field data on hylobatid pair bonds are few, but Palombit’s (1996) study of sympatric white-handed gibbon and siamang provides a starting point partly because it employed several of the same behavioral measures described above for chacma baboons and mountain gorillas. These demonstrate that male hylobatids are responsible for proximity maintenance to the same degree that female chacma baboons are with their male friends (Palombit 1999). Essentially the same is true of allogrooming between white-handed gibbon pairmates: males perform the vast majority of within-pair grooming (Figure 11.2) largely because females rarely initiate grooming sessions, routinely solicit grooming at higher rates, and ignore male solicitations for reciprocated grooming. Among siamang, grooming exchanges tend to be more reciprocal, but where an asymmetry exists, it is, again, the male that contributes more.

The available data, therefore, suggest that the contributions of the sexes to maintaining pair bonds in hylobatids, particularly in white-handed gibbons, are inconsistent with the infanticide protection hypothesis and contrary to patterns exhibited in chacma baboons and mountain gorillas, where male–female association implicates infanticide defense. Further tests require data from a larger number of hylobatid pair bonds, and should also consider whether defense-inspired male–female bonds develop differently in socially monogamous versus polygynous settings.

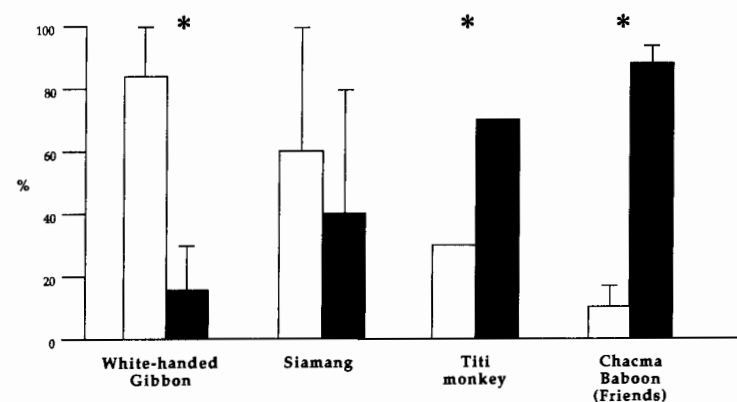


Figure 11.2. Sex differences in grooming investments of bonded adult males and females. Shown is mean (with SD where available) percentage of within-pair grooming performed by the male (white) and the female (black) for siamang and white-handed gibbons (Palombit 1996), titi monkeys (Kinzey & Wright 1982) and chacma baboons (Palombit *et al.* 1997). A star indicates a statistically significant difference ($P < 0.05$).

For example, compared with gibbons, female chacma baboons and mountain gorillas may be more vulnerable to coercion from a (much larger) male protector, whom they may attempt to mollify through a more cohesive social bond. Also, females in the two polygynous species may invest more in proximity maintenance because their male companions are frequently pursuing copulations with other females, which may motivate the behavior of male hylobatids less frequently (but see Palombit 1994a,b and Reichard 1995) or because of intense female–female competition (Palombit *et al.* 2000). These possibilities may account for some patterns of female behavior in chacma baboons and mountain gorillas, but they fail to explain why male white-handed gibbons’ investment in pair bonds exceeds rather than equals that of their female mates.

Primate studies suggest that where a female benefits from some meaningful service provided by a male, her investment in their social relationships either exceeds his (e.g., infanticide protection in chacma baboons, extensive carrying of infants in titi monkeys) or equals his (limited carrying of infants in siamang) (Figure 11.2) (see also Hamilton 1984). It may be significant that in white-handed gibbons, pair bonds offer no conspicuous benefit to females, and are maintained predominantly by males. This gibbon may be an example of the “useless male” (Hrdy 1981), “unavoidable partner” (Mock & Fujioka 1990) or “pair bondage” phenomenon

(Gowaty 1996a,b): 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. Komers & Brotherton (1997) suggested that mammalian social monogamy generally derives from male ability to successfully monopolize a solitary female, with any accompanying advantages to females constituting evolutionary "side-effects".

The possibly negligible benefits of pair bonds to female white-handed gibbons implicate alternative selective forces operating in hylobatids. One scenario identifies mate guarding as the primary selective force behind the origin and maintenance of pair bonds in hylobatids (Palombit 1999). Where males then additionally allocate direct care to infants, as in siamang, females increase their investment in the those bonds. Ecological differences relaxing intragroup feeding competition in siamang may have facilitated the subsequent evolution of paternal care in this species but not in white-handed gibbons (Palombit 1996). A number of findings support the paternity guard hypothesis: the greater role of males in maintaining proximity to females, observations of extra-pair copulations (Palombit 1994b; Reichard 1995), frequent turnover in gibbon pair bonds (Palombit 1994a), and recent research suggesting that mate guarding may not function simply to forestall extra-pair fertilizations, but may persist *beyond* the period of female fertility to prevent loss of mate and pair-bonded status (Wagner 1991; Slagsvold & Lifjeld 1997). This argument is consistent with the view that mammalian monogamy is generally a "risk aversion" strategy of males, whereby staying with one female minimizes variance in mating success (Komers & Brotherton 1997). Thus, even if a male mammal is capable of maintaining a home range encompassing those of, say, two females, restriction of ranging to one female may still be selected for, *if* mate guarding effectively prevents loss of mate or pair-bonded status as well as extra-pair fertilizations.

In summary, four patterns taken together challenge the hypothesis that male infanticide is the selective force maintaining hylobatid pair bonds: (1) the rarity of males most likely to commit infanticide, i.e., physically as well as sexually mature unmated individuals; (2) the extremely low incidence of actual or attempted takeover infanticidal attacks under conditions apparently favoring it; (3) low infant mortality; and (4) the convergence of chacma baboons and mountain gorillas toward male-female bonds that apparently function to protect infants from infanticide, but that differ significantly from those of hylobatids.

Lemurs

A final group of primates, the gregarious lemurs, provides useful subjects for analyzing the infanticide protection hypothesis. Infant mortality is generally high, infanticide occurs (Pereira & Weiss 1991; Hood 1994; Wright 1995; Andrews 1998; Erhart & Overdorff 1998) and heterosexual pair bonds are the core of social systems in many diurnal species (Kappeler, 1993; Jolly, 1998). Preliminary support for the hypothesis derives from the correlation between permanent male-female associations and infant carrying (versus caching) in prosimians, which van Schaik & Kappeler (1997) interpreted as evidence that heterosexual bonds evolved because males protect infants transported continuously by their mothers.

The few field tests of the infanticide protection hypothesis have, however, yielded equivocal results. Contrary to a central prediction of the hypothesis, the resident male in a group of Milne-Edwards sifaka (*Propithecus diadema edwardsi*) failed to protect infants in two observed infanticidal episodes, in spite of the apparent opportunity to do so (Wright 1995). In a study of rufous lemurs (*Eulemur fulvus rufus*), Overdorff (1998) rejected the infanticide protection hypothesis because male-female bonds did not intensify during the birth season when infants were vulnerable to infanticide, females failed to limit copulation to potential male protectors, and heterosexual relations were insufficiently cohesive to constitute "pair bonds".

Additional studies should evaluate other possible causes for the co-occurrence of infant-carrying and male-female association. For example, predator avoidance through crypsis may select for both female caching and avoidance of conspicuous social relationships with males; females that rely on predator detection may carry offspring and be able associate with male protectors. Given that females in most of the species with male-female association are relatively large, diurnal, and/or intra-sexually gregarious, this anti-predation possibility merits further scrutiny.

Discussion: future directions

The female perspective

Most of the supportive evidence for the infanticide protection hypothesis addresses benefits to females of postcopulatory bonds with males. The female harassment, male coercion, and predator protection hypotheses

are particularly relevant alternatives because aspects of protection may be organized in broadly similar ways to counter different threats. Discriminating among these contingencies is often difficult. For example, observational data may be insufficient to demonstrate unambiguously that "sentinel" males keep watch for infanticidal males instead of copulatory rivals, potential mates, female competitors of their companions, or predators. Experimentation is crucial, but a single manipulation may prove insufficient. For example, field observations and a male removal experiment initially suggested that male presence in the orange-tufted sunbird (*Nectarinia osea*) functions to reduce infanticide by floater males (Goldstein *et al.* 1986; Table 11.3). Building upon this work, Markman *et al.* (1996) conducted a more systematic series of male removal experiments, but with an intriguing methodological twist: they removed intruding floater males as they arrived on the widowed females' territories with the explicit intent of *preventing* infanticide. The result was that the offspring of experimental females still suffered higher mortality than controls, not because of infanticide, but because of predation from jays (*Garrulus glandarius*). This finding not only suggests that male sunbirds confer multiple benefits to their mates, but raises the possibility that infanticide defense might maintain pair bonds that originated as an anti-predation strategy. In any event, the study underscores the challenges of testing functional hypotheses (Hinde 1975).

There is a critical need for mutually exclusive predictions about benefits to females under specific conditions. For example, risk of sexually selected infanticide and the need for male defense should both decline as offspring mature and approach weaning or fledging, but anti-predator protection may either increase (Andersson *et al.* 1980) or decrease (Tolonen & Korpimäki 1995) with offspring age, depending upon circumstances. Future research must also test directly the assumptions of the infanticide protection model. For example, van Schaik & Kappeler (1997) assumed that continuous proximity to the female (and her infant) is necessary for male infanticide protection in primates, but they relaxed that assumption in arguing that solitary male orang-utans (*Pongo pygmaeus*) may defend widely dispersed females from infanticide. Studies of jacanas (*Jacana* spp.) suggest that small home ranges relative to individual mobility allow infanticidal defense without requiring continuous proximity to beneficiaries (Stephens 1982; Emlen *et al.* 1989).

The male perspective

The least studied and understood aspect of the infanticide protection hypothesis concerns benefits to males. Researchers generally assume that male infanticidal defense reflects parental effort, but direct, genetic data are generally lacking (an exception is the burying beetle; for data on paternity of resident males in species with infanticide, see also Gilbert *et al.* 1991; Borries *et al.* 1999b). Copulatory patterns more often suggest the potential importance of paternity in cases of infanticide defense. In chacma baboons, for example, at least 68% of friendships established by lactating females were with males they had copulated with during consecutive cycles (Palombit *et al.* 1997).

An important goal of future research is to clarify how infanticide defense varies with probability of paternity. A suggestive preliminary result emerges again from experimental studies of chacma baboons. A male's response to playback of his female friend's scream was unassociated with his or her dominance rank at the time of the friendship (and playback), or with the strength of their social relationship, but it was positively correlated with male rank at the time his female friend conceived her infant many months earlier (Palombit *et al.* 2000). That is to say, the higher a male's rank at the time his future friend conceived her infant, the stronger was his response to playback of her distress call over 6 months later. Given the association between rank and copulatory success in male chacma baboons (Bulger 1993), this result implicates paternity as a potentially important determinant of aiding of females.

There is currently no clear evidence that males derive mating benefits by providing infanticide defense, though investigation of the mating effort function of male care has only recently begun. Smuts (1985) originally suggested that future mating preference by the female partner was an important benefit of friendships to male olive baboons, but comparable behavioral evidence was absent among chacma baboons. For example, male responses to playback experiments and male contributions to maintaining friendships fail to support the prediction of the mating effort hypothesis that males should direct greater attention to the infants of more attractive females (e.g., high-ranking females). Indeed, we might expect that male intervention in attacks on female friends would increase immediately after infants died and resumption of cycling was imminent, but males were significantly *less* responsive to their female friend's screams at this time. Nevertheless, at least one case, the Arctic ground squirrel, suggests an unspecified role of mating effort; in these

Table 11.5. *Some potential costs of bonds between females and male defenders against infanticide*

Female	Male
Ecological	
1. Feeding competition with male	1. Feeding competition with female
2. Reduced foraging efficiency	2. Reduced foraging efficiency
3. Increased predation risk	3. Increased predation risk
Social	
4. Time and energy to maintain social relationship with male protector	4. Defense of females/infants from infanticide:
5. Reduced social interaction with kin	(a) aggressive deterrence
6. Restriction of mating opportunities and mate choice:	(b) territoriality
(a) "Voluntary" by female	(c) vigilance
(b) Coerced by male partner	5. Increased social interaction with higher-ranking (infanticidal) male
7. Female-female competition for male protectors	6. Restriction of mating opportunities
8. Social exploitation:	(a) "Voluntary" by male
(a) Victim of redirected aggression	(b) Female-female competition
(b) Use of infants in triadic interactions	(c) Coerced by female partner

rodents males defend from infanticide young they are "unlikely to have sired" (McLean 1983).

The importance of studying costs

I have not considered costs in any detail in this chapter, but these will ultimately prove critical for understanding the evolution of male-female associations. The adaptive value of male infanticide defense will depend upon the costs as well as benefits to females of associating with him relative to the economics of alternative anti-infanticide strategies available to these females. Table 11.5 provides a preliminary outline of some potential costs.

Rodents may exemplify the importance of evaluating costs. Although infanticide is widespread in this order, the limited field data suggest that female bonds with male protectors are relatively less common than in mammals such as primates. If this is confirmed by future research, I suggest that the infrequency of this counterstrategy among rodents may be due to greater female reliance on maternal aggression to deter infanticide (Maestriperieri 1992). The overall deterrent value of maternal aggression is controversial (Ebensperger 1998a), but it clearly succeeds in

forestalling male infanticide in some cases (e.g., Wolff 1985; Maestriperieri & Alleva 1991; vom Saal *et al.* 1995). In contrast, female primates are strikingly ineffective in defense against male infanticide, even in coalitions (Hrdy 1979; Maestriperieri 1992; Palombit 1999; see also Yamamura *et al.* 1990). Thus a capacity to defend her own young may select for avoiding the potentially high costs of associating with male defenders in favor of maternal aggression. It is important to note that this hypothesis does *not* predict that maternal aggression is more effective or even equally as effective in deterring infanticide as is male defense: all that is necessary is that the benefit-cost ratio for maternal defense exceeds that for male defense. Costs of associating with males are thus crucial. Consistent with this view, the currently most likely case of male-female association functioning as an anti-infanticide strategy in rodents occurs in a species in which "females could not prevent incoming males from killing" pups (McLean 1983, p. 42).

Costs to males, particularly limitations in breeding, are equally relevant. In primates, several patterns suggest that infanticide defense has evolved in systems where costs to males are relatively low (e.g., mountain gorillas, chacma baboons). First, because males in these species live in multifemale groups, restriction of breeding opportunities is less severe than it would be if infanticide protection required monogamy. Second, females appear to incur more of the time, energy and social costs of maintaining the heterosexual relationship. Third, sexual dimorphism and male social dominance over females assure priority of access to food resources for which they compete more intensively because of their association.

Infanticide defense based on social monogamy may rarely evolve precisely because of the serious breeding costs to males (even when they have paternity certainty of the protected young; Hawkes *et al.* 1995), and the ecological costs associated with co-dominance (or dominance) of females resulting from sexual monomorphism. Comparative data suggest that infanticide defense selects for social monogamy primarily when infanticidal pressure is extremely high, e.g., when relatively abundant floaters of *both* sexes pursue takeover strategies, as in house wrens and burying beetles. As with other forms of paternal care (Dunbar 1995), infanticide protection by monogamous males may be more likely to evolve *after* monogamy, rather than select for it.

Conclusion

In the near-absence of direct tests of the infanticide protection hypothesis, pertinent evidence may concern three distinct issues: (1) the effect of male presence on the risk of infanticide relative to the costs to females of bonding with males; (2) the benefits to males from providing infanticide protection relative to the costs (especially in mating); and (3) the ability to reject alternative functional hypotheses for male–female relationships.

Most studies so far have focused on only one of these questions. Current data generally oppose the hypothesis in hylobatids and are equivocal in lemurs, but support it in burying beetles, barn swallows, house wrens, Arctic squirrels, mountain gorillas, and chacma baboons. The phylogenetic diversity represented by these taxa suggests that heterosexual bonds have evolved as an anti-infanticide strategy numerous times in both polygynous and socially monogamous systems. Existing studies also focused on fitness benefits for females rather than for males.

There are clearly multiple evolutionary pathways to strong postcopulatory bonds between the sexes. Much more work is needed, including quantification of costs and variation in male–female bonds, experimental techniques such as playbacks and male removals, and explicit tests of functional possibilities against one another.

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