Chapter 23 Nonparental Infanticide

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Male marmot 100 moved into the Grass Group. Male 69 seemed to oppose 100's sudden entry, but the females of the group appeared to accept 100. Before male 100 moved in there were 9 healthy marmot pups crawling around the Grass Group's main burrows. Within two weeks there was one injured marmot pup limping around—apparently avoiding marmot 100. The injured pup did not survive hibernation. (Blumstein 1993:14)

A female invaded an adjacent coterie territory and entered a burrow containing a recently emerged, healthy juvenile. The marauder emerged 5 minutes later with a distinctly bloody face, and then showed licking the front claws [behavior]. Several minutes later the disoriented juvenile emerged with fresh, severe wounds on the face and neck. The juvenile disappeared a few days later. (Hoogland 1995:134)

INFANTICIDE CAN STRIKE quickly and may have profound demographic consequences (Sherman 1981b; Hoogland 1995; Blumstein 1997). Nonparental infanticide, the killing of infants by conspecifics other than the parents, occurs in a variety of vertebrate and invertebrate taxa (Hausfater and Hrdy 1984; Elgar and Crespi 1992; Parmigiani and Vom Saal 1994; Van Schaik and Janson 2000). Among mammals, infanticide has been reported in primates, terrestrial and marine carnivores, artiodactyls, cetaceans, lagomorphs, perissodactyls, and tree shrews (Ebensperger 1998b). More recent additions to the literature include reports of infanticide in banded mongooses (*Mungos mungo,* Cant 2000), bottle-nose dolphins (*Tursiops truncatus,* Patterson et al. 1998), giant otters (*Pteronura brasiliensis,* Mourão and Carvalho 2001), hippos (*Hippopotamus amphibius,* Lewison 1998), plains zebras (*Equus burchelli,* Pluháček and Bartoš 2000), sportive lemurs (*Lepilemur edwarsi,* Rasoloharijaona et al. 2000), and suricates (*Suricata suricatta,* Clutton-Brock et al. 1998). Infanticide has been noted in the wild or under laboratory conditions in two species of hystricognath rodents and 35 species of sciurognath rodents (table 23.1). Despite the difficulty of observing and quantifying infanticide in these typically semifossorial and often nocturnal species, we know a considerable amount about the proximate regulation, evolution, and function of infanticide in rodents. Understanding the causes and consequences of infanticide in rodents provides a basis for developing and testing alternative hypotheses for the functional significance of infanticide in mammals generally.

Several field-based studies that recorded the frequency of infanticide by rodents have concluded that infanticide is a major source of juvenile mortality (Sherman 1981b; Agrell et al. 1998; Hoogland 1995; Blumstein 1997). Other seminatural and field-based studies have reached similar conclusions indirectly by showing a significant impact of adult female density on juvenile recruitment (Labov et al. 1985; Mappes et al. 1995). These studies show that the removal of breeding females usually increases the survival of resident juveniles in deer mice (*Peromyscus maniculatus;* Galindo and Krebs 1987), golden hamsters (*Mesocricetus auratus;* Goldman and Swanson 1975), gray-tailed voles (*Microtus canicaudus;* Wolff et al. 2002), and meadow voles (*Microtus pennsylvanicus;* Rodd and Boonstra 1988). In contrast,

Table 23.1 Summary of reports of nonparental infanticide in rodents

Family	Species	Common name	MN	MC	FN	FC	I	Sources
Caviidae	*Galea musteloides*	Yellow-toothed cavy				1	X	Künkele and Hoeck 1989
Hydrochaeridae	*Hydrochaeris hydrochaeris*	Capibara				1		Da Cunha-Nogueira et al. 1999
Muridae	*Acomys cahirinus*	Spiny mouse		1		1		Porter and Doane 1978; Makin and Porter 1984
	Apodemus sylvaticus	European wood mouse		1		1		Wilson et al. 1993
	Clethrionomys glareolus	Bank vole	1	1	1	1		Ylonen et al. 1997
	Dicrostonyx groenlandicus	Collared lemming		1		2		Mallory and Brooks (1978), 1980
	Glis glis	Dormouse			1?			Pilastro et al. 1996
	Lemmus lemmus	Norwegian lemming		1?		1		Arvola et al. 1962; Semb-Johansson et al. 1979
	Meriones unguiculatus	Mongolian gerbil		1		2		Elwood 1977, 1980; Elwood and Ostermeyer 1984b
	Mesocricetus auratus	Golden hamster				1		Goldman and Swanson 1975; Marques and Valenstein 1976
	Microtus agrestis	Field vole				1	X	Agrell 1995
	Microtus brandtii	Brant's vole		1		1		Stubbe and Janke 1994
	Microtus californicus	California vole		1?				Lidicker 1979a; Heske 1987
	Microtus pennsylvanicus	Meadow vole	1	1	1	1		Louch 1956; Caley and Boutin 1985; Ebensperger et al. 2000
	Microtus ochrogaster	Prairie vole		1		2		Roberts 1994 (cited in Carter and Roberts 1997)
	Mus musculus/ domesticus	House mouse (lab stocks)		2		1		Gandelman 1972; Svare and Mann 1981; Parmigiani et al. 1989; Perrigo et al. 1993
	Mus musculus/ domesticus	House mouse (wild stocks)		1		1		Southwick 1955; Perrigo et al. 1993; Vom Saal et al. 1995; Jakubowski and Terkel 1982; Soroker and Terkel 1988
	Neotoma lepida	Desert woodrat				1?		Flemming 1979
	Ondatra zibethicus	Muskrat	?		?			Errington 1963; Caley and Boutin 1985
	Peromyscus californicus	California mouse		1		1		Gubernick 1994
	Peromyscus leucopus	White footed mouse	1	1	2	2		Wolff 1986; Wolff and Cicirello 1991
	Peromyscus maniculatus	Deer mouse	1	1	2	2		Wolff and Cicirello 1991
	Phodopus campbelli	Djungarian hamster		1		1		Gibber et al. 1984
	Phyllotis darwini	Leaf-eared mouse		1		1		D. Bustamante, R. Nespolo, and L.A. Ebensperger, unpublished ms
	Rattus norvegicus	Norway rat		2		1		Calhoun 1962; Jakubowski and Terkel 1985a
Sciuridae	*Cynomys gunnisoni*	Gunnison prairie dog	1?		1			Fitzgerald and Lechleitner 1974
	Cynomys ludovicianus	Black-tailed prairie dog	1		2			Hoogland 1985, 1995
	Cynomys parvidens	Utah prairie dog	1					Hoogland (chap. 37, this volume)
	Marmota caligata	Hoary marmot	1		1			T. Karels, unpublished ms
	Marmota caudata	Golden marmot	1					Blumstein 1997
	Marmota flaviventris	Yellow-bellied marmot	1?		1			Armitage et al. 1979; Brody and Melcher 1985
	Marmota marmota	Alpine marmot	1					Coulon et al. 1995
	Paraxerus cepapi	Tree squirrel	1					de Villiers 1986

Table 23.1 (continued)

Family	Species	Common name	MN	MC	FN	FC	I	Sources
	Spermophilus armatus	Utah ground squirrel	?		?			Balph 1984; Eshelman and Sonnemann 2000
	Spermophilus beecheyi	California ground squirrel			1			Trulio et al. 1986; Trulio 1996
	Spermophilus beldingi	Belding's ground squirrel	1		1			Sherman 1981b
	Spermophilus columbianus	Columbian ground squirrel	1		2			Steiner 1972; Balfour 1983; Waterman 1984; Hare 1991; Stevens 1998
	Spermophilus parryii	Arctic ground squirrel	1					Steiner 1972; Holmes 1977; McLean 1983; Lacey 1992
	Spermophilus richardsonii	Richardson's ground squirrel				1		Michener 1973b
	Spermophilus townsendii	Townsend's ground squirrel	1?					Alcorn 1940
	Spermophilus tridecemlineatus	Thirteen-lined ground squirrel	1					Vestal 1991

NOTES: MN = male infanticide observed in nature; MC = male infanticide observed in captivity; FN = female infanticide observed in nature; FC = female infanticide observed in captivity; I = studies where individuals of the opposite sex were not examined; ? = indicate uncertainties in the database. Numbers in the MN, MC, FN, and I columns are used to indicate when one sex is more infanticidal than the other (i.e., 2 > 1). Species for which infanticide was reported but the infanticidal sex was not specified are listed, but the sex of the infanticidal animal was left blank.

juvenile recruitment per pregnancy has been shown to decrease under wild conditions as the number of adult female (but not male) gray-tailed voles sharing a patch increases (Wolff and Schauber 1996). In the laboratory, litter mortality in prairie voles (*Microtus ochrogaster*) is more negatively affected by the presence of additional females than males (Hodges et al. 2002). These observations are consistent with the assertion that infanticide by females is the mechanism for reduced recruitment of juveniles.

We view infanticide as potentially adaptive (e.g., Hrdy 1979; Sherman 1981b; Hoogland 1995), and we review functional hypotheses and evidence about the current adaptive utility of infanticide in rodents. Males and females are considered separately when infanticide serves different functions in each sex. We also address some consequences of infanticide on behavioral counter-strategies and demography.

Explanations of Infanticide: Hypotheses and Evidence

Nonadaptive explanations

As Hrdy (1979) and Sherman (1981b) pointed out, historically infanticide was considered aberrant because it was inconceivable that such a behavior could be adaptive (e.g., Fox 1968). Formally, infanticide could be neutral or maladaptive (i.e., pathological) during conditions of high density (Southwick 1955; Louch 1956; Calhoun 1962b), it could be an accidental occurrence of dominance disputes (Rijksen 1981; Campagna et al. 1988), or result from disturbances in physical or social environments (e.g., habitat reduction coupled to high density conditions; Curtin and Dolhinow 1978; Ciani 1984).

However, four lines of evidence make it unlikely that the nonadaptive hypothesis is a general explanation for rodent infanticide. First, most studies claiming that infanticide is not an adaptive trait come from confined populations kept under seminatural conditions in which the identity of killers, and the precise circumstances (i.e., the possibility of evaluating potential benefits), of infanticide are not recorded (Southwick 1955; Calhoun 1962b; Semb-Johansson et al. 1979). Second, explanations of infanticide based on overcrowding, per se, may not be relevant because in the field, infanticide is apparently unrelated to local density (Dobson 1990; Wolff and Cicirello 1991; Hoogland 1995). Moreover, infanticide could be adaptive under conditions of high density if resources are limited. Third, there is no evidence in rodents that infanticide is accidental (e.g., pups simply get in the way of fighting adults; Sherman 1981b; Hoogland 1995). Fourth, individuals that commit infanticide do so under predictable circumstances and exhibit a number of context-specific traits. For instance, black-tailed prairie dogs engage in a specific type of self-cleaning following infanticide (Hoogland 1995). In the rest of this review we focus on potentially adaptive explanations of infanticide.

Adaptive explanations

Hypothesis 1. Direct acquisition of nutritional resources

In rodents, infanticide by males and by females has evolved together, a finding consistent with the hypothesis that infanticide originally evolved as a foraging strategy (Blumstein 2000). If infanticide initially evolved as a foraging strategy, subsequent functions of infanticide must be viewed as exaptations. Juveniles are easy prey, and infanticide may enable killers to obtain nutritious food resources (Hrdy 1979; Sherman 1981b). This hypothesis predicts that infanticide should be followed by cannibalism, and that it might be more frequent among energetically stressed individuals.

Support for the predation hypothesis is provided by field studies showing that cannibalism is negatively correlated with food availability (Holmes 1977). Most species in which infanticide and cannibalism have been noted are those with diets that normally include some animal matter (Sherman 1981b; Elwood 1992). For instance, adult rodents occasionally prey on the infants or adults of other rodents (DeLong 1966; Rood 1970; Ewer 1971; Paul and Kupferschmidt 1975; Wolff 1985c; Elwood and Ostermeyer 1986), and these same species are infanticidal.

Females

Females from 5 of 10 well-studied rodent species have been observed killing and cannibalizing pups (table 23.2). Among these, 69% ($n = 13$) of female deer mice (Wolff and Cicirello 1991) and from 67% ($n = 18$) to 100% ($n = 10$) of female white-footed mice (*Peromyscus leucopus;* Wolff and Cicirello 1989, 1991) that kill and cannibalize pups are either pregnant or lactating. Among sciurid rodents, most female black-tailed prairie dogs (*Cynomys ludovicianus;* 78%, $n = 65$; Hoogland 1985, 1995), California ground squirrels (*Spermophilus beecheyi;* 100%, $n = 36$; Trulio 1996), and Columbian ground squirrels (*Spermophilus columbianus;* 100%, $n = 7$; Stevens 1998) that committed nonparental infanticide did so while nursing their own young. Perpetrators typically consumed their victims, suggesting that they were obtaining nutritional benefits at a time of energetic stress. Interestingly, in laboratory pup-retrieval experiments, female Richardson's ground squirrels (*Spermophilus richardsonii*) that were virgins or nonparous sometimes cannibalized the young (Michener 1973b).

Predation is not a current universal function of infanticide by female rodents. Cannibalism has not been recorded in some female microtines, including collared lemmings (*Dicrostonyx groenlandicus;* Mallory and Brooks 1978, 1980), Norway lemmings (*Lemmus lemmus;* Arvola et al. 1962), bank voles (*Clethrionomys glareolus;* Ylönen et al. 1997), and field voles (*Microtus agrestis;* Agrell 1995), and it occurs only rarely in yellow-bellied marmots (*Marmota flaviventris;* Armitage et al. 1979; Brody and Melcher 1985) and Belding's ground squirrels (*Spermophilus beldingi;* Sherman 1981b). In the laboratory, most female meadow voles kill (73%, $n = 11$) and consume (75%, $n = 8$) alien pups when they are pregnant, but they stop killing and consuming pups when they are lactating and/or not breeding (Ebensperger et al. 2000).

Males

Males from 9 of 11 well-studied species have been observed to kill and cannibalize pups (table 23.2), including Mongolian gerbils (*Meriones unguiculatus;* Elwood and Ostermeyer 1984a), meadow voles (Ebensperger et al. 2000), Norway rats (*Rattus norvegicus;* Paul and Kupferschmidt 1975), Belding's ground squirrels (Sherman 1981b), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus;* Vestal 1991), Townsend's ground squirrels (*Spermophilus townsendii;* Alcorn 1940), Utah prairie dogs (*Cynomys parvidens;* Hoogland chap. 37 this volume), and yellow-bellied marmots (Armitage et al. 1979). As might be expected, food deprivation increases the frequency of infanticide and cannibalism in male gerbils (Elwood and Ostermeyer 1984a), Norway rats (Paul and Kupferschmidt 1975), house mice (*Mus musculus/domesticus;* Svare and Bartke 1978, but see the following), and common voles (*Microtus arvalis;* Litvin et al. 1977).

Obtaining energy is thus a common function of infanticide by male rodents. However, not all males eat the young they kill. Small proportions of male deer mice (2 out of 6) and white-footed mice (1 out of 8) ate pups after killing them (Wolff and Cicirello 1989, 1991). Thus although cannibalism does occur in some species under some circumstances by both males and females, it is not universal and does not totally explain the current motivation or functional significance of infanticide in all species or situations.

Hypothesis 2: Acquisition of space and other physical resources

Infanticide also may provide the perpetrator, or its offspring, increased access to potentially limited resources such as food, nesting sites, or space by eliminating current or future competitors for those resources (Rudran 1973; Hrdy 1979; Sherman 1981b). In such cases, infanticide is expected to be more prevalent under conditions when resource quality varies considerably, or when resources are extremely limited (Butynski 1982). This hypothesis would also be supported by observations of individuals that commit infanticide by selectively killing the sex of young that will be competitors for the critical resource, and then taking over the resources of their victims' mother. This expectation as-

Table 23.2 Predictions of hypotheses posed to explain rodent infanticide and species where evidence supports or rejects them

Hypothesis	Main predictions	Supportive studies	Unsupportive studies
Direct acquisition of nutritional resources	Killers must consume their victims.	Females: *P. leucopus, P. maniculatus, C. ludovicianus, M. flaviventris, S. beecheyi*	Females: *D. groenlandicus, L. lemmus C. glareolus, M. agrestis*
		Males: *M. unguiculatus, R. norvegicus, M. pennsylvanicus, C. parvidens, S. beldingi, S. tridecemlineatus, S. townsendii*	Males: *P. leucopus, P. maniculatus*
	Infanticide and cannibalism common when food abundance is low, or when experimentally food-deprived.	Males: *M. unguiculatus, R. norvegicus, M. musculus-domesticus*	
	Infanticide and cannibalism common in pregnant and lactating females.	Females: *P. leucopus, P. maniculatus, C. ludovicianus, S. beecheyi, S. columbianus*	Females: *M. pennsylvanicus*
	Motivational and neurological basis of infanticide should resemble that of predatory attack.		Males: *M. musculus/domesticus*
Indirect acquisition of space and other physical resources	Infanticide more common when per capita availability of resources is low.		Females: *P. leucopus, P. maniculatus*
	Resources previously used by individuals losing litters should be taken over by killers.	Females: *S. beldingi*	
	Infanticide should be directed toward infants of the sex most likely to become competitors for the perpetrator or its offspring.		Females: *S. beecheyi*
Insurance against misdirecting parental care	Infanticide should be common in females before and after lactating their own litters.	Females: *M. auratus, M. musculus-domesticus, M. unguiculatus, R. norvegicus*	
	Infanticide by breeding females should occur when nonfilial offspring cannot be confused with own.	Females: *C. ludovicianus, S. beldingi, S. columbianus*	Females: *S. beecheyi*
	Infanticide should be common in breeding females whose nests are clumped.	No information available	
	Infanticide more frequent among species with precocial as opposed to altricial offspring.	No information available	
Acquisition of mates	Infanticidal males should not kill offspring they have sired.	Males: *M. musculus/domesticus, A. cahirinus, P. maniculatus, P. leucopus, M. pennsylvanicus*	
	The elimination of offspring should shorten the interbirth period of the victimized females.	Males: *M. musculus/domesticus, D. groenlandicus, R. norvegicus*	
	Infanticidal males should mate with and sire the subsequent offspring of the mother whose litter was killed.	Males: *M. musculus/domesticus*	

sumes that adult marauders are able to determine the sex of potential victims prior to killing them.

Females

Female Belding's ground squirrels apparently commit infanticide to obtain access to a critical resource—a burrow site that is safe from predation. In this species, females that lose their young to coyotes and badgers move to safer areas and attempt to kill young there. Indeed, 70% of females ($n = 20$) losing their litters to predators or conspecifics moved to new sites as compared with 33% of females that did not lose their litters. Nonresident adult females were responsible for 42% of observed infanticide. Infanticidal female Belding's ground squirrels seldom (9%, $n = 8$) consumed their victims (Sherman 1981b). In most cases perpetrators established nest burrows the subsequent year near their victim's natal burrow (Sherman 1981b).

Infanticide to reduce competition for space has also been suggested in white-footed mice and deer mice. Females of both species are territorial against other females, the most common perpetrators of infanticide (Wolff and Cicirello

1989, 1991). While functions are not mutually exclusive, female white-footed mice that are pregnant or lactating usually consume their victims (Wolff and Cicirello 1989, 1991). Data showing increased access by infanticidal females (or their offspring) to the territories of their victimized females are required to support the hypothesis that infanticide in these mice is a form of resource competition.

Among sciurids, such as black-tailed prairie dogs, California ground squirrels, and Belding's ground squirrels, females do not direct their infanticidal attacks selectively toward female pups (Sherman 1981b; Hoogland 1995; Trulio 1996), as would be expected from the pattern of female philopatry (Greenwood 1980; Dobson 1982). Sherman (1981b) suggested that this lack of sex-specificity was because it is more important for females to kill entire litters rapidly than to spend time sexing their victims, especially in a dark burrow. Alternatively, and what often may be the case, females kill pups as a form of direct competition with territorial females and as a means of acquiring the burrow/nest site immediately and therefore must kill all offspring and not just the philopatric sex.

The theoretical framework provided by the resource-competition hypothesis seems appropriate for exploring causal associations between infanticide and communal nesting/breeding. Infanticide is one of a series of mechanisms by which individuals may suppress reproduction in others. Females of communally breeding species might use infanticide to prevent breeding by less dominant females, and thus control the partitioning of reproduction within the group (Johnstone and Cant 1999). The observations that nursing females kill pups within the same nesting group (*Glis glis;* Pilastro et al. 1996), pups of less dominant females (house mouse, Palanza et al. 1996), and pups of the same burrow (coterie) system (black-tailed prairie dog; Hoogland 1995) support this scenario. However, lactating females do not kill pups in other communally breeding species such as meadow voles (Ebensperger et al. 2000) and Norway rats (Menella et al. 1990; Schultz and Lore 1993). The conditions under which infanticide functions as a mechanism of reproductive suppression in rodents are unclear. One aspect that requires further elucidation is the relatedness between perpetrators and victims, especially in communally nesting species or those species in which females nest close together.

Males

Two studies have examined the resource-competition hypothesis to explain infanticide by males. McLean (1983) and Lacey (1992) invoked competition for resources to explain infanticide committed by immigrant male Arctic ground squirrels (*Spermophilus parryii*). McLean (1983) recorded 10 cases of infanticide, all of which were perpetrated by immigrant adult males. Male marauders did not cannibalize their victims, but became resident in the area after the killings. Lacey (1992) found that females who lost their litters to infanticidal males dispersed and did not mate with the killers. McLean (1983) suggested that males of this species kill infants to decrease competition for food. Lacey (1992) suggested that infanticide by male Arctic ground squirrels resulted from competition for burrow systems whereby males took over female burrows, destroyed their litters, and remained there until the next breeding season. In short, both studies have provided valuable, but still preliminary, insights into the function of male infanticide in Arctic ground squirrels. More generally, the role of resource limitation on male infanticide in rodents remains to be assessed. The function of male infanticide in sciurids (e.g., see Hoogland chap. 37 this volume), and other seasonally breeding rodents, is particularly puzzling since sexual selection seems unlikely in this case (see the following).

Hypothesis 3: Insurance against misdirecting parental care

Sherman (1981b) and Elwood and Ostermeyer (1984b) suggested that individuals sometimes commit infanticide to avoid "adopting" or otherwise providing parental care to unrelated offspring. If so, infanticide should be committed mostly by the sex that bears the primary costs of adoption (Pierotti 1991). Among mammals, lactation is the most energetically costly phase of parental care (Trillmich 1986; Gittleman and Thompson 1988), and thus females should be the ones that benefit most by committing infanticide. An additional prediction from this hypothesis is that infanticide should be more frequent in species where nests of breeding females are spatially clumped (which increases the opportunity for unrelated pups to steal milk). This hypothesis does not require that victims be consumed.

Evidence in support of the misdirected parental care hypothesis is largely circumstantial. Among species in which females are infanticidal, both laboratory and field studies show that lactating females will indeed adopt and/or provide parental care to unrelated infants (table 23.2). This is the case in spiny mice (*Acomys cahirinus;* Porter and Doane 1978), Norway lemmings (De Kock and Rohn 1972), meadow voles (McShea and Madison 1984; Sheridan and Tamarin 1986), house mice (Sayler and Salmon 1971; König 1989a, 1994b), desert woodrats (*Neotoma lepida;* Fleming 1979), white-footed mice (Hawkins and Cranford 1992; Jacquot and Vessey 1994), deer mice (Hansen 1957; Hawkins and Cranford 1992; Millar and Derrickson 1992), black-tailed prairie dogs (Hoogland et al. 1989), Belding's ground squirrels (Sherman 1980a), Columbian ground squirrels (Hare 1991), yellow-bellied marmots (Armitage and Gurri-Glass 1994), and in the yellow-toothed cavy (*Galea musteloides;* Künkele and Hoeck 1995). The biological meaning of such adoption, particularly in laboratory studies, remains to be properly evaluated. Ultimately, knowing how frequently adoption occurs in nature is essential.

Other laboratory observations provide more direct evidence for the misdirected care hypothesis. Specifically, observations have shown that female golden hamsters (Richards 1966), house mice (McCarthy and Vom Saal 1985; Soroker and Terkel 1988; Manning et al. 1995; but see Palanza et al. 1996), Mongolian gerbils (Elwood and Ostermeyer 1984b), and Norway rats (Peters and Kristal 1983) kill unrelated young when they are sexually inexperienced, pregnant, or after weaning their own litters, but rarely when they are lactating. This makes sense, because lactating females of these altricial species are those most likely to make mistakes because pups of their own are available. In the house mouse (Sayler and Salmon 1971; Ostermeyer and Elwood 1983; Manning et al. 1995; but see Palanza et al. 1996) and the cavy (Künkele 1987; cited in Künkele and Hoeck 1989), lactating females in the laboratory adopt and nurse alien pups of similar age to their own, but may attack infants that do not match the age of their own young. Thus lactating female house mice and cavies seem to kill infants that potentially could steal milk, but only at times when they can recognize pups as not their own.

Among sciurids in which lactating females kill infants, the deaths occur before young mingle (Sherman 1981b; Hoogland 1985; Hare 1991). An exception to this is in the California ground squirrel in which most victims of infanticide by lactating females are postemergent infants (Trulio 1996). Elwood (1992) suggested that committing infanticide to prevent adoption could be expected in precocial rather than altricial species; in the former, infants are mobile and may attempt to nurse from nonrelatives. However, too few precocial rodents have been studied to evaluate this prediction. Under seminatural conditions, breeding females of precocial capybaras (*Hydrochaeris hydrochaeris*) kill pups of unfamiliar females (Da Cunha-Nogueira et al. 1999), female yellow-toothed cavies kill infants that do not match the age of their own offspring (Künkele and Hoeck 1989), and female maras (*Dolichotis patagonum*) are aggressive toward alien pups that attempt to nurse from them (Taber and Macdonald 1992a). However, infanticide by females has not been observed in the similarly precocial degu (*Octodon degus;* Ebensperger 2001b). Although some evidence exists to support the predictions of the misdirected care hypothesis, the theory has not been well developed and sufficient empirical and phylogenetic data are lacking for a thorough test of its application to rodents in general.

Hypothesis 4: Acquisition of mates

Hrdy (1977b, 1979) suggested that males might kill infants to destroy another male's offspring and cause females to return to reproductive readiness. Key predictions of this "sexual selection" hypothesis are: (1) infanticidal males should not kill offspring they have sired; (2) the elimination of offspring should shorten the interbirth period of the victimized females; and (3) infanticidal males should mate with and sire the subsequent offspring of the mother of the infant(s) that were killed (Hrdy 1979; Sommer 1994).

Sexual selection has been invoked to explain infanticide by males in several species of murid rodents (Vom Saal and Howard 1982; Huck 1984; Wolff and Cicirello 1989, 1991; Elwood 1992). There is considerable evidence from laboratory studies demonstrating the existence of mechanisms enabling males to target unrelated young and avoid killing their own offspring, including direct recognition of pups (house mouse, Paul 1986; spiny mouse, Makin and Porter 1984; deer mouse, El-Haddad et al. 1988), use of indirect cues such as association with previous sexual partners (house mouse, Huck et al. 1982; meadow vole, Webster et al. 1981), location of pups (McCarthy and Vom Saal 1986a), or inhibition of male pup killing due to recent mating and cohabitation with a female (Mongolian gerbil, Elwood 1977, 1980; house mouse, Elwood 1985, 1986, Elwood and Kennedy 1991, Palanza and Parmigiani 1991; meadow vole, Webster et al. 1981; Djungarian hamster, *Phodopus campbelli,* Gibber et al. 1984; spiny mouse, Makin and Porter 1984; McCarthy and Vom Saal 1986b; Brown 1986b; and Norway rat, Jakubowski and Terkel 1985b, Mennella and Moltz 1988).

In nature, infanticide by male white-footed mice and deer mice is typically committed by individuals who are recent immigrants. Thus they are unlikely to have sired any offspring in the area (Wolff and Cicirello 1989, 1991). In seminatural (captive) populations of house mice, infanticide is committed by territorial males outside their own territories, and by nonterritorial males that have not sired any offspring (Manning et al. 1995). Again, these male rodents kill infants they are unlikely to have sired.

The second requirement of the sexual selection hypothesis—that infanticide reduces the interbirth period of the females—is supported in murid but not sciurid rodents. Captive male collared lemmings (Mallory and Brooks 1978), meadow voles (Webster et al. 1981), house mice (Vom Saal and Howard 1982; McCarthy and Vom Saal 1986b; Coopersmith and Lenington 1996), and Norway rats (Mennella and Moltz 1988) that are introduced into the cage of an unfamiliar female and her neonates attack and kill the pups. If the infanticidal males are allowed to stay and mate with the victim's mother, they produce offspring sooner than males that do not eliminate the female's original litter (Mallory and Brooks 1978; Webster et al. 1981; Vom Saal and Howard 1982; McCarthy and Vom Saal 1986b; Mennella and Moltz 1988).

Embryonic implantation in rats, house mice, and Mongolian gerbils is delayed by lactation, and by the presence of infants (Mantalenakis and Ketchel 1966; Elwood and Ostermeyer 1984b; Mennella and Moltz 1988). As the number of suckled pups decreases, females subsequently produce larger litters (Elwood and Ostermeyer 1984b). Thus by killing pups, males not only shorten the interbirth interval but also increase the female's subsequent litter size (Elwood and Ostermeyer 1984b).

Only one study with rodents has attempted to look at subsequent mating by infanticidal males (Manning et al. 1995). In seminatural enclosures, male house mice sired the subsequent litters of victimized females after committing infanticide, which supports the sexual selection hypothesis.

The sexual selection hypothesis cannot be a general explanation of infanticide by males in sciurids and other seasonally breeding mammals. In most, but not all, (e.g., de Villiers 1986) sciurids in which infanticide by adult males has been recorded, the females become estrus only once per year and the elimination of their litters does not cause them to resume their sexual receptivity until the next breeding season (Sherman 1981b; McLean 1983; Hoogland 1985; Vestal 1991; Coulon et al. 1995; Blumstein 1997). Thus males cannot increase their opportunities to reproduce in the short term by killing a female's litter (Hiraiwa-Hasegawa 1988). Moreover, models show that a year-long lag between the death of a female's offspring and her next conception may make infanticide untenable as a male reproductive strategy (Chapman and Hausfater 1979; Hausfater 1984). Nonetheless, there is a possibility that infanticidal males of seasonally breeding rodents increase their reproduction during the following breeding season, because reproductive failure one year increases a female's chance of success in the following year (e.g., in black-tailed prairie dogs [Hoogland 1985], Richardson's ground squirrels [Michener 1978], and Alpine marmots [*Marmota marmota*, Hackländer and Arnold 1999; Coulon et al. 1995]), but not in golden marmots (*M. caudata;* Blumstein 1997).

The results from the previously mentioned studies provide strong evidence that infanticidal murid males avoid killing offspring they have sired, and that the elimination of offspring may shorten the interbirth period of the victimized females. The critical prediction that infanticidal males should mate with and sire the subsequent offspring of the mother of the infants has been scarcely examined and clearly more tests, ideally involving different species, are needed.

Counterstrategies to Infanticide

Several behavioral and physiological mechanisms have been implicated as counterstrategies to infanticide, including the direct attack of potential perpetrators (either by single individuals or by group coalitions); the avoidance of infanticidal animals; multiple mating; territoriality; or the early termination of pregnancy (Hrdy 1979; Hausfater 1984; Agrell et al. 1998; Ebensperger 1998b).

The frequency and intensity of agonistic behavior by female rodents typically increases during late gestation and lactation. Reports of greater aggression by breeding females under natural conditions exists for hoary (*Marmota caligata*) and Olympic marmots (*M. olympus*), Columbian ground squirrels, grey squirrels (*Sciurus*), red squirrels (*Tamiasciurus hudsonicus*), and yellow-pine chipmunks (*Tamias amoenus*), among sciurid rodents, wood rats, and jumping mice (*Zapus*), and among murid species (Ostermeyer 1983; Maestripieri 1992). Observations of maternal aggression among animals in large pens include Hystricognath species, such as green acouchis (*Myoprocta pratti*) and Bahaman hutias (*Geocapromys ingrahami*). One explanation for such heightened aggression is that it serves to protect offspring from infanticidal conspecifics (Svare 1977; Paul 1986; Huck 1984; Parmigiani 1986). In European wood mice (*Apodemus sylvaticus;* Wilson et al. 1993) females selectively chase and attack the conspecific gender that is most likely to kill preweaned pups. Female house mice and meadow voles are more likely to attack and direct more harmful bites toward males that are infanticidal than toward noninfanticidal and less aggressive males of the same reproductive status (Parmigiani, Sgoifo, and Mainardi 1988; Parmigiani, Brain, Mainardi, and Brunoni 1988; Elwood et al. 1990; Storey and Snow 1990).

The key expectation—that maternal aggression should result in a higher likelihood of infant survival has been harder to document. A number of laboratory studies have shown that maternal aggression reduces the likelihood of infanticide (bank voles, Ylönen and Horne 2002; deer mice and white-footed mice, Wolff 1985c; golden hamsters, Giordano et al. 1984; house mice, Maestripieri and Alleva 1990; vom Saal et al. 1995; meadow voles, Storey and Snow 1987; Norway rats, Takushi et al. 1983; Flannelly and Flannelly 1985; and woodrats, Fleming 1979). However, other studies found that females were only able to delay, but not prevent, infanticide under laboratory or seminatural conditions (collared lemming, Mallory and Brooks 1980; European wood mice, Wilson et al. 1993; house mice, Brooks and Schwarzkopf 1983; Parmigiani, Sgoifo, and Mainardi 1988; Parmigiani et al. 1989; Elwood et al. 1990; Palanza and Parmigiani 1994; Palanza et al. 1994; Manning et al. 1995;

Ebensperger 1998a; and Norway rats, Erskine et al. 1978; Mennella and Moltz 1988), even if infanticidal males are not artificially confined with the female and her pups (Ebensperger 1998a). We suspect that such a delay is probably sufficient for females to prevent infanticide under more natural conditions. However, some field studies also suggest that mothers cannot completely protect their litters from infanticide (Arctic ground squirrel, McLean 1982, 1983; Richardson's ground squirrel, Michener 1983a; and yellow-bellied marmot, Armitage et al. 1979). If this is generally so, the whole topic could set the stage for future studies that would consider these male-female aggressive interactions as a coevolutionary arms race.

A second mechanism that lactating females may employ is avoiding infanticidal males (Hrdy 1974, 1977b; Butynski 1982; Sommer 1987). However, demonstrating that females leave an area to avoid infanticidal males is a difficult task because individuals can move to a different area for other reasons, including a better food supply or better nest availability. Results from two studies support this prediction. Female Arctic ground squirrels and Alpine marmots moved their litters to new locations when their territories were taken over by foreign males, who might commit infanticide (McLean 1983; Coulon et al. 1995). In at least Alpine marmots, females successfully weaned their infants after moving them (Coulon et al. 1995). Clearly, future studies need to consider other valid explanations simultaneously as to why breeding females may change their location.

A third mechanism by which individuals may prevent infanticide is by forming coalitions that cooperate to repel infanticidal conspecifics (Hrdy 1977b). Two types of evidence provide support for this mechanism in rodents. Female house mice communally nest with other female relatives (Wilkinson and Baker 1988); and in the laboratory, females nesting in pairs are successful in attacking and repelling male and female intruders (Parmigiani 1986; Maestripieri and Rossi-Arnaud 1991). As a result, in enclosed populations, infanticide occurs in single-mother nests twice as often as in communal nests (Manning et al. 1995). Sires also may participate in the direct defense of litters (Pflanz 2002), and male-female pairs of house mice are effective in repelling intruders (Palanza et al. 1996). Whereas related female Belding's ground squirrels live in close proximity and successfully defend their litters by cooperatively chasing away conspecific intruders (Sherman 1980a), pairs of female Arctic ground squirrels are rarely successful in chasing away infanticidal males (McLean 1983).

A fourth mechanism to prevent infanticide is defending a territory such that potential intruders are kept away from vulnerable infants (Sherman 1980a, 1981b; Wolff 1993b). The pup-defense hypothesis has been invoked to explain female territoriality among rodents (Sherman 1980a, 1981b; Webster and Brooks 1981; McLean 1983; Michener 1983a; Brooks 1984; Wolff 1993b), and mammals in general (Wolff and Peterson 1998). Supporting evidence is that the intensity of female territoriality generally increases during pregnancy, peaks during early to mid lactation, and decreases after the weaning of infants (Sherman 1980a, 1981b; Ostermeyer 1983; Maestripieri 1992), and that female territoriality is more intense close to the females' nest site rather than in the periphery of their territories (Wolff et al. 1983; Murie and Harris 1994).

Further support for the hypothesis that female territoriality functions to prevent infanticide among rodents includes studies on three species that show a fit between the identity of infanticidal intruders and the target of territoriality. Thus both males and females may commit infanticide among Belding's ground squirrels (Sherman 1980a, 1981b), black-tailed prairie dogs (Hoogland 1985, 1995), and wild house mice (Soroker and Terkel 1988), and as expected, both male and female conspecifics are excluded from the territory of lactating females (Sherman 1981b; Chovnick et al. 1987; Hoogland 1995). In Arctic ground squirrels, male rather than female territoriality is suggested to prevent infanticide by other males (McLean 1983). However, a mismatch between the identity of infanticidal intruders and the target of territoriality occurs in at least five other species. Male rather than female Alpine marmots are infanticidal, but female territoriality is directed against other females rather than males (Arnold 1990a; Coulon et al. 1995). Further, although male white-footed mice (Wolff 1985b; Wolff and Cicirello 1991), deer mice (Wolff 1985b; Wolff and Cicirello 1991), meadow voles (Madison 1980b; Ebensperger et al. 2000), and European wood mice (Wolton 1985; Wilson et al. 1993) can be as infanticidal as females, they are not excluded from the territory of the females. Such discrepancies may be explained, to some extent, if the females use more than one strategy to deal with different types of individuals (i.e., territoriality against females, multiple mating against males). However, discrepancies also may occur if female territoriality serves different functions in different species.

According to the pup-defense hypothesis, and under a similar amount of intruder pressure, the risk of infanticide should increase with a decrease in territory size, or with the intensity of territorial defense. One study has assessed this prediction directly with supportive results. In Belding's squirrels, the size of a lactating female's territory is inversely correlated with the probability of losing infants to infanticide (Sherman 1981b). Further indirect evidence comes from field studies of voles in which neonate survival and juvenile recruitment decrease as density of adult females increases concomitant with an overlap in female territories (Rodd and Boonstra 1988; Schauber and Wolff 1996; Wolff et al. 2002).

More subtle ways by which individuals are suggested to prevent infanticide include mating with several males and pregnancy termination. By mating with multiple males, females may confuse paternity of their litters and "persuade" males to tolerate their young once born (Hrdy 1974, 1977b, 1979). This hypothesis has been frequently suggested as an evolved mechanism in female rodents (and other mammals) to prevent male infanticide (Wolff 1993b; Agrell et al. 1998; Wolff and Macdonald 2004). The promiscuity hypothesis is well supported by several laboratory studies documenting an inhibition of male pup killing due to recent mating with a female (Mongolian gerbil, Elwood 1977, 1980; house mouse, Elwood 1985, 1986; Elwood and Kennedy 1991; Palanza and Parmigiani 1991; meadow vole, Webster et al. 1981; Djungarian hamster, Gibber et al. 1984; spiny mouse, Makin and Porter 1984; McCarthy and Vom Saal 1986b; Brown 1986b; and Norway rat, Jakubowski and Terkel 1985b; Mennella and Moltz 1988). In addition, one study has supported the expectation that infanticidal male rodents should not kill the offspring of previous sexual partners. Male house mice that were introduced into the cage of either their previous mate, or a strange female, were more likely to kill pups in the cage of the strange female, even if it contained foster pups actually fathered by the test male (Huck et al. 1982). Nevertheless, several other studies have failed to replicate these results (Brooks and Schwarzkopf 1983; McCarthy and Vom Saal 1986b; Parmigiani 1989; Elwood and Kennedy 1991).

According to the promiscuity hypothesis, a relationship is expected between multiple mating and the risk of infanticide. Two studies have addressed such an expected relationship, one in the field and the other in the lab. Pregnant female water voles that moved their nest location into the home range of a new male mated with that male; but pregnant females that stayed within their original male's range did not exhibit additional mating (with the presumed resident male) once they were pregnant (Jeppsson 1986). In a lab study with field voles, Agrell et al. (1998) found that when males were close together females mated with both of them and nested between them; however when males were far apart, females mated with the dominant male and nested near him (Agrell et al. 1998). These two cases are suggestive that females assess the potential for infanticide and use multimale mating as a deterrent tactic. Assuming that mating activity involves costs to females (e.g., increased susceptibility to predators), we might expect that females will associate and mate preferentially with infanticidal rather than noninfanticidal males. The observation that female meadow voles and house mice did not prefer infanticidal over noninfanticidal conspecific males as social or potential mating partners is inconsistent with the female promiscuity hypothesis (Ebensperger 1998d).

Wolff and Macdonald (2004) recently provided correlative support for the promiscuity hypothesis. By using examples from across sciurid and murid rodents (and from nonrodent mammals) they found that in species in which males commit infanticide, females mate with multiple males. In contrast, they recorded that multimale mating by females is not frequent in species in which male infanticide does not occur. A further analysis of their data controlling for phylogeny (e.g., Blumstein 2000) will provide a more complete test of this hypothesis.

Male-induced pregnancy disruption (also referred to as "pregnancy block," "Bruce effect." or "abortion") was initially observed in house mice, and occurs when recently inseminated females are exposed to an unfamiliar male (or to his odor), which may prevent implantation and cause a return to estrus 4–5 days later (Bruce 1959, 1960). Among other potential functions, pregnancy disruption may prevent waste of additional investment on infants that will likely be killed by invading or strange males (Hrdy 1979; Schwagmeyer 1979; Labov 1980, 1981b; Mallory and Brooks 1980). In support of this hypothesis, dominant male house mice are more infanticidal than subordinate males (Huck et al. 1982; Elwood 1986), and female encounters with dominant males are more likely to cause pregnancy disruption than encounters with subordinate males (Huck 1982; but see Labov 1981a). Infanticidal male house mice are more likely to induce pregnancy block than noninfanticidal males, which suggests an ability of females to evaluate differences in the risk of infanticide on their litters should pregnancy not be interrupted (Huck 1984; Elwood and Kennedy 1990). In golden hamsters, females are more infanticidal than males (Marques and Valenstein 1976), and pregnancy block is caused more frequently by females than males (Huck et al. 1983; Huck 1984). Apparently, females can use odor, as well as behavioral (e.g., level of aggression) cues from conspecifics to make this discrimination (Storey 1986b; Storey and Snow 1990; de Catanzaro et al. 1995).

Only two field studies have attempted to test the pregnancy disruption hypothesis and both found no or limited support for it. De la Maza et al. (1999) experimentally exposed breeding female gray-tailed voles to treatments in which males were removed and replaced by either socially unfamiliar males or females. In response to this manipulation, the researchers found no differences in intervals between parturitions, in the frequency of pregnancies, or in juvenile recruitment. Gray-tailed voles are promiscuous (Wolff et al. 1994) and males are infanticidal (J. Wolff, unpublished) and thus should fit predictions of the pregnancy disruption hypothesis. In a similar study with a population of prairie voles in outdoor enclosures, Mahady and Wolff (2002) replaced resident males with unfamiliar males every 10 days. They reported that 7 of 33 (21%) nulliparous females did not conceive during the study, but whether this was due to pregnancy failure or disruption of pairbonding in this monogamous species is not known. Production of second litters and breeding by parous females were not affected by exposure to strange males. Certainly, more field studies are needed to test the validity of the Bruce effect or pregnancy disruption hypothesis as a counterstrategy to infanticide, but at least these two field studies with two *Microtus* species do not provide strong support that pregnancy disruption occurs regularly or is an adaptive response to exposure to strange males, at least in this taxon.

Among sciurids, most takeovers by male Alpine marmots (62%, n = 21) occur after the mating period or before the end of lactation (Hackländer and Arnold 1999). Interestingly, female breeding is reduced after these male takeovers despite clear signs of pregnancy early in the season, and females failing to reproduce right after these takeovers increase their chance of breeding in the following year (Hackländer and Arnold 1999). Nonetheless, male takeovers in other populations of Alpine marmots seem to occur mostly (75%, n = 20) when juveniles are already born (King and Allainé 2002). Taken together, these field studies provide only moderate support for the idea that pregnancy disruption is a strategy to prevent losses to infanticide. Moreover, predators and other potentially stressful factors also may cause pregnancy disruptions in female rodents (de Catanzaro and MacNiven 1992), which suggests that pregnancy disruption may indeed be part of a more general strategy to prevent the waste of energy in producing offspring likely to be lost.

Finally, socially subordinate individuals may suppress breeding as a strategy to avoid wasting energy and resources on litters that are likely to be eliminated by more dominant females within the group (Agrell et al. 1998). Such may be partially the case of subordinate females of Alpine marmots that achieve copulations and become pregnant within their social units, but only the dominant females give birth (Hackländer and Arnold 1999; King and Allainé 2002). Formal phylogenetic analyses may shed light onto the evolutionary relationships between the occurrence of within-group infanticide, social living, and breeding suppression.

Concluding Remarks

Functions of infanticide

The functional significance of infanticide in rodents is complex and cannot be explained by any one single hypothesis. Each hypothesis has its own assumptions, predictions, and tests (fig. 23.1; table 23.2). In some species individuals obtain nutritional benefits from infanticide (table 23.2). In some cases, nutritional benefits are gained by females (e.g.,

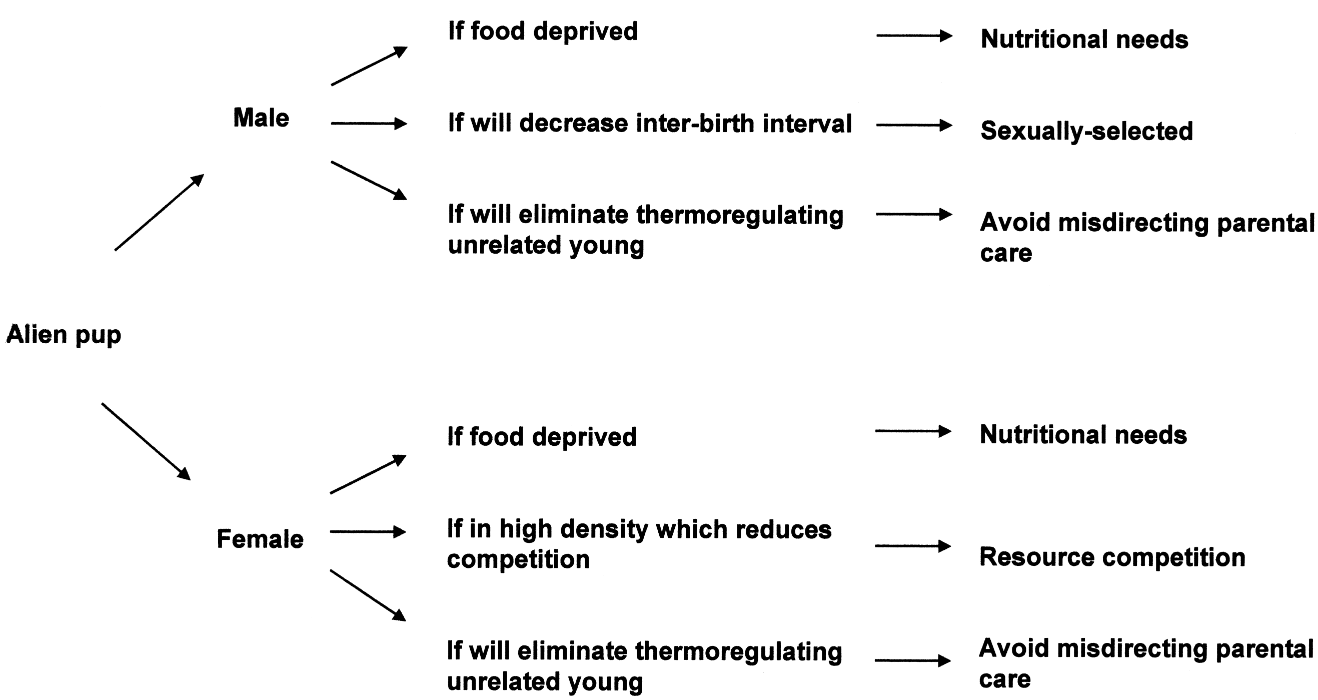

Figure 23.1 Key conditions and the subsequent benefits from infanticidal behavior reported to occur in male and female rodents. Not all benefits are equally well supported (see text).

deer mouse, the white-footed mouse, the black-tailed prairie dog, the California ground squirrel, the Columbian ground squirrel), while in other species males may gain nutritional resources (e.g., Mongolian gerbil, meadow vole, Belding's ground squirrel).

In a few species, infanticide is a mechanism of resource competition (table 23.2). The most compelling evidence supporting the idea that individuals commit infanticide to avoid misdirecting parental care to unrelated offspring comes from the infanticidal behavior of female pinnipeds, which react aggressively and bite unrelated pups that attempt to steal milk from them (e.g., Reiter et al. 1981; Bruemmer 1994). Evidence for this hypothesis among rodents is limited to associations between the breeding condition of killers and the timing of infanticide (table 23.2). Moreover, this hypothesis might explain why a female would kill a pup that wandered into her burrow, but it would not explain why a female would travel a long way from her nest burrow, enter another female's burrow, and kill young in there (as in Belding's ground squirrels and prairie dogs).

The sexual selection hypothesis in which males kill infants they have not sired as a means of reproducing with the victims' mother seems well supported in primates and African lions (reviewed in Ebensperger 1998b), but is less clear in rodents, especially sciurids. The possibility that sexually selected infanticide takes place among male rodents (particularly Muridae) is supported by laboratory studies showing that male rodents are prevented from killing their own infants (table 23.2). Nonetheless, studies that measure fitness benefits in terms of increased mating opportunities or of a reduced latency for the females to bear offspring of infanticidal males under wild or more seminatural conditions (e.g., Manning et al. 1995) are needed. Studies of sexually selected infanticide by males of seasonally breeding species also deserve further study, particularly in terms of increased chances of killers to mate with the victimized females and whether reproductive success of victimized females increases during the following breeding season.

We encourage future investigators to design studies that will simultaneously evaluate multiple functional hypotheses and their specific predictions (e.g., table 23.2). Experimental studies under natural conditions and/or those that accurately represent the social and physical environment of species are needed to discern among alternative hypotheses. Indeed, quantifying the incidence of infanticide among wild populations is a difficult task, and there are serious ethical issues with experimental studies of infanticide (Elwood 1991). However, using traps "baited" with pups (e.g., Wolff and Cicirello 1991; Ylönen et al. 1997), recording characteristic behaviors and external signs given by the perpetrators (e.g., Hoogland 1995), and potentially employing other innovative techniques while being careful to avoid pain and suffering of experimental subjects will allow future investigators to control for various social and ecological variables to test the adaptive significance of the various hypotheses for infanticide. Moreover, there is a need for future comparative studies to test the various hypotheses for the adaptive significance of infanticide.

Consequences of infanticide

Overall, the nature of the mechanisms by which parents should attempt to prevent infanticide has been controversial, and deserves further study. In particular, we believe that some important current controversies will be solved if future studies consider three major issues. First, we need information from animals whose behavior is recorded under realistic conditions of space, habitat heterogeneity, and density. This is critical to fully appreciate the meaning of any results within an evolutionary context. We acknowledge that these are difficult data to acquire in nature. Secondly, alternative hypotheses should be stated a priori, and strong inferential tests devised. The behaviors that have been suggested to be counterstrategies in rodents have other hypothesized functions as well. Multiple mating by females has many hypothesized functions (Jennions and Petrie 2000; Fedorka and Mousseau 2002). Maternal aggression could be a mechanism used by dams to assess quality of males as future mates (Parmigiani et al. 1989; Parmigiani et al. 1994). Territory defense (as opposed to defending nests and the space immediately nearby) by female rodents might be directed toward defending physical resources as well as pups (e.g., Sherman 1981b; Ostfeld 1990). Considering the great cost to females of losing their offspring, and the apparently high incidence of infanticide in natural populations, natural selection has likely favored several defensive strategies by females to protect their young in the evolutionary arms races within and between the sexes.

Summary

Nonparental infanticide, the killing of infants by conspecifics other than the parents, occurs in a variety of vertebrate and invertebrate taxa. In rodents, infanticide has been noted in the wild or under laboratory conditions in 2 species of hystricognaths and 35 species of sciurognaths. Our review supports the hypothesis that nonparental infanticide is adaptive in rodents. However, its functional significance seems complex and cannot be explained by any one single hypothesis. In some cases, nutritional benefits are gained by females, while in other species males may gain nutritional resources. In a few species, infanticide is a mechanism of re-

source competition. Evidence supporting the idea that individuals commit infanticide to avoid misdirecting parental care to unrelated offspring among rodents is rather limited. The sexual selection hypothesis in which males kill infants they have not sired as a means of reproducing with the victims' mother remains unproven in rodents; studies that measure fitness benefits in terms of increased mating opportunities or of a reduced latency for the females to bear offspring of infanticidal males under wild or more seminatural conditions are strongly needed. The nature of the mechanisms by which parents prevent infanticide has been controversial, and future studies need to consider two critical issues. First, information is needed from animals whose behavior is recorded under realistic ecological conditions. Second, alternative hypothesis should be stated a priori: the behaviors that have been suggested to be counterstrategies in rodents have other hypothesized functions as well. Overall, we encourage future investigators to design studies that will simultaneously evaluate multiple functional hypotheses and their specific predictions.

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