Infanticide as Sexual Conflict: Coevolution of Male Strategies and Female Counterstrategies

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One of the earliest recognized forms of sexual conflict was infanticide by males, which imposes serious costs on female reproductive success. Here I review two bodies of evidence addressing coevolved strategies of males and females. The original sexual selection hypothesis arguing that infanticide improves male mating success by accelerating the return of females to fertilizable condition has been generally supported in some taxa—notably, some primates, carnivores, rodents, and cetaceans—but not in other taxa. One result of recent research has been to implicate other selective benefits of infanticide by males in various taxa from insects to birds to mammals, such as acquisition of breeding status or improvement of the female breeding condition. In some cases, however, the adaptive significance of male infanticide remains obscure. The second body of data I review is arguably the most important result of recent research: clarifying the possible female counterstrategies to infanticide. These potential counterstrategies span diverse biological systems, ranging from sexual behavior (e.g., polyandrous mating), to physiology (e.g., the Bruce effect), to individual behavior (e.g., maternal aggression), to social strategies (e.g., association with coalitionary defenders of either sex). Although much remains to be studied, these current data provide compelling evidence of sexually antagonistic coevolution surrounding the phenomenon of infanticide.

At its most elemental level, infanticide is the killing of a newborn individual by a conspecific. With the growing appreciation of its biological significance, however, infanticide came to be defined more broadly as any "behavior that makes a direct and significant contribution to the immediate death of an embryo or newly hatched or born member of the performer's own species" (Mock 1984, p. 4) or "any form of lethal curtailment of parental investment in offspring brought about by conspecifics" (Hrdy and Hausfater 1984, p. xv). These definitions highlight the heterogeneous and variable nature of the phenomenon, which can be perpetrated by either sex, by parents or other kin, by individuals unrelated to the victim, in a wide variety of social and mating systems, under a range of seasonal or aseasonal breeding regimes, and across diverse taxa straddling vertebrates and invertebrates.

One adaptive form of infanticide—the killing of infants by unrelated males—is arguably

the archetype of sexual conflict. In 450 BCE, Herodotus not only documented the behavior among Egyptian cats, but explained it as a male "trick" to obtain sexual access to females otherwise preoccupied with maternal duties (Delibes et al. 2012). Among the myriad ideas inaugurating sociobiology in the 1970s, the hypothesis that infanticide is a male strategy that improves reproductive success at the expense of female fitness (Hrdy 1974) constituted one of the first demonstrations of the "battle of the sexes" theory developed by Williams (1966) and Trivers (1972). Partly because of the controversy surrounding the appearance of this hypothesis (Rees 2009), however, subsequent research focused more on male strategy than on the other party in this sexual dialectic, the female. Thus, field and laboratory research has helped to establish its many forms and conditional occurrence, describe its distribution across taxa, and clarify its adaptive significance, but it is only relatively recently that female counterstrategies have become the subjects of rigorous study, even though their potential importance was grasped early on (Hrdy 1979).

In this article, I review selected aspects of this body of data and analysis. My focus is on nonparental male infanticide targeting dependent young—in mammals, nursing individuals—as opposed to older, weaned offspring, the killing of which is variably rendered "juvenilicide," "pedicide," or "filicide" (e.g., Agoramoorthy and Mohnot 1988; Palombit 2014, in press).

amenorrhea: adet görmeme

THE SEXUAL CONFLICT OF INFANTICIDE: MALE STRATEGIES

Several functional hypotheses have been proposed to explain male infanticide. Foremost among them historically is the sexual selection hypothesis. I consider this hypothesis first, with special, although not exclusive, taxonomic focus on the group of animals that originally generated the hypothesis—the primates. I then move on to several alternative hypotheses for male infanticide, the discussion of which will incorporate consideration of data from other animals as well as additional data from primates.

Sexual Selection Hypothesis

Although male infanticide clearly has no unitary explanation, the biological relevance of intrasexual selection in males makes the sexual selection hypothesis a good starting point for discussion. As originally formulated for langurs (*Semnopithecus entellus*), Hrdy's (1974, 1977) argument is that the killing of an infant prematurely ends lactational amenorrhea (the cessation of ovulatory cycles during nursing) in its mother, thereby significantly advancing the time when she is available for subsequent fertilization by the perpetrator. The potential benefit of this strategy to male fitness will depend on many variables, but salient among them is the degree to which sexual access to fecund females is limited by two factors: male–male competition and the reproductive life history of females.

The latter of these factors provides a useful context for analyzing the problem of male infanticide. The L/G ratio, which compares the durations of lactation and gestation, summarizes the potential value (to males) and vulnerability (to females) of infanticide in mammals. When lactation greatly exceeds gestation, postpartum mating and early pregnancy impose potentially prohibitive costs on females in the form of simultaneous support of two sets of offspring differing in ages, requirements, and competitive capacities (van Schaik 2000b). The adaptive solution to this female problem is lactational amenorrhea, which, however, generates the reproductive problem for males that infanticide can solve. Plainly expressed: An infant is a "perfect contraceptive," and infanticide simply serves to remove this effect (Altmann et al. 1978, p. 1029).

The taxonomic distribution of sexually selected infanticide across mammals is not fully resolved, but current reports of infanticide whose patterning is consistent with this hypothesis are predictably concentrated among taxa with relatively long L/G ratios— namely, primates, fissiped carnivores, and odontocete

Two factors limit the sexual access to fecund (dogurgan) females : male-male competition and rep. life history of females.

**L: emzirme
G: gebelik**

whales (Fig. 1) (van Schaik 2000b). Several caveats warrant mention. First, this result does not mean that male infanticide is uniformly expressed within these taxa; on the contrary, there is often considerable variation over time and across populations (see below). Second, it is also not the case that male infanticide is unreported in other taxa with lower L/G ratios, but in those cases the sexually selected mechanism has been less implicated than alternative hypotheses (see below). Finally, L/G ratios are important, but other factors may explain the rarity of infanticide in some mammals, for example, ecologically determined sexual segregation, (Kunz and Ebensperger 1999), caching of infants as an antipredator strategy (Schülke 2005), need for hibernation (Thalmann 2001), or even phylogenetic inertia (Ebensperger 2001).

It is not possible here to review comprehensively the empirical tests of the sexual selection hypothesis (see Hausfater and Hrdy 1984; Parmigiani et al. 1994; Connor et al. 2000; van Schaik and Janson 2000; Ebensperger and Blumstein 2007; Palombit 2012), but some general patterns can be highlighted. The largest body of data supporting this hypothesis has come from study of the nonhuman primates. In the last 25 years, the number of species in which infanticide had been observed directly or inferred from substantive indirect evidence in the wild has risen from a dozen (Hiraiwa-Hasegawa 1988) to 54, including 84 distinct populations distributed across nine of the 14 families of strepsirrhines, monkeys, and apes (updated from Palombit 2012).

The circumstances surrounding infanticide in primates are typically (although not invariably) consistent with the sexual selection hypothesis: (1) replacement of a male occupying the position of sole or dominant breeder in the group by a male who is unlikely to have sired the infants he subsequently attacks; (2) resumption of ovulatory cycling by the mother; and (3) copulation between the mother and perpetra-
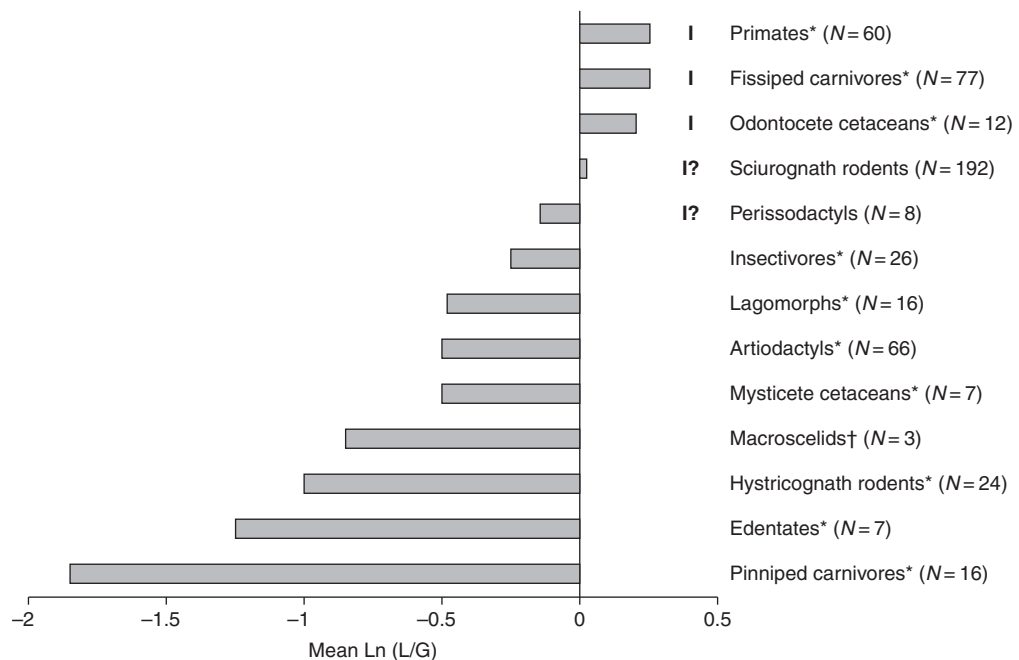
Figure 1. Mean lactation/gestation (L/G) ratios for selected mammalian groups. Log-transformed L/G ratios significantly different from 1 are indicted by *($p < 0.05$) or †($p < 0.01$). The letter "I" denotes taxa in which deliberate sexually selected infanticide by males has been recorded. Sample sizes (number of species) are indicated in parentheses. (Modified from data in van Schaik 2000b.)

tor, and thus shortening of the interbirth interval. Most but not all reports provide supportive data for all three predictions, but cases in which behavioral data are unavailable or contradictory more often concern the third prediction. Advances in field methodology have permitted collection of ancillary (nonbehavioral) data to further test the hypothesis. For example, DNA data establish that males are unrelated to the infants they attack (Pereira and Weiss 1991; Borries et al. 1999a; Soltis et al. 2000) or are fathers of the female's next infant (Morelli et al. 2009), whereas hormonal data provide direct evidence of maternal resumption of ovulatory cycling following infanticide (Harris and Monfort 2003) as well as elevated stress response in mothers following heightened infanticide risk or actual attacks (Beehner et al. 2005; see also Brockman et al. 2009). Thus, as a general explanation of infanticide, the sexual selection hypotheses has received more support than alternative hypotheses (see below) (van Schaik 2000a; Palombit 2012).

Although originally observed for primates living in unimale, polygynous groups, male infanticide has been observed in almost all of the other social systems found in this order, from dispersed societies, to multimale groups, to fission–fusion communities, and perhaps even socially monogamous pairs. Its occurrence in some multimale societies is noteworthy. The permanent presence of multiple males was expected to hinder infanticide by increasing its costs (through male defense of infants) or decreasing its potential benefits (through reduced ability to monopolize matings). Thus, across gregarious primates, infanticide rate is negatively correlated with the number of males in groups (Janson and van Schaik 2000). Nevertheless, significant male infanticide has been documented in a number of multimale societies in two general contexts: (1) by new immigrants (or, somewhat less commonly, by long-term residents) that rise to the alpha position in the male dominance hierarchy (e.g., Palombit et al. 2000; Soltis et al. 2000; Teichroeb and Sicotte 2008); or (2) by coalitionary cohorts of alien males that collectively replace the entire male membership of a group (Fedigan et al. 2008)

in a manner reminiscent of lions (Pusey and Packer 1994b). One factor apparently promoting infanticide in this social context is pronounced mating skew toward dominant males (sensu Broom et al. 2004).

Compelling evidence for sexually selected infanticide in the nonprimate mammals has come from field studies of fissiped carnivores (particularly bears and well-studied lions); there are also some suggestive recent data for toothed whales (particularly dolphins) (Table 1). Among rodents, the altriciality of young and lengthy periods of female investment make sexually selected infanticide likely in many species, particularly in the murids (Wolff and MacDonald 2004). Male infanticide is known in 14–17 species of Muridae (Ebensperger and Blumstein 2007). The Norway rat (*Rattus norvegicus*), house mouse (*Mus musculus/domesticus*), and Mongolian gerbil (*Meriones unguiculatus)* have been the subjects of extensive and well-controlled laboratory research (see references in Table 1), which has shed important light on the proximate mechanisms underlying infanticide and on female counterstrategies. These data for murids are largely consistent with the sexual selection hypothesis, but almost all of them come from the laboratory; only four murid species have provided limited data on male infanticide in the wild (see Caley and Boutin 1985; Wolff and Cicirello 1991; Ylönen et al. 1997). It is partly because "virtually nothing is known" about infanticide in natural populations of murids (Berdoy and Drickamer 2007, p. 389) that the broader implications of the laboratory results are debated, particularly vis-à-vis the predicted postinfanticide reproductive benefits. Thus, Ebensperger and Blumstein (2007, p. 178) conclude that although current data reject nonadaptive explanations, the sexual selection hypothesis "remains unproven in rodents" (see also below for sciurid rodents).

Alternative Explanations for Male Infanticide

Besides the sexual selection hypothesis, there is a large number of alternative adaptive explanations for male infanticide (Table 1). Only a few of these can be addressed here. It is perhaps

Table 1. Adaptive and nonadaptive hypotheses for nonparental infanticide by males

Hypothesis	Theoretical rationale	Proposed example taxa	References
Benefits related to mating			
Sexual selection I. Accelerate female return to breeding condition	When sexual access to fecund females is limited by intrasexual competition, killing eggs or infants accelerates female return to fertilizable condition (mammals: shortens lactational amenorrhea) for subsequent insemination	Arachnids; birds (*Hirundo rustica*, *Passer domesticus*); hippos (*Hippopotamus amphibius*); horses (*Equus caballus*); dolphins (*Tursiops* spp.); lions (*Panthera leo*); bears (*Ursus arctos*); murid rodents (*M. musculus*, *R. norvegicus*, *Peromyscus* spp., *M. unguiculatus*, *Myodes glareolus*); tree squirrels (*Paraxerus cepapi*); relatively many primate species	Crook and Shields 1985; Veiga 1993; Pusey and Packer 1994b; Schneider and Lubin 1997; Lewinson 1998; Patterson et al. 1998; Swenson et al. 2001; Dunn et al. 2002; Erez et al. 2005; McLellan 2005; Bellemain et al. 2006a; Solomon and Keane 2007; Dudzinski et al. 2009; Gray 2009; Zedrosser et al. 2009; see references in Ebensperger and Blumstein 2007 and Palombit 2012
II. Improved female condition and future fertility	Premature termination of lactational amenorrhea improves female condition and thereby enhances future reproductive success following insemination by infanticidal male	Arctic ground squirrels (*Spermophilus parryii*); red deer (*Cervus elaphus*); horses (*E. caballus*, *E. ferus przewalskii*); ring-tailed lemurs (*Lemur catta*); sifakas (*Propithecus edwardsi*)	McLean 1983; Bartoš and Madlafousek 1994; Wright 1995; Jolly et al. 2000; Cameron et al. 2003; Hoesli et al. 2009; Morelli et al. 2009
Breeding social status acquisition	Infanticide facilitates acquisition of high rank or breeding status in multimale groups for resident males or new immigrants	Howler monkeys (*Alouatta arctoides*); baboons (*Papio hamadryas hamadryas*); Hanuman langurs (*S. entellus*)	Angst and Thommen 1977; Crockett 2003; Rajpurohit et al. 2008
Breeding site acquisition	Infanticide is part of a strategy to take over a breeding site by destroying existing offspring, and then mating with the resident female(s) or new immigrant female(s)	Burying beetles (*Nicrophorus* spp.); fish (*Lamprologus callipterus*); birds (*Tachycineta bicolor*, *Troglodytes aedon*)	Freed 1986, 1987; Robertson and Stutchbury 1988; Trumbo 1990a; Trumbo and Valletta 2007; Maan and Taborsky 2008
Mate acquisition Direct	Infanticide by an extragroup male promotes female transfer to the killer partly by advertising his superior ability to protect against infanticide	Birds (*H. rustica*); colobine monkeys (*Presbytis thomasi*, *Colobus polykomos*); mountain gorillas (*Gorilla gorilla*)	Crook and Shields 1985; Watts 1989; Steenbeek 2000; Møller 2004; Korstjens et al. 2005

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R.A. Palombit

Table 1. *Continued*

Hypothesis	Theoretical rationale	Proposed example taxa	References
Indirect	In species with female dispersal, infanticide by an extragroup male disrupts the mother–subadult daughter bond, facilitating the dispersal of latter to infanticidal male	Chimpanzees (*Pan troglodytes*)	Goodall 1986
Sexual monopolization of female	Infanticide induces female to restrict future copulations to infanticidal males(s) than to other male(s)	Chimpanzees (*P. troglodytes*)	Hamai et al. 1992
Removal of mating competitors	Selective killing of male infants: (a) eliminates possible future sexual competitors of infanticidal males or their sons; (b) undermines coalitionary power of rival males?	Arctic ground squirrels (*S. parryii*); Hanuman langurs (*S. entellus*); white-thighed colobus monkeys (*Colobus vellerosus*)	McLean 1983; Sommer 1994; Teichroeb and Sicotte 2008
Decrease reproductive success of rivals	Infanticide removes genes of rival male(s)	Tree squirrel (*P. cepapi*); fur seals (*Callorhinus ursinus*); patas monkey (*Erythrocebus patas*)	de Villiers 1986; Enstam et al. 2002; Kiyota and Okamura 2005
Benefits related to resources			
Removal of competitors for limiting resources	Infanticide improves access to limiting food resources to infanticidal male and/or his offspring	Gerbils (*M. unguiculatus*); purple-faced langurs (*Semnopithecus vetulus*); howler monkeys (*Alouatta arctoides, A. palliata*)	Rudran 1973b; Clarke 1983; Elwood and Ostermeyer 1984b; Agoramoorthy and Rudran 1995
Improved intergroup competition for limited resources	Killing of infants in neighboring groups enhances access to resources by: (a) causing their mothers to withdraw permanently from borders areas, thereby facilitating killers' home range to expand; (b) facilitating intergroup dominance and thereby priority of access of resources in border areas	(a) Chimpanzees (*P. troglodytes*); (b) guereza (*Colobus guereza*)	(a) Watts et al. 2002; Williams et al. 2002, 2004; Mitani et al. 2010; (b) Harris and Monfort 2003
Nutritional exploitation	Infants are cannibalized to obtain direct nutritional benefits	Fish (*Telmatherina sarasinorum*); yellow sciurid rodents (*Spermophilus beldingi*,	Paul and Kupferschmidt 1975; Svare and Bartke 1978; Sherman 1981; Elwood and

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Table 1. *Continued*

Hypothesis	Theoretical rationale	Proposed example taxa	References
		S. tridecemlineatus, Cynomys parvidens); murid rodents (*R. norvegicus, M. musculus, M. unguiculatus, Microtus pennsylvanicus*); baboons (*Papio cynocephalus*)	Ostermeyer 1984a; Vestal 1991; Ebensperger et al. 2000; Hoogland 2001; Altmann et al. 2006; Gray et al. 2007
Benefits related to paternal investment			
Avoidance of misdirected paternal investment	Infanticide prevents male parental investment in offspring sired by another male	Birds (*T. aedon*, *P. domesticus*); humans (*Homo sapiens*)	Daly and Wilson 1984, 1994; Rohwer 1986; Freed 1987; Pierotti 1991; Veiga 1993
Benefits related to learning			
Acquisition of mating tactics and skills	Inexperienced subadult males lethally use pups as proxies for adult females to acquire skill in mating tactics (e.g., female stealing and herding, territory maintenance)	Otariid seals (*Mirounga* spp., *Callorhinus ursinus*)	Le Boeuf and Campagna 1994; Kiyota and Okamura 2005
Nonadaptive hypotheses			
Social pathology	Lethal attacks on infants are: (a) abnormal behavior resulting from human-induced disturbance (e.g., overcrowding) or selection; (b) results of changes in nature/rate of aggression (e.g., takeover, intergroup hostility) caused by anthropogenic disturbance and habitat degradation	Horses (*E. ferus przewalskii*); episodic in others (e.g., Hanuman langurs) (*S. entellus*); Tibetan macaques (*Macaca thibetana*); chimpanzees (*P. troglodytes*)	Jansen et al. 2002; (a) Dolhinow 1977; Curtin and Dolhinow 1978; Feh and Munkhtuya 2008; (b) Boggess 1984; Berman et al. 2007; Williams et al. 2008
Generalized aggression	Infant killing is an incidental byproduct of selection for overall intra- or intersexual aggressiveness in males or (for intergroup infanticide) of general male xenophobic territoriality	Otariid seals (*Mirounga* spp., *Otaria byronia*); horses (*E. ferus przewalskii*); episodic in others (e.g., baboons) (*Papio h. hamadryas*); macaques (*Macaca radiata*); mona monkey (*Cercopithecus campbellii*); chimpanzees (*P. troglodytes*)	Galat-Luong and Galat 1979; Rijksen 1981; Goodall 1990; Bartlett et al. 1993; Le Boeuf and Campagna 1994; Singh et al. 2006; Hoesli et al. 2009

unsurprising that the two taxa in Figure 1 that ostensibly straddle the "high L/G" and "low L/G" groupings have generated conflicting results and debate about sexually selected infanticide. These are the sciurid rodents and the perissodactyls.

Among ungulates, the perissodactyls—particularly equids—show the highest incidence of male infanticide (Pluháček and Bartoš 2005). The majority of reports have come from captivity, however, which has lead to suggestions that the behavior is an artifact of captivity or domestication (Table 1). Moreover, there is little unambiguous evidence from either the captive or few wild studies that infanticide shortens interbirth intervals in females, as predicted by the sexual selection hypothesis (e.g., Feh and Munkhtuya 2008). If there is an adaptive basis to the behavior, a variant of this hypothesis may be more relevant. This alternative hypothesis arose originally from an appreciation that the sexually selected mechanism is unlikely to operate in seasonal breeders, because infanticide cannot easily accelerate female return to fertilizable condition when mating is determined primarily by photoperiodicity or other cyclical cues. However, premature termination of lactation can potentially benefit males in seasonal breeders if it improves the female condition and thus her *future* reproductive success (Hrdy and Hausfater 1984; Hoogland 1985). Bartoš and Madlafousek's (1994) experimental study of red deer (*Cervus elaphus*) was the first to provide some empirical support for this hypothesis, which has been invoked for other mammals, including some primates, rodents, and equids (see Sexual selection II in Table 1). Another context in which sexually selected infanticide may operate among seasonal breeders is, of course, when interbirth intervals exceed 1 yr, as in langurs living at high elevations (Borries 1997). Under this scenario, infanticide can accelerate the return of females to fertilizable condition, and thereby enhance the reproductive success of a male (assuming he retains breeding status in the subsequent reproductive season).

Among the Sciuridae, male infanticide is known to occur in 11–14 species (Ebensperger and Blumstein 2007). In stark contrast to the mostly laboratory-based research on murids,

almost all of the sciurid data are from the wild, particularly from studies of prairie dogs (*Cynomys* spp.), ground squirrels (*Spermophilus* spp.), and marmots (*Marmota* spp.). With few exceptions (e.g., nonseasonally breeding tree squirrels) (Solomon and Keane 2007), these naturalistic data are generally less consistent with the sexual selection hypothesis than with alternative explanations (e.g., nutritional exploitation) (see Table 1). Indeed, Hoogland (2007) has argued that his large data set on wild black-tailed prairie dogs (*Cynomys ludovicianus*) and Utah prairie dogs (*C. parvidens*) does not clearly support *any* of the existing hypotheses for male infanticide. Perhaps Blumstein's (2000, p. 195) appeal of more than a decade ago—"we simply need better data"—remains the most compelling conclusion.

Another functional hypothesis for male infanticide has arisen from avian research. Sexually selected infanticide has been suggested for at least 13 species of birds (Veiga 2000). It has been reported in polygynous species (as expected theoretically), but notably also in socially monogamous breeders as well, where more often than advancing the female's next fecund period, infanticide functions as part of a takeover strategy for achieving breeding space and/or acquiring a mate in the first place. This role of infanticide has also been suggested for several species of mammals (see Table 1).

Perhaps no single species has yielded more proposed explanations for male infanticide than the chimpanzee (*P. troglodytes*) (Table 1). Much about infanticide in this ape has long been puzzling (Arcadi and Wrangham 1999). This is particularly true of the violent attacks on the infants of *neighboring* groups, which have seemed to produce no obvious mating- or resource-related benefits for the male perpetrators. Intriguing new data, however, suggest a "range expansion" function, whereby infanticide induces victimized mothers to abandon their home ranges to the killers, which in one Ugandan community facilitated a 22% increase in their territory size (Mitani et al. 2010).

Finally, two hypotheses explain infanticide as maladaptive behavior or accidental by-product (Table 1). Inspired partly by laboratory demonstrations of infanticide arising from

debilitating overcrowding (e.g., Myers and Poole 1961; Calhoun 1962), the social pathology hypothesis links the behavior in the wild to anthropogenic disturbance of either a direct (e.g., provisioning) or indirect (e.g., habitat degradation) nature. Although this explanation may apply to some individual cases (especially in captivity), it has largely failed as a general explanation, partly because the prediction that "the infanticidal individual is behaving in a manner that indicates malfunction" (Pierotti 1991, p. 1141) has not been consistently supported. Sterck (1998) argues that rather than produce infanticide by disrupting "normal" regulatory pathways of behavior, local human disturbance often alters rates of infanticide through its effects on important causal variables and conditions, such as the occurrence of male takeovers. Some anthropogenic intervention has also provided difficult-to-obtain "experimental" support of the sexual selection hypothesis (e.g., the selective removal of males through trophy hunting in fissiped carnivores) (e.g., Wielgus and Bunnell 2000; Loveridge et al. 2007; Wielgus et al. 2013; but see Miller et al. 2003).

The second nonadaptive hypothesis, the "generalized aggression" hypothesis, suggests that infanticide arises accidentally as a byproduct of the intra- or intersexual aggression surrounding male mating competition (Bartlett et al. 1993). Again, although some individual episodes are consistent with this model (Table 1), it has not proved an adequate general explanation of larger data sets, which typically establish the highly "directed" nature of infanticidal attacks and their predictable long-term patterning. One notable exception seems to be the well-studied otariid seals, in which evidence suggests that infants (and juveniles) are trampled to death accidentally by huge males (although even in this case, adaptive hypotheses have been proffered but not tested) (see Table 1).

The Occurrence of Male Infanticide as a Potential Selective Agent for Female Counterstrategies

A defining feature of infanticide is its variability, expressed across taxa and over time. Rates of occurrence may vary significantly across populations of the same species. For example, in chacma baboons of southern Africa (*Papio hamadryas ursinus*), male infanticide accounts for an average of 38% of infant mortality, but among east African yellow (*P. h. cynocephalus*) and olive baboons (*P. h. anubis*), it is not only much less demographically significant but less clearly a male reproductive strategy (Palombit 2003; for other examples, see also Butynski 1990; Arcadi and Wrangham 1999). Even in populations with relatively high rates of infanticide, it is not invariably expressed by *all* males experiencing the putative causal conditions. This has led some researchers to propose that infanticide is a facultative strategy (a behavioral polymorphism?) (e.g., McLean 1983; Palombit et al. 2000; Cords and Fuller 2010), as also suggested by theoretical models (e.g., Chapman and Hausfater 1979; Glass et al. 1985; Yamamura et al. 1990; Broom et al. 2004). Consequently, rates of occurrence in an "infanticidal" population may vary considerably over time. For example, although male infanticide accounted for an average of 38% of infant mortality in the previously mentioned chacma baboon population, this figure ranged from nearly 0% to as high as 75% in certain years (Cheney et al. 2004). The reasons for variation in infanticide are not well understood, but one relevant variable for interpopulation differences in primates as well as carnivores is the rate of breeding male turnover (Packer et al. 1988; Sterck 1998; Crockett and Janson 2000).

Long-term studies of populations in which male infanticide occurs have generally suggested it is a major—if not *the* major—source of infant mortality. Among Serengeti lions (*P. leo*), it accounts for 27% of cub mortality overall, but nearly 100% of the mortality of cubs under the age of 9 mo (Pusey and Packer 1994b). In a sample of 29 primate populations in which infanticide is known, 19 had relative rates ≥30% (Palombit 2012). In some of these taxa, male replacement produces a 3-, 11-, or 32-fold increase in infant mortality (Beehner and Bergman 2008; Fedigan et al. 2008; Pavé et al. 2012). In sciurid rodents, male (as well as female) infanticide is a major cause of infant and juvenile mortality (Ebensperger and Blumstein 2007).

In total, the empirical evidence for adaptive strategies of male infanticide provides a compelling rationale for evaluating its possible importance as a selective agent on the evolution of female biology.

THE SEXUAL CONFLICT OF INFANTICIDE: FEMALE COUNTERSTRATEGIES

A very large number of possible female counterstrategies to male infanticide have been proposed and studied to varying degrees. These can be grouped into three broad categories addressing: (1) sexual behavior and reproduction; (2) individual prevention and deterrence; and (3) social counterstrategies. Space limitations preclude discussion of all of these phenomena, and so I focus on some of the major empirically supported patterns.

Sexual and Reproductive Counterstrategies of Females

Among the numerous potential counterstrategies related to sex and reproduction (Table 2), arguably the best known is "confusing paternity" through copulation with males (Hrdy 1979). Direct tests of this hypothesis are limited primarily to laboratory murids (see below), but field data have generally suggested that infanticide is perpetrated by males who have no sexual history with the victimized infants' mothers. In one of the few direct tests in primates, DNA paternity data showed that male attacks on infants were directed at eight times the rate toward unrelated individuals than toward offspring (Soltis et al. 2000).

A logical extension of this hypothesis is that females vulnerable to infanticide will pursue a strategy of "promiscuous" or "multimale" mating, which Hrdy (1979, 1981) invoked to explain the pronounced sexual assertiveness of haplorrhine primates. Broad comparative analyses provide indirect support for this hypothesis. For example, in eutherian mammals, multimale mating is more pronounced in species characterized by male infanticide; among primates alone, 62% of species with female susceptibility to infanticide show promiscuity,

compared to 11% of nonvulnerable species (van Noordwijk and van Schaik 2000). Recent data have even suggested a heretofore unappreciated potential for this benefit to accrue to females living in *unimale* groups, through copulations with extragroup males (Palombit 2012). Similarly, Wolff and MacDonald (2004) argue on the basis of their correlative analysis that multimale mating in rodents is best understood as anti-infanticidal confusion of paternity, but it is important to remember that multimale mating has many other possible functions which are implicated in numerous species (e.g., Bryja et al. 2008; Lane et al. 2008). Notably, Hoogland (2007) rejects this hypothesis for Utah prairie dogs based on observations of males attacking *some* of the pups of females with whom they previously mated. However, students of species in which females produce multiply sired litters have speculated that males may be able to recognize kin phenotypically and then selectively target unrelated infants in a litter (e.g., Vestal 1991; Berdoy and Drickamer 2007). If true, this outcome would imply a possible male counterstrategy to counteract the female anti-infanticide counterstrategy of promiscuity (Table 2).

A large number of laboratory tests of this hypothesis in murid rodents suggest that copulation inhibits subsequent infanticidal behavior of males in at least seven species (reviewed in Ebensperger and Blumstein 2007). These results have not been replicated in several studies, however, which sometimes indicate the importance of not just copulation but a period of postcopulatory cohabitation in facilitating inhibition of infanticidal tendencies (e.g., Elwood and Kennedy 1994).

More intriguingly, a series of experiments on the house mouse suggest that this female counterstrategy of promiscuity may have itself selected for additional male counterstrategies. Copulation is known to inhibit infanticide in males (vom Saal and Howard 1982). That inhibition, however, does not commence until about 12 d after the sexual encounter, and it terminates spontaneously 60 d later, a schedule that corresponds roughly to the periods of gestation and lactation, respectively (vom Saal

Table 2. Sexual and reproductive counterstrategies of females with selected example taxa

Proposed counterstrategy	Theoretical rationale	Proposed example taxa	References
Strategies obscuring paternity among males			
Promiscuity/ multimale mating	Elevated sexual receptivity and proceptivity and/or polyestrous cycling promotes insemination by multiple males, thereby confusing paternity	Birds (*Tachycineta bicolor*); murid rodents (*Mus musculus*); prairie dogs (*Cynomys parvidens*); bears (*Ursus arctos*); lions (*Panthera leo*); badgers (*Meles meles*); dolphins (*Tursiops* spp.); primates	Bertram 1975; Robertson 1990; Connor et al. 1996; 2000; Dahle and Swenson 2003; Ebensperger and Blumstein 2007; Hoogland 2007; Dugdale et al. 2011; see references in Palombit 2012
Multiply sired litters	In polytocous breeders, females achieve fertilizations by multiple males in single litters	Mice (*M. musculus*); voles (*Myodes rufocanus*); bears (*U. arctos*)	Bellemain et al. 2006a; Ishibashi and Saitoh 2008; Thonhauser et al. 2013
Extended estrus period	Lengthened periods of estrus or polyestrous cycling increase opportunities for copulation with multiple males	Dolphins (*Tursiops*); catarrhine primates with sexual swellings, langurs (*S. entellus*)	Connor et al. 1996; van Schaik et al. 2000; Heistermann et al. 2001
Concealed ovulation	Paternity is obscured by absence of reliable signals of ovulation and/or by variability in the timing of ovulation	Hanuman langurs (*S. entellus*); vervet monkeys (*Chlorocebus pygerythrus*); capuchin monkeys (*Cebus capucinus*)	Andelman 1987; Heistermann et al. 2001; Carnegie et al. 2006
Postconception sexual behavior	Anovulatory copulations (and when relevant, signaling of "ovulation") occur regularly in early gestation	Many catarrhine primates, some platyrrhine primates	See references in Palombit 2012
Situation-dependent sexual receptivity ("pseudoestrus")	Exposure to new (or extragroup) males facultatively causes (a) "deceptive" anovulatory sexual behavior in pregnant females; or (b) longer receptive periods among cycling females	(a) Lemurs (*Propithecus verreauxi*); capuchin monkeys (*Cebus apella*); blue monkeys (*Cercopithecus mitis*); baboons (*Papio hamadryas hamadryas*); red colobus (*Procolobus badius*); (b) cercopithecine monkeys (*C. mitis*, *Macaca fuscata*)	(a) Struhsaker and Leland 1985; Fairgrieve 1995; Brockman and Whitten 1996; Zinner and Deschner 2000; Pazol 2003; Ramírez-Llorens et al. 2008; (b) Cords 1984; Takahata et al. 1994; Pazol 2003
Strategies focusing copulations and/or conceptions on particular male(s)			
Female mate choice targeting infanticidal male(s)	Females mate preferentially with males most likely to commit infanticide because of factors such as dominance status or spatial proximity	Murid rodents (*Lemmus, Microtus, Mus, Myodes*); bears (*U. arctos*); capuchin monkeys (*C. nigritus, C. olivaceous*)	O'Brien 1991; Agrell et al. 1998; Bellemain et al. 2006b; Izar et al. 2009

Continued

Table 2. *Continued*

Proposed counterstrategy	Theoretical rationale	Proposed example taxa	References
Female mate choice targeting protector male(s) (direct)	Females limit periovulatory matings to a male likely to be a future protector against infanticide	Hamadryas baboons (*P. h. hamadryas*)	Swedell and Saunders 2006
Female mate choice targeting protector male(s) (indirect)	Females incite male mate guarding by advertising ovulation or copulations (e.g., through sexual swellings, vocalizations), which reduces polyandry at ovulation and thereby concentrates paternity in future, high-quality male defender of infant	Catarrhine primates living in multimale societies	See references in Palombit 2012
Strategies manipulating reproduction			
Pregnancy block and pregnancy termination (Bruce effect)	Direct or indirect exposure to a new replacement male results in failure of implantation or absorption of fetus	Equids (*E. burchelli*, *E. caballus*); baboons (*P. h. hamadryas*, *P. h. cynocephalus*); langurs (*S. entellus*); geladas (*Theropithecus gelada*)	Berger 1983; Pereira 1983; Agoramoorthy et al. 1988; Colmenares and Gomendio 1988; Pluháček and Bartoš 2000; Bartoš et al. 2011; Roberts et al. 2012
Superfetation	Conception occurs during gestation accompanied by fertilized eggs entering embryonic diapause	European badger (*Meles meles*)	Yamaguchi et al. 2006
Abandonment of infant	Mothers abandon a healthy infant or an infant injured in infanticidal attack	Colobine monkeys (*Colobus vellerosus, S. entellus*)	Hrdy 1977; Sicotte et al. 2007
Acceleration of weaning	Following male takeover, mothers wean older infants sooner than usual	Vervet monkeys (*Chlorocebus pygerythrus*); baboons (*P. h. hamadryas*)	Fairbanks and McGuire 1987; Colmenares and Gomendio 1988
Temporarily reduced fecundity	Following male takeover, females temporarily suspend ovulatory cycles until new male(s) are established and unlikely to be replaced again	Lions (*Panther leo*); leaf monkeys (*P. thomasi*)	Pusey and Packer 1994b; Steenbeek 1999b
Breeding synchrony	Among group-living females, greater ovulatory synchronization prevents single males from monopolizing matings, generating multimale groups that are generally less vulnerable to takeover infanticide	Lions (*P. leo*); lemurs (*Eulemur fulvus rufus*); baboons (*Papio* spp.); blue monkeys (*Cercopithecus mitis*)	Bertram 1975; Cords 1986; Altmann 1990; Ostner and Kappeler 2004

1985; Perrigo et al. 1990, 1992). This timing suggests that the female (sexual) counterstrategy has, in turn, selected for counteradaptations in males that "fine-tune" the expression of infanticidal inhibition to periods when pups are most likely to be their genetic offspring, and that thereby avoid the "evolutionary mistake" of failing to attack unrelated pups. A further step in this coevolutionary scenario is suggested by the fact that aggressive mothers protecting their pups attack males who have copulated with them very recently (within the last 24 h) with the same severity they direct toward males who have not copulated with them at all (Parmigiani et al. 1988b). Taken together, these patterns imply the spiraling, antagonistic dynamic characterizing sexual conflict.

Recognition of the potential importance of male protectors in deterring infanticide in some species (see below) has led to modification of this hypothesized counterstrategy of paternity confusion. Under these conditions, females may benefit most from pursuing a dual sexual strategy that concentrates paternity in the best available male defender and also dilutes (confuses) it in other males (e.g., Clarke et al. 2009). Cues of ovulation, such as the sexual swellings characterizing many species of Old World monkeys and apes, may provide a mechanism for achieving what seem at first glance to be incompatible reproductive goals. The "graded signal hypothesis" holds that: (1) the probability of ovulation is highest at the time of maximal tumescence, and thus sexual swellings can promote fertilization by high-quality (protector) males; but (2) the probability of ovulation at other times is inherently *variable* and *nonzero*, and, hence, paternity can be confused among other males (Nunn 1999). Hormonal data from langurs confirmed that the timing of ovulation was sufficiently variable that low-ranking males occasionally achieved fertilizations despite the dominant male's sexual monopolization of females during periods when ovulation was statistically more likely (Heistermann et al. 2001). Further support for this hypothesis is provided by observations that female primates of several species mate selectively at periovulatory periods (coinciding with increased probability of ovu-

lation) and promiscuously at other times in their cycle (when ovulation is less likely to occur) (reviewed Palombit 2012). Moreover, in catarrhine primates exhibiting sexual swellings, the follicular phase of the menstrual cycle—during which follicles mature in the ovary and ending with ovulation—is significantly longer in species in which females are subject to higher risk of male infanticide (van Schaik et al. 2000). One interpretation of this pattern is that longer phases provide greater opportunities for matings to confuse paternity.

A recently suggested angle on this coevolutionary dialectic is that *males* may themselves exploit this female counterstrategy to protect their offspring. Evidence from chacma baboons suggests that alpha males may "cede" a proportion of mating opportunities to other males and thereby reduce the risk of infanticidal attack (Boyko and Marshall 2009; Henzi et al. 2010).

Individual Counterstrategies of Females

A number of possible deterrent counterstrategies are based on individual action (Table 3). Maternal (or postpartum) aggression, the "fierce and persistent" hostility of pregnant or lactating females to intruders is a conspicuous feature of rodent reproductive biology (Lonstein and Gammie 2002, p. 869) and is argued to underlie female territoriality in some species (Wolff and Peterson 1998; but see Ebensperger 1998a). Although maternal aggression is a heterogeneous phenomenon subserving multiple functions, a link to infanticide prevention is currently suggested in at least eight murid species and possibly several sciurid species (reviewed Ebensperger and Blumstein 2007; McGuire and Bemis 2007; Weber and Olsson 2008). Once again, numerous detailed data have emerged from laboratory investigations of murids. In species such as the house mouse, the aggressiveness of mothers is striking in light of the virtual absence of aggression when females are in other reproductive states (Heiming et al. 2013). Aggression is sensitive to the presence of pups (Elwood et al. 1990), increases with litter size (Maestripieri and Alleva 1990; see also

pick the best, but also confuse others.

If nobody understands which kid belongs to whom, why would anyone kill any kids?

Table 3. Individual counterstrategies of females with selected example taxa

Proposed counterstrategy	Theoretical rationale	Proposed example taxa	References
Maternal aggression	Females increase in heterosexual aggressiveness during lactation and/or directly defend infants from infanticidal attacks by males; females become territorial during periods of offspring rearing	Birds (*H. rustica*, *Tachycineta bicolor*); many murid rodents, gerbils (*Gerbilliscus leucogaster*); shrews (*Sorex araneus*)	Møller 1988; Robertson 1990; Wolff and Peterson 1998; Ebensperger and Blumstein 2007; Lötter and Pillay 2012; Oleinchenko 2012
Female dominance	Female maintains a relationship of social dominance over males either during lactation or more permanently	Gerbils (*M. unguiculatus*); ring-tailed lemurs (*Lemur catta*)	Pereira and Weiss 1991; Elwood and Kennedy 1994; Ichino 2005
Maternal protectiveness	Under conditions of heightened infanticide risk, mothers increase visual monitoring of potentially infanticidal male and/or offspring, and restrain and/or maintain proximity to infants more	Horses (*E. caballus*); many primates	Cameron et al. 2003, 2009; see references in Palombit 2012
Chemical suppression	Pregnant females produce pheromone that disrupts neurochemical pathways mediating infanticidal behavior in males	Rats (*R. norvegicus*)	Mennella and Moltz 1988
Sexual segregation	Lactating females (a) alter individual ranging to avoid areas with potentially infanticidal males; or (b) for gregarious females, adjust intragroup spatial relations to decrease proximity to infanticidal males or reduce participation in intergroup encounters	(a) Lions (*Panthera pardus*); bears (*U. arctos*); spider monkeys (*Ateles* spp.); chimpanzees (*P. troglodytes*); (b) baboons (*P. h. ursinus*); capuchin monkeys (*C. capucinus*)	(a) Wrangham and Smuts 1980; Packer and Pusey 1983, 1994b; McComb et al. 1993; Sakura 1994; Matsumoto-Oda 1999; Wielgus and Bunnell 2000; Dahle and Swenson 2003; Ben-David et al. 2004; Aureli et al. 2008; (b) Palombit et al. 2001; Crofoot 2007

Koskela et al. 2000), and wanes as pups mature (Parmigiani et al. 1994). Moreover, in their defensive responses to the infanticidal threat posed by sexually naïve males, lactating females direct "severe" bites to vulnerable body parts (such as the head and ventrum) at 3–5 times the rate

they do so in aggressive interactions with (less infanticidal) virgin females (Parmigiani et al. 1988a, 1990). Mothers can also differentiate among males on the basis of infanticidal potential and respond accordingly (Elwood et al. 1990). A possible indication of sexually antago-

nistic coevolution in this domain is that the magnitudes of male infanticidal behavior and maternal aggression are positively correlated with one another in genetic strains of mice (Parmigiani et al. 1999).

The actual effectiveness of maternal aggression in deterring male infanticide in rodents is debated, however. In the laboratory, male mice retaliate with extreme aggression, particularly against females with whom they have not mated (or have mated only recently), often overcoming maternal defense and successfully committing infanticide, leading Parmigiani et al. (1989) to conclude that maternal aggression may simply "delay," rather than prevent, infanticide (see also Ebensperger 1998b). Ebensperger and Blumstein (2007), however, suggest that under more naturalistic conditions, such a delay would probably often translate into maternal success. On the other hand, these researchers point out that ineffectiveness does seem to characterize maternal aggression in several species of squirrel, and they explicitly raise the possibility that this may reflect different outcomes or phases in sexually antagonistic coevolution.

Similarly, primate mothers mount concerted and protracted defense of their infants against infanticidal males, but once again evidence suggests that such efforts succeed in only a handful of species (Palombit 2012), some of which are characterized by the relatively rare social arrangement of stable female dominance over males (which also applies to some rodent examples, Elwood and Kennedy 1994). The reasons for this general ineffectiveness remain unclear, but they may partly reflect a greater reliance of female primates on socially based counterstrategies (see below).

A final individual counterstrategy has been suggested in several mammalian species characterized by solitariness or fission–fusion/dispersed gregariousness. In these species, lactating females may pursue a strategy of evasion based on sexual segregation (Table 2). There is evidence that even females in highly gregarious species may adopt this counterstrategy on a smaller spatial scale by adjusting behavior to decrease proximity to potentially infanticidal males residing in their groups (see Table 2).

Social Counterstrategies of Females

A large set of potential counterstrategies involve deterrence through cooperation with conspecifics. These can be grouped into two sets of strategies involving social interactions with other females and with males, respectively (Table 4).

Female gregariousness has traditionally been viewed as an adaptive solution to the problems of predation and feeding ecology (e.g., Alexander 1974; Wrangham 1980), and it is only recently that the selective role of infanticide risk has begun to be formally incorporated into these models (e.g., Sterck et al. 1997). There are several possible mechanisms through which group living potentially reduces infanticide risk: dilution effects (sensu Hamilton 1971), early detection through communal vigilance and alarm-based avoidance of infanticidal males; female–female coalitionary aggression to extragroup males to prevent takeover or to resident males to thwart attacks on infants. As with ecological models, related females may be more likely to join together in this manner (e.g., lions, see below), but aggregations of unrelated females to reduce infanticidal threat have also been suggested (e.g., Maestripieri and Rossi-Arnaud 1991; Cameron et al. 2009).

Although female gregariousness has been invoked as a counterstrategy for a number of species (Table 4), direct evidence for the predicted inhibitory effect on infanticide is still relatively rare. In a study of a seminatural population of house mice, Manning et al. (1995) reported that female communal nests experienced less than half the rate of infanticide (by both sexes) than did single-mother nests. A possible mechanism underlying this outcome is suggested by laboratory experiments demonstrating that paired females effectively repel male (and female) intruders (Parmigiani 1986; Maestripieri and Rossi-Arnaud 1991). Similarly, when food was experimentally manipulated to promote increased aggregation of female bank voles (*Myodes glareolus*), pup survival increased, which Rémy et al. (2013) attributed to improved anti-infanticide protection.

There are several lines of evidence that group living among lionesses (*Panthera leo*) is

Table 4. Social counterstrategies of females with selected example taxa

Proposed counterstrategy	Theoretical rationale	Proposed example taxa	References
Social strategies involving other females			
Female–female association	(a) Females living in permanent groups with other females reduce infanticide risk through derive dilution, vigilance, and/or defensive benefits; (b) lactating members of aggregate temporarily with other females	(a) Voles (*Microtus oeconomus*, *Myodes glareolus*); house mice (*M. musculus*); Arctic ground squirrels (*S. parryii*); horses (*E. caballus*); lions (*P. leo*); dolphins (*Tursiops* spp.); langurs (*S. entellus*); primates generally; (b) baboons (*P. hamadryas ursinus*)	(a) McLean 1982; Pusey and Packer 1994a,b; Brereton 1995; Manning et al. 1995; Treves and Chapman 1996; Connor 2000; Le Galliard et al. 2006; Cameron et al. 2009; Rémy et al. 2013; (b) Cowlishaw 1999; Palombit et al. 2001
Female coalitionary defense	Females collectively attack infanticidal males and/or deter male immigration with relative success	Lions (*Panthera leo*); sifakas (*Propithecus edwardsi*, *P. verreauxi*); chimpanzees (*P. troglodytes*); bonobo (*Pan paniscus*); blue monkeys (*Cercopithecus mitis*); red colobus (*Procolobus badius*); bonobos (*P. paniscus*)	Butynski 1982; Packer et al. 1990; Richard et al. 1993; Starin 1994; Grinnell and McComb 1996; de Waal 1997; Morelli et al. 2009; Cords and Fuller 2010
Residency in small (female) groups	If risk of male takeover increases with female group size, females maintain small groups via secondary transfer, group fission, and/or aggression to female immigrants	Lions (*P. leo*); many species of colobine monkeys, howler monkeys, gorillas	Pusey and Packer 1987; see references in Palombit 2012
Social strategies involving males			
Transfer with evicted male	In species in which infanticide is preceded by male takeover, lactating females temporarily accompany ousted male until infant is weaned	Capuchin monkeys (*Cebus capucinus*); colobine monkeys (*Semnopithecus vetulus*, *S. entellus*, *Presbytis rubicunda*)	Rudran 1973a; Hrdy 1977; Davies 1987; Jack and Fedigan 2009
Male–female association	Females associate with individual male defender(s) as: (a) relatively loose association in dispersed societies; (b) temporary relationship with particular males in multimale groups during lactation; or (c) permanent male–female pairs or unimale groups	Burying beetles (*Nicrophorus* spp.); birds (*Troglodytes aedon*); Arctic ground squirrels (*S. parryii*); muroid rodents; bears (*U. arctos*); lions (*P. leo*); dolphins (*Tursiops* spp.); many primates including mouse lemurs (*Cheirogaleus major*); howler monkeys (*Alouatta* spp.); mangabeys	McLean 1983; Freed 1986; Watts 1989; Trumbo 1990b, 2007; Gust 1994; Pusey and Packer 1994b; Kappeler 1997; Sommer 1997; Agrell et al. 1998; Borries et al. 1999b, 2011; Steenbeek 1999a; Connor et al. 2000; Crockett and Janson 2000; Delgado and van Schaik 2000; Weingrill

Continued

Table 4. *Continued*

Proposed counterstrategy	Theoretical rationale	Proposed example taxa	References
		(*Cercocebus atys, C. galeritus*); baboons (*P. hamadryas hamadryas, P. h. ursinus*); colobine monkeys (*Colobus vellerosus, Procolobus badius, P. thomasi, S. entellus*); gibbons (*Hylobates* spp.); great apes (*Gorilla gorilla* subspp., *Pongo pygmaeus*)	2000; Stokes 2004; Bellemain et al. 2006b; Swedell and Saunders 2006; Teichroeb and Sicotte 2008; Palombit 2009; Yamagiwa et al. 2009; Fruteau et al. 2010; Opie et al. 2013
Residency in multimale groups	In female-dispersal systems, females immigrate to groups with more males; in female-philopatric systems, females promote multimale group structure	Lemurs (*Eulemur fulvus, P. verreauxi*); howler monkeys (*Alouatta arctoidea, A. caraya, A. palliata*); cercopithecine monkeys (*Chlorocebus pygerythrus, Macaca fuscata*); gorillas (*Gorilla gorilla beringei*)	Crockett and Janson 2000; Treves 2001; Isbell et al. 2002; Ostner and Kappeler 2004; Yamada and Nakamichi 2006; Lewis 2008; Robbins et al. 2009a; Pavé et al. 2012
Residency in groups with better male defender	Primarily among females living in unimale societies, cycling females immigrate to a new group with a better protector male	Colobine monkeys (*Colobus vellerosus, Procolobus badius, P. rufomitratus, P. thomasi*); gorillas (*Gorilla gorilla* subspp.)	Marsh 1979; Starin 1994; Sterck 1997; Stokes et al. 2003; Robbins et al. 2009b; Teichroeb et al. 2009; Yamagiwa et al. 2009

an effective deterrent to infanticide (Packer and Pusey 1983). Cub mortality is much lower for females living in groups of two or more than for solitary mothers (Pusey and Packer 1994b). This is partly achieved through coalitionary attack on alien males, which successfully protects cubs from attack by single individuals or small groups of males, who "may have to fight for their lives" against lionesses capable of inflicting fatal injuries (Pusey and Packer 1994b, p. 297). The counterstrategic response of males is to use vocal cues to avoid groups of females (Grinnell and McComb 1996) or to travel in large male cohorts, against which female defense is less effective. Like house mouse dams, however, lionesses appear capable of discriminating among males on the basis of infanticide threat and may use evasion to reduce such interactions (McComb et al. 1993). Finally, socioecological

data suggest that pride size does not maximize individual food intake through communal hunting, but rather infanticidal protection (Packer et al. 1990).

Somewhat surprisingly, female coalitionary defense against infanticidal males in most primates appears as generally unsuccessful as individual maternal defense (Palombit 2012). It is possible that the anti-infanticide advantage conferred by gregariousness involves the harder-to-test mechanism of improved vigilance and nonaggressive intervention (e.g., retrieving infants from dangerous situations before attacks can be launched, as has been noted in a number of field studies). In some primate species, however, an alternative version of this female–female counterstrategy may operate.

This alternative version is based on the idea that larger groups of females are predicted to be

more attractive as takeover targets to potentially infanticidal males. Thus, females may theoretically garner increased protection for their infants by breeding in relatively small groups (Janson and Goldsmith 1995; Treves and Chapman 1996). This goal can be achieved via several possible mechanisms, such as the fissioning of large groups, individual female transfer to smaller groups, or the aggressive deterrence of alien female immigration by resident females. Supportive evidence for this counterstrategy has been found in a number of primate species in which: (1) the predicted negative correlation between infant mortality or infanticide rates and female group size has been documented; and (2) one or more of the above three mechanisms has been identified (reviewed Palombit 2012; see also Pusey and Packer 1987 for lions). This counterstrategy carries a potentially important implication that may help to explain the surprising ineffectiveness of female coalitionary aggression against infanticide in many primates. The individual female transfer that underlies this counterstrategy in primates tends to produce small groups of females who share relatively low genetic relatedness with one another (cf. lions). Such conditions may impede the formation of the kinds of female–female coalitions that are effective deterrents to infanticidal males (Palombit 2012). This hypothesis has not been tested directly, but it underscores the possibility that various female counterstrategies may be incompatible with one another, such that adoption of one may preclude another.

A final set of counterstrategies has been inspired by a growing body of data demonstrating the important role males may play in preventing infanticide. The majority of relevant data on these counterstrategies has come from studies of nonhuman primates, possibly because other animals, such as rodents, are less likely to rely on socially based counterstrategies to infanticide (Blumstein 2000). There are several variants on this strategic theme, which can be distinguished by general features of social system, such as the feasibility of transfer as a strategic option for females at risk of infanticide (reviewed in Palombit 2012).

The ecological and social costs of intergroup transfer vary considerably for females, but they are generally expected to be higher for frugivorous species than for folivores. This is because the greater rarity of fruits (relative to leaves) in most environments engenders elevated feeding competition and greater difficulties in finding food in the unfamiliar habitats that a transferring female would necessarily encounter. Moreover, the social costs of female transfer are potentially higher for frugivores because the "female-bonded" social organization of many fruit-eating primates (particularly Old World monkeys) is centered on networks of social relationships among related females. Thus, female transfer may necessarily require cessation of cooperative interactions with female kin, which can impose costs on both individual and inclusive fitness. It is for these reasons that transfer is less of an option for females in the female-philopatric, multimale societies. In this case, an antiinfanticide counterstrategy based on cooperation with resident males would be more likely. One such possible counterstrategy is to maintain a temporary relationship with a male protector (or a small number of adult males) during the period of infant vulnerability (Table 4), as exemplified by the chacma baboon of southern Africa. When a female gives birth, she establishes such a relationship, or "friendship," with a particular male, which lasts as long as she has her nursing infant; if the infant weans or dies, the relationship ends. Observational and experimental playback data suggest that male friends are significantly more predisposed than other males to come to the aid of females under attack by the potentially infanticidal alpha male (Palombit et al. 1997), possibly because of paternity of the infants involved (Moscovice et al. 2010). Immigration of a new male who attains alpha status results in elevated cortisol among the group's mothers (but not among cycling females); cortisol levels climb even higher if an infanticide is successfully perpetrated or, notably, among the (very few) mothers who lack a male friend (Beehner et al. 2005; Engh et al. 2006). Lactating females compete for male friends, such that a mother's rank is positively correlated with the rank of her male friend (Palombit et al. 2001).

It is partly because the vast majority of mothers have male friends that it is difficult to assess directly the fitness benefits of friendship for females, and data are still too few to evaluate how variation in the characteristics of friendships or male friends affect infant survival. Nevertheless, the evidence is suggestive that this system reflects an anti-infanticidal counterstrategy.

For folivorous primates, the costs of female transfer are predicted to be lower, opening the way for dispersal-based counterstrategies, such as the previously described transfer to smaller female groups. Many of these species are characterized by unimale breeding units, which are particularly prone to takeover infanticide. Females in these societies may reduce the risk of infanticide by choosing a group with a high-quality male protector. This hypothesis has not been subject to rigorous testing, partly because of the difficulties in measuring variation in male quality as protector. There are suggestive supportive data for a few species, however, notably Thomas's leaf monkeys (*P. thomasi*), in which infanticide is not perpetrated as part of a male "takeover" by a new immigrant, but rather by extragroup males. Victimized females respond to infanticide by abandoning their group and joining the killer. And, as predicted, cycling females who transfer from older males to "prime" (younger) males subsequently experience fewer infanticidal attacks.

For relatively folivorous primates in which female transfer remains an ecologically viable option, but in which the number of males in groups varies, an alternative counterstrategy is to preferentially target groups with more males. This hypothesis is supported in several species, such as howler monkeys (*Alouatta* spp.) and mountain gorillas (*G. gorilla beringei*) in which there is empirical evidence that infanticide occurs at predictably lower rates in groups with more males (independently of female group size). Even so, puzzles remain, such as the apparent lack of preference among female gorillas for multimale groups as destinations for transfer (Robbins et al. 2009a).

The above examples have focused on gregarious animals, but even in dispersed societies in which the sexes are relatively solitary and inter-act sporadically, female association with a male may nevertheless afford some protection against infanticide (Table 4). For example, ousted male lions will re-establish or maintain residency near a pride that offers few mating opportunities if it contains vulnerable cubs they likely sired (Pusey and Packer 1994b). Male–female pairs of house mice repulse infanticidal intruders (Palanza et al. 1996) so successfully that Parmigiani et al. (1994) suggest that the apparent failure of maternal aggression to thwart infanticide in previous laboratory experiments may derive from the artificial absence of the stud male.

Finally, infanticide has been suggested to be the primary selective force behind the evolution of social monogamy (Table 4) (reviewed in Palombit 2000). Perhaps the most compelling evidence for this hypothesis comes from research on burying beetles (*Nicrophorus* spp.). In a manner reminiscent of avian monogamy, a male–female pair of beetles maintains a long period of postcopulatory association with one another on a vertebrate carcass that provides nourishment for developing larvae (Eggert and Müller 1997). Both parents provision the larvae by regurgitating predigested carrion obtained from this carcass, although the paternal contribution is not crucial for offspring success (Trumbo 1991; Müller et al. 1998). On the other hand, male presence significantly reduces the risk of takeover infanticide by another male, suggesting an anti-infanticide benefit of social monogamy in some populations (Trumbo 1990a,b, 1991; Robertson 1993; Trumbo and Valletta 2007). Similarly, in some birds such as tropical house wrens (*Troglodytes aedon*), protection against infanticide appears to be a more important advantage of social monogamy than biparental provisioning of offspring (Freed 1986; see also Veiga 2000). This hypothesis as it applies to primates, notably the monogamous gibbons (*Hylobates* spp.) (van Schaik and Dunbar 1990), has been questioned on the basis of comparative data (Palombit 1999; Fuentes 2000; Brockelman 2009), but recent indirect evidence of infanticide in one population of white-handed gibbons suggests an intriguing possibility (Borries et al. 2011). Contradictory conclusions about the

selective role of infanticide in the evolution of mammalian social monogamy have emerged from recent phylogenetic and life history analyses (Lukas and Clutton-Brock 2013; Opie et al. 2013).

CONCLUSIONS

Male infanticide appears to be an arresting example of interlocus conflict (sensu Arnqvist and Rowe 2005). There is still a great deal we do not understand about the array of behaviors constituting this system. The adaptive significance, occurrence, and variability of male infanticide remains unclear in many species, and we still lack enough data to compare directly the lifetime reproductive success of the "infanticidal" versus alternative "noninfanticidal" strategies. Nevertheless, evidence accumulated over the last several decades yields several general conclusions. First, in the well-studied populations, it seems clear that infanticide is not simply an aberration or byproduct of other biological characters or conditions, but represents an adaptive strategy for males in some circumstances. Second, the adaptive significance of the strategy is multifarious; male infanticide is not unitary. The sexual selection hypothesis may be the best known explanation, but there is sufficient evidence to consider a multiplicity of other functions (Table 1). Third, whatever the benefit of infanticide to males, there is little doubt that it usually imposes a substantive fitness cost on females (as well as infants, of course), particularly in the slowly reproducing species in which one form of infanticide—sexually selected—is expected to operate. This provides a strong rationale for expecting that male infanticide has acted as a selective agent in the evolution of female biology in these species, perhaps operating as strongly as the conventionally recognized contingencies related to predation and feeding ecology.

Female counterstrategies to infanticide have been the subject of rigorous study for a relatively short time, however. What is perhaps most striking about current data is the great variety of possibilities that have been proposed (Tables 2–4). These mechanisms range from counterstrategies that increase the potential costs of infanticide to would-be perpetrators (e.g., promiscuity, maternal aggression, coalitionary defense with other females or males), to those that decrease its benefits (promoting small female group sizes or multimale social structure), to some that simply "cut the losses" of infanticide (e.g., pregnancy termination). It is also striking that females in the well-studied populations appear multiple times throughout Tables 2–4, suggesting that females at risk of infanticide rely not on one counterstrategy but on an array of counterstrategies. Lions provide an excellent example of this principle. When cycling, lionesses mate promiscuously to confuse paternity (Table 2). During lactation, females with older cubs (≥10 mo) capable of independent locomotion opt for a strategy of evasion, living largely solitarily on the periphery of their home ranges (sexual segregation) (Table 3). Should alien males be encountered visually or aurally, females attempt to escape or resort to individual maternal aggression (Table 3) (although the latter counterstrategy carries potentially high costs). For females with younger, less mobile cubs, however, sexual segregation is less feasible, and they rely on membership in a pride of female relatives (especially if it is a larger pride) (Table 4). They thereby benefit from the coalitionary defense that is "always able to overcome or drive off one or a few males" (Pusey and Packer 1994b, p. 297). But if prides become too large and thus more attractive for male takeover, then females may disperse (Table 4). The more general conclusion suggested here is that sexually antagonistic coevolution may be a mechanism accounting for much of the great diversity of animal behavior.

There is an unquestionable need for further research on possible female counterstrategies. There are alternative explanations for most of the behaviors listed in Tables 2–4, which must be carefully tested (and rejected) to substantiate the anti-infanticide hypothesis. Analyses are additionally complicated by the fact that predictions of the anti-infanticide hypotheses are often similar to those of alternatives based on ecology. Finally, although it seems likely that female counterstrategies will help to explain variation in the occurrence of male infanticide,

data from the wild are insufficient to address this issue quantitatively.

It should also be noted that the implications for sexually antagonistic coevolution may extend well beyond infanticide and its immediate counterstrategies. A case in point concerns the suite of behaviors collectively known as male "sexual coercion" of females. Those aspects of sexual coercion that involve restricting multi-male mating by females may be best understood as the male evolutionary response to promiscuity as a female counterstrategy to the male strategy of infanticide (Wolff and MacDonald 2004; Palombit 2014). Similarly, female promiscuity may have exerted selection on systems of sperm competition among males in some taxa, which in turn may have then "counter selected" for mechanisms of cryptic female choice (Kappeler 2012). Thus, the potential cascading effects of the sexual conflict originating with infanticide may be extensive, broad, and diverse.

In many ways, the study of male infanticide and female counterstrategies does not lend itself well to the kinds of methodologies and reproductive profiles that allow direct assessment of sexually antagonistic coevolution (Palombit 2010). The relevant organisms often reproduce slowly, are not easily amenable to experimental manipulation, and are difficult to study in the wild. Despite these difficulties, however, these systems offer opportunities to study the action of sexual conflict in the context of highly gregarious life styles and, more generally, to broaden our appreciation of the diversity of pathways over which sexually antagonistic coevolution has operated.

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