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The evolution of infanticide in rodents: a comparative analysis

Introduction

We simultaneously know more about the proximate causes of infanticide in rodents and less about its adaptive consequences and evolution than in any other taxon. Rodents are the largest mammalian order with over 440 genera and 2021 of the 4629 described species (Musser & Carleton 1993; Wilson & Reeder 1993). Infanticide by either or both males and females may be found in 46 species from 22 genera in 3 rodent groups (see below). A number of previous reviews illustrate the detailed understanding of proximate causation, development, and function gained by studying infanticide in rodents (Sherman 1981; Brooks 1984; Elwood & Ostermeyer 1984; Huck 1984; Labov 1984; Svare *et al.* 1984; vom Saal 1984; Labov *et al.* 1985; Trulio 1987; Elwood 1992; Elwood & Kennedy 1994; Ebensperger 1998a). In this review, I take a slightly different approach to study the evolution of infanticide in rodents. I first use the taxonomic distribution of infanticide by males and infanticide by females along with available phylogenetic evidence to parsimoniously reconstruct the evolution of infanticide by males, infanticide by females, and a potential female response to infanticide by males – male-induced pregnancy termination (Bruce effects; Bruce 1960). Then, using these evolutionary reconstructions, I test specific functional hypotheses about infanticide.

A thumbnail sketch of infanticide in rodents

Rodents provide some of the richest information about infanticide because studies of the proximate causation of infanticide are integrated with studies designed to document ultimate function. Studies of proximate factors influencing infanticide by male rodents have supported a number of key predictions associated with functional hypotheses – particularly the sexual selection hypothesis (Hrdy & Hausfater 1984). For instance, strain differences in infanticidal behavior in male mice (Svare *et al.* 1984; Perrigo *et al.* 1993) suggested that infanticide may be a heritable trait; a key requirement of the sexual selection hypothesis. Elegant studies examined how the timing of mating behavior (Elwood & Ostermeyer 1984; Elwood 1994), the process of ejaculating (Perrigo *et al.* 1990; Perrigo & vom Saal 1994), and familiarity with the mother (D'Amato 1993) influence male infanticidal behavior. These findings are generally consistent with another key prediction of the sexual selection hypothesis – males should not kill their own offspring. Another key prediction, verified in some rodents (e.g., vom Saal & Howard 1982), is that when a female loses a litter she becomes sexually receptive sooner than had she not lost a litter.

Functional hypotheses have been studied in the field, but field studies typically have not had the necessary control to study proximate mechanisms, although they suggest a variety of functions both for infanticide by males and for infanticide by females (Sherman 1981; Trulio 1987). Hoogland's (1995) review of his long-term studies of black-tailed prairie dogs (Latin names not in the text are given in Table 8.1) is notable. Infanticide in prairie dogs is a major source of pup mortality that accounts for as much as the partial or total loss of 39% of litters. Both males and females are infanticidal, but infanticide by females is more common. Lactating females kill and cannibalize unweaned offspring of close kin, as well as offspring of immigrant females living in their social group. Interestingly, while one lactating black-tailed prairie dog female is out killing another female's offspring, another individual may be killing the former's offspring! In contrast to Hoogland's finding, Sherman (1981) noted that ground squirrel females never killed offspring of their close relatives. Hoogland concluded that several hypotheses related to resource competition or exploitation might explain infanticide by female prairie dogs. Trulio (1987) also concluded that for female sciurid rodents, resource exploitation was the most common function of female infanticide.

Infanticide by males may be sexually selected but the link is not as clear as in some mice, carnivores or primates. Male prairie dogs who disperse into a new social group are often infanticidal. Prairie dogs – like their close relatives the marmots and *Spermophilus* ground squirrels – are monestrous and thus breed only once a year. In a study of golden marmots, another sciurid rodent, I found no strong support that females were more likely to wean young the year after male infanticide

(Blumstein 1997), but the effect size may be small. However, using a much larger dataset, Hackländer & Arnold (1999) found that female alpine marmots who terminated their pregnancy upon exposure to a novel male (see below), were in better physiological condition the next year and had higher reproductive success than females who did not terminate their pregnancies. Hoogland (1995) concluded that nourishment may also be a potential function of male infanticide. Surviving the winter is a major challenge for some sciurids and young of the year are particularly vulnerable (Arnold 1993). Some marmots hibernate socially and help to thermoregulate young. Thermoregulation is, however, costly, and alloparental care is directed at younger relatives (Arnold 1993). I found support for Sherman's (1981) hypothesis that males may kill offspring to avoid providing misdirected care. In the case of social golden marmots, males may kill unrelated juveniles to reduce costs of over-winter alloparental care (Blumstein 1997). This conclusion is supported by the pattern of infanticide reported in marmots: male alpine marmots – another social marmot that provides parental/alloparental care – are infanticidal (Coulon *et al.* 1995), while females but apparently not males of the less social yellow-bellied marmot are infanticidal (Armitage *et al.* 1979; Brody & Melcher 1985).

The evolution of infanticide in rodents

The interdisciplinary approach used to study infanticide has generated a considerable amount of knowledge since Hrdy (1974, 1979), Wilson (1975) and Sherman (1981) emphasized the potential adaptiveness of infanticide. A model for interdisciplinary research was proposed by Tinbergen (1963), who recognized four types of question that could be asked about any behavioral phenomena. Of them, evolutionary history has heretofore been a relatively neglected subject in infanticide research (but see Boonstra 1980; van Schaik & Kappeler 1997; van Schaik *et al.* 1999; van Schaik 2000). In this chapter I apply modern comparative methods (Harvey & Pagel 1991) to study the evolution of infanticide in rodents. Specifically, I reconstruct the ancestral states of infanticidal behaviors in rodents, and test hypotheses about correlated evolution between infanticide by males and male-induced pregnancy termination. In doing so, I hope to provide another line of evidence with which to evaluate the sexual selection hypothesis, as well as another way to study infanticide in rodents.

Comparative analyses may help to evaluate functional hypotheses. I make the following predictions about the evolutionary history of infanticide in rodents. First, if the sexual selection hypothesis was responsible for the evolution of infanticide in rodents, infanticide by males should be the ancestral condition in those clades where infanticide is found, and infanticide by females should evolve independently of infanticide by males. Second, if infanticide evolved as a generalized foraging strategy, or if resource competition and exploitation were responsible for the evolution of infanticide in rodents, then infanticide would be predicted to be seen in both sexes and to have evolved together in both sexes. Third, sexual selection also predicts that Bruce effects in females evolved in response to the evolution of infanticide by males. Thus there should be a significant association between the evolution and loss of infanticide by males and the evolution and loss of Bruce effects in females. In all cases, because infanticide reduces the fitness of those who lose young, we should see broad evidence of adaptations to counter infanticidal tendencies.

Methods and data

Some important caveats

All comparative analyses are fundamentally dependent on valid observations of the traits which they seek to study. It is extremely difficult to obtain an unbiased comparative dataset with which to study infanticide in rodents. Because most rodents are small, nocturnal and semi-fossorial, studying their behavior and observing infanticide poses a variety of problems. Direct observations of infanticide in many muroid rodents are lacking in nature. Fortunately for infanticide researchers, house mice and other common laboratory rodents commit infanticide. In contrast to the majority of rodents, sciurid rodents are diurnal, live in predictable locations and are generally easy to observe. This has made them an ideal group in which to study socioecological questions (Armitage 1981; Sherman 1981; Michener 1983; Blumstein & Armitage 1998, 1999), including infanticide.

Some sciurid researchers have directly observed infanticide and, as already discussed, infanticide may be a major cause of juvenile mortality. However, many reported cases of infanticide were not directly observed. This led to a discussion over the validity of inferring infanticide from indirect observations (Michener 1982; Sherman 1982). The fundamental problem is that infanticide generally occurs in underground nesting burrows and observations may, at best, be only indirect. In lieu of actually observing infanticide, a researcher may see an animal emerge with blood on its face and a litter known to be in the burrow subsequently never emerges (e.g., Hoogland 1995). Infanticide has also been inferred by seeing recently emerged young fleeing certain adults with the observer later finding carcasses with "escape wounds" (small bites on the back of the legs and back; e.g., Blumstein 1997), and by finding an animal in possession of a recently killed pup (Trulio 1996). To validate behavioral observations and inferences, Hoogland (1995) used a backhoe to immediately excavate burrows in which he and his research assistants strongly suspected infanticide had just occurred. He also caught and examined stomach contents from females assumed to be infanticidal. Excavations supported his behavioral observations: Hoogland found recently killed pups in an excavated burrow and found the remains of cannibalized young in the stomach of a suspected perpetrator. Thus, *contra* Michener (1982), it may be valid to use behavioral correlates as evidence of infanticide.

Defining infanticidal traits

To study the evolution of infanticide I first defined three traits and then "mapped" them (i.e., optimized them using parsimony) onto a series of rodent phylogenies. Because infanticide reflects an individual reproductive strategy (e.g., Sherman 1981), and because infanticide by males and females usually has different functions (e.g., Hrdy 1979), I examined the evolution of infanticide separately for males and females, based on reports both in the laboratory and the field (Table 8.1).

The first trait I defined was the presence of infanticide by males. I did not distinguish between observations of infanticide in the field or in captivity. Additionally, to minimize the number of infanticidal species excluded from analysis, I was rather liberal in my adoption of evidence for infanticide and included both direct observations, less direct inferences and anecdotes of pup cannibalism. I used both previous reviews of infanticide in rodents and current literature searches to generate the comparative dataset. Because we know relatively little about the behavior or ecology of most rodents, this review is necessarily incomplete.

I defined the second trait as the presence of female infanticide. Again, I did not distinguish between field and laboratory reports. Moreover, I did not distinguish between infanticide committed by the mother and infanticide committed by a female other than the mother (see Ebensperger 1998a) because this would introduce error into the comparative dataset (in many instances in the field the perpetrator's identity is unknown).

I defined the third trait as the presence of Bruce effects in female rodents. Bruce effects are hypothesized to have evolved to minimize the

Table 8.1. *Summary of reports of infanticide and Bruce effects in rodents*

Family	Subfamily	Species	Common name	Infanticide/ Bruce effects	Sources
Sciuridae	Sciurinae	*Paraxerus cepapi*	Tree squirrel	MN	de Villiers 1986
Sciuridae	Sciurinae	*Spermophilus beecheyi*	California ground squirrel	FN, MN	Trulio 1996
Sciuridae	Sciurinae	*Marmota caudata*	Golden marmot	MN	Blumstein 1997
Sciuridae	Sciurinae	*Marmota marmota*	Alpine marmot	B, MN	Perrin *et al.* 1994; Coulon *et al.* 1995; Hackländer & Arnold, 1999
Sciuridae	Sciurinae	*Marmota flaviventris*	Yellow-bellied marmot	FC, FN	Armitage *et al.* 1979; Brody & Melcher 1985
Sciuridae	Sciurinae	*Spermophilus franklinii*	Franklin's ground squirrel	MN	Sowls 1948
Sciuridae	Sciurinae	*Spermophilus tridecemlineatus*	13-lined ground squirrel	MN	Vestal 1991
Sciuridae	Sciurinae	*Spermophilus armatus*	Utah ground squirrel	FN	Burns 1968
Sciuridae	Sciurinae	*Spermophilus beldingi*	Belding's ground squirrel	FN	Sherman 1981
Sciuridae	Sciurinae	*Cynomys ludovicianus*	Black-tailed prairie dog	FN, MN	Hoogland 1995
Sciuridae	Sciurinae	*Cynomys gunnisoni*	Gunnison prairie dog	FN	Fitzgerald & Lechleitner 1974
Sciuridae	Sciurinae	*Spermophilus richardsonii*	Richardson's ground squirrel	FC, FN	Quanstrom 1968; Michener 1973
Sciuridae	Sciurinae	*Spermophilus parryii*	Arctic ground squirrel	MN	Steiner 1972; McLean 1983
Sciuridae	Sciurinae	*Spermophilus columbianus*	Columbian ground squirrel	FN, MN	Betts 1976; Balfour 1983; Dobson 1990
Sciuridae	Sciurinae	*Spermophilus townsendii*	Townsend's ground squirrel	MN	Alcorn 1940
Muridae	Arvicolinae	*Microtus pennsylvanicus*	Meadow vole	B, MC, MN	Clulow & Langford 1971; Mallory & Clulow 1977; Webster *et al.* 1981; Caley & Boutin 1985; Storey *et al.* 1994
Muridae	Arvicolinae	*Microtus montanus*	Montane vole	B	Stehn & Jannett 1981
Muridae	Arvicolinae	*Microtus townsendii*	Townsend's vole	FN	Boonstra 1978, 1980
Muridae	Arvicolinae	*Microtus canicaudus*	Gray-tailed vole	FN	Wolff & Schauber 1996
Muridae	Arvicolinae	*Microtus californicus*	California vole	B, MN	Lidicker 1979; Heske 1987
Muridae	Arvicolinae	*Microtus ochrogaster*	Prairie vole	B	Kenney *et al.* 1977; Heske & Nelson 1984
Muridae	Arvicolinae	*Microtus pinetorum*	Pine vole	B	Schadler 1981; Stehn & Jannett 1981

Table 8.1 (*cont.*)

Family	Subfamily	Species	Common name	Infanticide/ Bruce effects	Sources
Muridae	Arvicolinae	*Microtus agrestis*	Field vole	B, FN	Clulow & Clarke 1968; Milligan 1976; Myllymaki 1977; Agrell 1995
Muridae	Arvicolinae	*Microtus oeconomus*	Root vole	B	Jensen & Gustafsson 1984
Muridae	Arvicolinae	*Lemmiscus curtatus*	Sagebrush vole	No B	Stehn & Jannett 1981
Muridae	Arvicolinae	*Lasiopodomys brandti*	Brandt's vole	B, FC, MC	Stubbe & Janke 1994
Muridae	Arvicolinae	*Clethrionomys rutilus*	Northern red-backed vole		Koshkina & Korotkov 1975 cited in Brooks 1984
Muridae	Arvicolinae	*Clethrionomys gapperi*	Red-backed vole	B	Clulow *et al.* 1982
Muridae	Arvicolinae	*Clethrionomys glareolus*	Bank vole	B, FC, FN, MC, MN	Ylönen *et al.* 1997
Muridae	Arvicolinae	*Ondatra zibethicus*	Muskrat	FN	Errington 1963; Caley & Boutin 1985
Muridae	Arvicolinae	*Arvicola terrestris*	Water vole		Jeppson 1986
Muridae	Arvicolinae	*Dicrostonyx groenlandicus*	Collared lemming	B, FC, MC	Mallory & Brooks 1978, 1980
Muridae	Arvicolinae	*Lemmus lemmus*	Norwegian lemming	B, FC	Semb-Johansson *et al.* 1979; Jensen & Gustafsson 1984
Muridae	Cricetinae	*Phodopus campbelli*	Djungarian hamster	FC	Edwards *et al.* 1995
Muridae	Cricetinae	*Phodopus sungorus*	Siberian hamster	FC, MC	Gibber *et al.* 1984
Muridae	Cricetinae	*Mesocricetus auratus*	Syrian/golden hamster	No B, FC	Richards 1966; Huck 1984; Huck *et al.* 1988 reported pregnancy block induced by females, *not* males
Muridae	Sigmodontinae	*Neotoma lepida*	Desert woodrat	FC	Fleming 1979
Muridae	Sigmodontinae	*Peromyscus maniculatus*	Deer mice	B, FC, MC	Ayer & Whitsett 1980; Wolff 1985; Wolff & Cicirello 1989; Cicirello & Wolff 1990
Muridae	Sigmodontinae	*Peromyscus leucopus*	White-footed mouse	FC, FN, MC, MN	Wolff 1986; Wolff & Cicirello 1989; Cicirello & Wolff 1990
Muridae	Sigmodontinae	*Peromyscus californicus*	California mouse	FC, MC	Gubernick 1994; Gubernick *et al.* 1995

Muridae	Murinae	*Mus musculus/domesticus*	House mouse	B, FC, MC	Jakubowski & Terkel 1982; vom Saal & Howard 1982; Elwood 1986; McCarthey *et al.* 1986; Palanza *et al.* 1996
Muridae	Murinae	*Apodemus sylvaticus*	European wood mouse	FC, MC	Wilson *et al.* 1993; Montgomery *et al.* 1997
Muridae	Murinae	*Rattus norvegicus*	Norway rat	FC, MC	Jakubowski & Terkel 1985; Schultz & Lore 1993
Muridae	Murinae	*Acomys cahirinus*	Spiny mouse	MC	Makin & Porter 1984
Muridae	Gerbillinae	*Meriones unguiculatus*	Mongolian gerbil	FC, MC	Elwood 1980; Elwood & Ostermeyer 1984
Caviidae	Caviinae	*Cavia* sp.	Guinea pig		Bufon 1852, cited in Labov *et al.* 1985, but see Rood 1972
Caviidae	Caviinae	*Galea musteloides*	Cui	FC	Künkele & Hoeck 1989

Notes:

B, Bruce effect reported; No B, Bruce effect studied but not reported; FC, female infanticide observed in captivity; FN, female infanticide observed in nature; MC, male infanticide observed in captivity; MN, male infanticide observed in nature.

I did not distinguish between reports of Bruce effects in captivity or the wild. For subsequent comparative analyses, I combined reports of infanticide in the field and in captivity. I scored male infanticide (or female infanticide) present if it was reported, and absent if it was not reported when female infanticide (or male infanticide) was reported. Species for which infanticide was reported but the infanticidal sex was not reported are listed, but the sex of the infanticidal animal is not noted. Patterns of presence and absence generate hypotheses about a given trait for species with no data.

cost of losing a litter to the new infanticidal male and thus reflect a female reproductive strategy to counter male infanticide (Labov 1981; Huck 1984). Alternatively, Bruce effects may be a mechanism of female choice (Schwagmeyer 1979), and evidence of pregnancy termination induced by exposure to novel females but not males (Huck *et al.* 1988) suggest other possible functions (for a review, see Labov 1981). Most experimental tests of Bruce effects found a positive effect. I also include species tested for Bruce effects where Bruce effects were not found (Stehn & Jannett 1981; Huck *et al.* 1988) and hypothesize the pattern of Bruce effects for species in which they have not been studied.

The comparative dataset

I make several assumptions when compiling observations of infanticide. First, I assume that infanticide in the laboratory is not a pathological behavior resulting from overcrowded rearing conditions (e.g., Calhoun 1962), and that as a first approximation, patterns in the laboratory may reflect patterns of infanticide in nature (e.g., Ylönen *et al.* 1997). We have come a long way in the past 20 years, and one realization is that the laboratory offers a tremendous opportunity to study apparently adaptive mechanisms of infanticide. Second, I assume no sex bias in reports of infanticide. Thus, if infanticidal behavior for a given species is reported in one sex but not the other, then it occurs in one sex and not the other. This assumption is only as good as the reports, which at times are anecdotal. Third, I also include species where infanticide was reported but the perpetrator's sex was not recorded. In including these species I illustrate lacunae in the comparative dataset that future researchers may later fill in. Moreover, by using patterns of infanticide among close relatives and assuming parsimony (Wiley *et al.* 1991), I hypothesize the sex of infanticidal perpetrators for species where the sex(es) are not specified.

Skeptics may discount many observations of infanticide in nature and Bruce effects in captivity. Nevertheless, compiling these reports generates testable hypotheses about the evolution of infanticide. Below I use a combination of observations of infanticide and Bruce effects in nature and in captivity to study the evolution of infanticide in rodents.

Comparative analyses

I conducted a series of comparative analyses. First, I used a recent phylogenetic hypothesis of higher level rodent relationships (Carleton 1984) to determine how many times infanticide (either by males or by females) evolved in the order Rodentia. Then I examined separately the evolution of infanticide within each of the two families in which infanticide was commonly reported (sciurids and muroids).

There is no published sciurid or muroid phylogeny that includes all species of interest. For these analyses, I initially inferred phylogeny from taxonomy and modified branching patterns to reflect more detailed phylogenetic information (Black 1972; Corbet 1978; Carleton 1980; Honacki *et al.* 1982; Carleton & Musser 1984; Anderson 1985; Bonhomme *et al.* 1985; Catzeflis *et al.* 1992; DeBry 1992; Musser & Carleton 1993; Engel *et al.* 1998; Steppan *et al.* 2000; C. Conroy & J. Cook unpublished data; S. Davis unpublished data; R. S. Hoffmann, pers. comm.). I do not include species in the phylogeny for which there is no information – the vast majority of muroid species. The best available microtine rodent phylogeny is not completely resolved. To permit subsequent concentrated changes tests (Maddison & Maddison 1992, and see below), I randomly resolved three polytomies in the partial phylogeny. Doing so did not change the overall parsimonious trait reconstruction found when polytomies were not randomly resolved. Available evidence suggests that the sciurid genus *Spermophilus* is polyphyletic, explaining the location of the "genus" *Cynomys*. Future investigators interested in studying specific evolutionary hypotheses of infanticide within these taxonomic groups will certainly benefit from better-supported phylogenetic hypotheses and a more complete dataset.

Given uncertain relationships between most rodents, excluding most species for which there are no reports of infanticide or Bruce effects seems an acceptable strategy. Excluding species should not change the overall parsimonious reconstruction. However, excluding species will reduce the number of branches between species. The concentrated changes test estimates the probability of two traits evolving independently by calculating a null model that changes are randomly distributed along branches (Maddison & Maddison 1992). Excluding species may therefore bias the results of the concentrated changes test, making it less likely to detect a significant association between two traits.

The evolution of infanticide

Assuming parsimony and using MacClade 3.0 (Maddison & Maddison 1992), I first optimized infanticide on the higher-level phylogeny and then optimized each of the three traits on the partial rodent phylogenies. For all optimizations, I assumed the traits were unordered and that changes were equally likely in either direction. I did not specify an outgroup and allowed MacClade to hypothesize the ancestral condition.

Did male and female infanticide evolve together?

I used Maddison and Maddison's concentrated changes test (Maddison & Maddison 1992; see also van Schaik & Kappeler 1997) to test the hypothesis that the pattern of origins and losses of infanticide by males was associated with the pattern of origins and losses of infanticide by females in both sciurid and muroid rodents. MacClade provided an exact calculation of the probability that infanticide by males and infanticide by females was independent for sciurid rodents. There were too many independent gains and losses of infanticide by males in muroid rodents to permit an exact calculation. To estimate the probability that infanticide by males and by females was independent, I selected the 1000 sample simulation option in MacClade, and calculated the probability assuming that infanticide by females was ancestral (as suggested by the parsimonious reconstruction for muroids), and that infanticide by females was either ancestral or derived.

Did Bruce effects evolve as a counterstrategy to infanticide by males?

I tested this hypothesis by using the concentrated changes test. To estimate the probability that infanticide by males and Bruce effects by females were independent, I selected the 1000 sample simulation option in MacClade, and calculated the probability assuming that Bruce effects were ancestral, and assuming that Bruce effects were either ancestral or derived.

Results and discussion

How many times did infanticide evolve in rodents?

Available evidence suggests that infanticide evolved independently in three rodent infraorders: the Sciuromorpha, the Myomorpha (muroid rodents only), and the Caviomorpha (Figure 8.1). Despite the opportunity for bias in observing infanticide, I am aware of no reports of infanticide in other rodent groups. Future workers studying the behavior and ecology of other species would be well advised to look for evidence of infanticide; reports would greatly clarify our understanding of the evolution of infanticide. Moreover, because little is known about the independent evolution of infanticide in caviomorph rodents, future study would be particularly useful and might resolve the conflicting reports of Bufon (1852 cited in Labov *et al.* 1985) and Rood (1972). Because

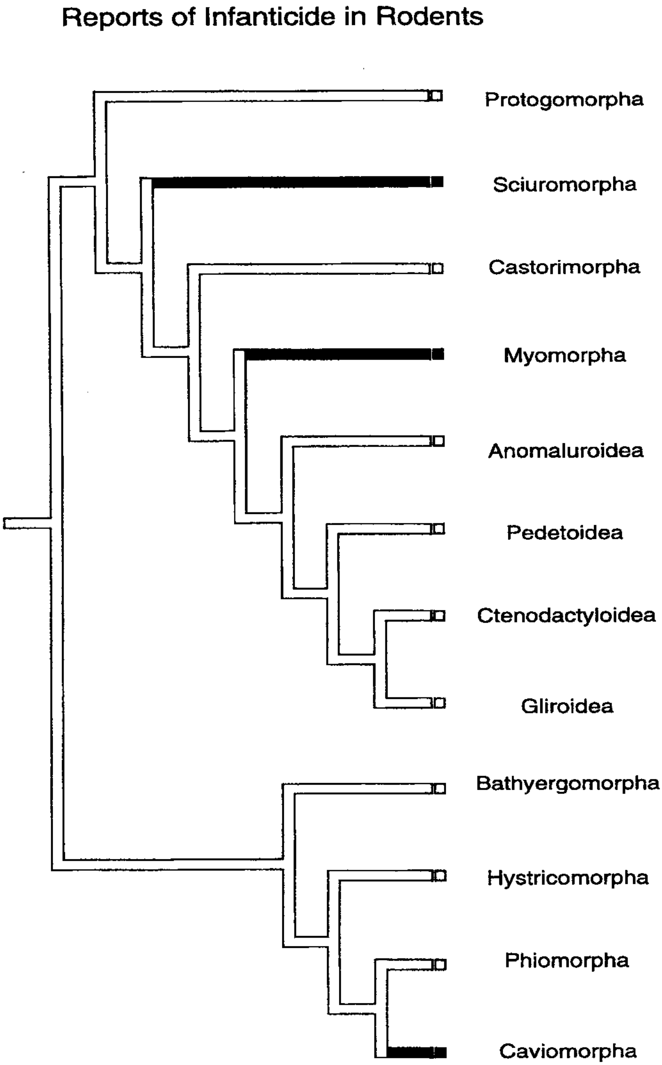

Figure 8.1. Phylogeny of rodent infraorders (-morpha suffix) and superfamilies (-oidea suffix) illustrating independent evolutionary origins of infanticide (phylogeny from Carleton 1984). Infanticide by both males and females is reported in muroid rodents of the infraorder Myomorpha and the sciurid rodents of the Sciuromorpha. There are two reports of infanticide in the Caviomorpha. Filled bars indicate any reports of infanticide in a group, empty bars indicate no reports of infanticide in a group.

infanticide evolved independently in sciuromorphs and myomorphs, and because there were numerous reports of infanticide in each group, I analyzed each separately in the analyses below.

How many times did infanticide and Bruce effects evolve in sciurids and muroids?

Available evidence suggests that infanticide evolved and was lost multiple times in sciurid (Figure 8.2) and muroid (Figure 8.3) rodents. Infanticide by males seems to be the ancestral condition in both sciurids and muroids. Infanticide by females is ancestral in muroids but not sciurids. Muroid reconstructions leave some ambiguity about the ancestral states for some species. Bruce effects were reported in only one sciurid – the alpine marmot – but a better dataset exists for Bruce effects in muroid rodents (Table 8.1). In muroids, patterns of extant Bruce effects suggest that the ability for females to terminate pregnancy after encountering a novel male is ancestral (Figure 8.3).

Did male and female infanticide evolve together?

In both sciurids and muroids, the pattern of origins and losses of infanticide by males and infanticide by females is non-random, suggesting that they evolved together. In sciurids, the concentrated changes test suggests that the number of gains and losses of infanticide by females evolved in unison with infanticide by males ($P = 0.024$ if infanticide by females was derived; $P = 0.024$ if either trait is ancestral). In muroids, the concentrated changes test suggests that the number of gains and losses of infanticide by females evolved in unison with infanticide by males ($P = 0.036$ if female infanticide is ancestral; $P = 0.032$ if either trait is ancestral). Because infanticide by males evolved with infanticide by females, it is likely that infanticide evolved as a generalized type of foraging strategy or as a means of competition or exploitation which later was adapted for different functions (e.g., sexual selection). Infanticide by non-parents in several mammalian taxa currently includes cannibalism (Ebensperger 1998a), suggesting that, for some species, infanticide is an ancestral foraging strategy.

Did Bruce effects evolve as a counterstrategy to infanticide by males?

The pattern of gains and losses of Bruce effects is random with respect to the pattern of gains and losses of infanticide by males in muroid rodents

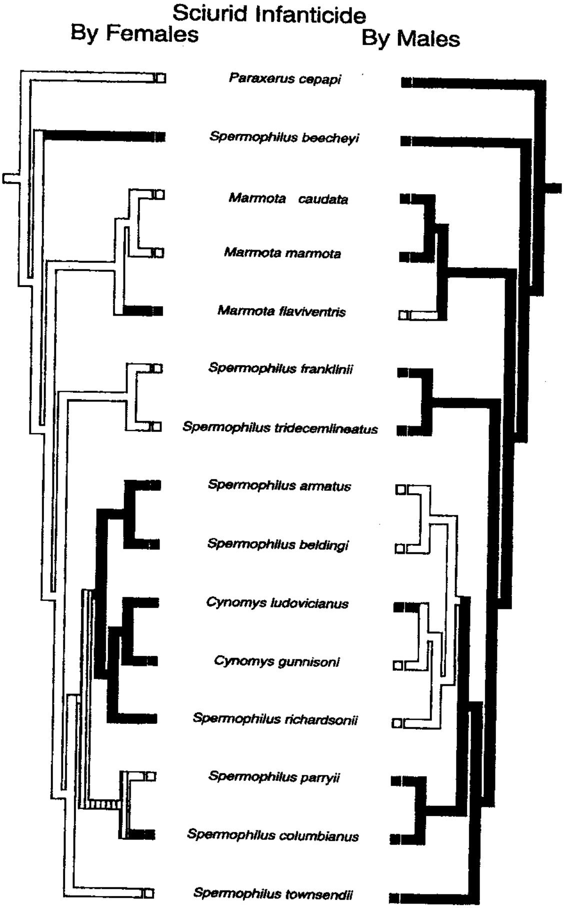

Figure 8.2. Evolutionary reconstructions of infanticide by males and by females in sciurid rodents. For this and Figure 8.3, whether or not the square next to the species name is filled indicates the presence or absence of a trait in the species; no square illustrates no data. Infanticide by males (or infanticide by females) was scored present if it was reported, and absent if it was not reported when infanticide by females (or infanticide by males) was reported. Species for which infanticide was reported but the infanticidal sex was not reported were scored as no data. Patterns of presence and absence generate hypotheses about a given trait for species with no data. A filled bar illustrates the presence of the reconstructed trait in that lineage; an empty bar indicates the absence of the reconstructed trait in the lineage. A striped bar illustrates ancestral lineages that could not be reconstructed using parsimony. Traits are optimized assuming parsimony and using MacClade 3.0 (for details, see text and Maddison & Maddison 1992).

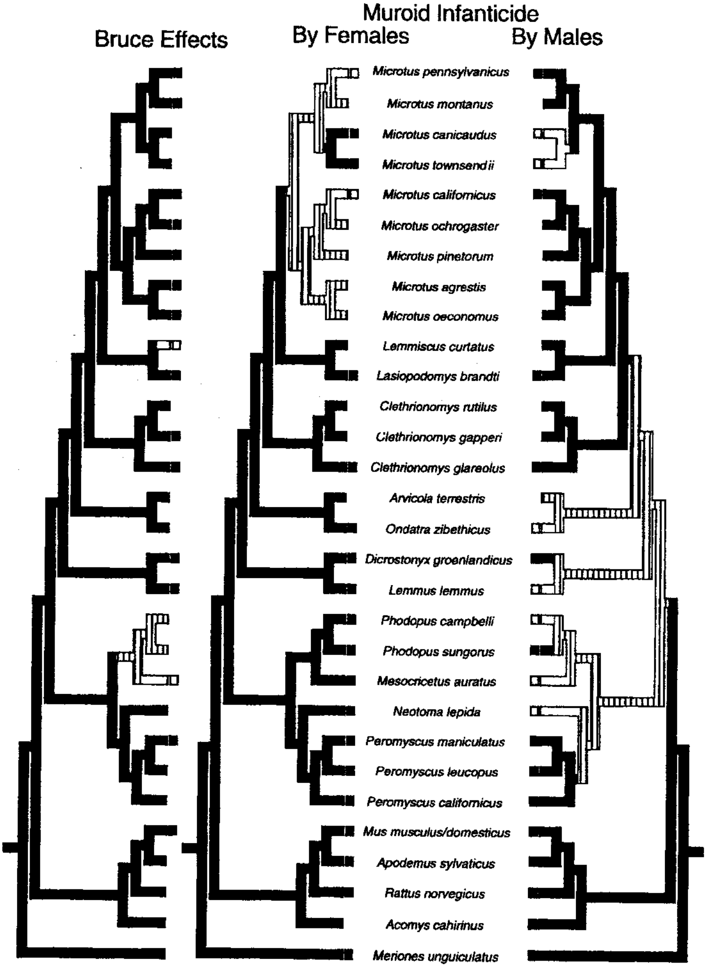

Figure 8.3. Evolutionary reconstructions of infanticide by males and by females in muroid rodents, and the evolutionary reconstruction of Bruce effects in muroid rodents. For interpretation, see legend of Figure 8.2.

($P = 0.298$ if either trait is ancestral; $P = 0.316$ if Bruce effects are considered ancestral). It is important to note that, while these data suggest that Bruce effects evolved for another unspecified purpose, they say nothing about current utility. Bruce effects may function quite well now as a strategy to minimize the costs of infanticide by males.

Bruce effects were only recently reported in alpine marmots

(Hackländer & Arnold 1999), and it is perplexing that Bruce effects are not widely reported in sciurids, particularly for those tropical species that are not monestrous. A monestrous female would have to wait at least 1 year to breed again. Rearing any young might lead to a larger pay-off to a female compared with the pay-off of resorbing or otherwise aborting her young and waiting a year to possibly mate again. It is likely, therefore, that, on average, the cost of losing a litter to a new and possibly infanticidal male is less than waiting an entire year to attempt to reproduce. The frequency of embryonic resorption in some Eurasian marmots (gray marmots (*Marmota baibacina*), Bibikov & Berendaev 1978; long-tailed/golden marmots, Davidov *et al.* 1978; Kizilov & Berendaev 1978) suggests that searching for Bruce effects and embryo abandonment more broadly might be a profitable line of research.

Other female counterstrategies

Rodent infanticide has different functions and different consequences (Labov *et al.* 1985). Agrell *et al.* (1998) argued that because females pay the greatest cost, females should evolve strategies to minimize costs associated with infanticide. Rodents illustrate several of these strategies. Multiple matings may be a strategy that a female can adopt to minimize the risk of infanticide by males by confusing paternity (Agrell *et al.* 1998) and is discussed in detail by van Noordwijk & van Schaik (Chapter 14). Mate choice may be another tactic used to counteract male infanticidal risks (Agrell *et al.* 1998). In addition to "standard" reasons given for female choice of dominant males (Andersson 1994), there are two hypothesized infanticide-avoidance benefits of mating with dominant males. First, dominant males may be more likely to kill unrelated offspring (Huck *et al.* 1988). Second, dominant males may ultimately have a longer breeding tenure than subordinate males; a female who mated with a dominant male would be less likely to have her offspring killed by a new resident male (Agrell *et al.* 1998). Female bank voles prefer mating with dominant males, a strategic decision suggested to minimize the risks of male infanticide (Horne & Ylönen 1996). While sciurid females may choose mates, there is no evidence that mate choice reduces the risks of infanticide by males.

How does infanticide influence rodent social organization?

While infanticide may be a potent selective force, there are no obvious generalizations about how infanticide by males influences rodent social organization. Perhaps this reflects the various strategies that females employ to counter infanticidal risks. More likely, this reflects the limited detailed knowledge of the socioecology of most rodents.

Some species in which males are infanticidal live in year-round complex social groups (e.g., some marmots, prairie dogs), but there is no obvious relationship between sociality and infanticide by males as reported in primates (van Schaik & Kappeler 1997). Infanticide by males is reported in some of the most socially complex (Blumstein & Armitage 1998) sciurid rodents as well as in some of the least complex sciurid rodents. For muroid rodents, infanticide by males and Bruce effects are found among both cooperative breeders with singular breeding (i.e., only a single adult female breeds in a social group) and plural breeding (i.e., more than a single adult female breeds in a social group; Table 8.1 in Solomon & Getz 1997) as well as in less social species.

Viewed more broadly as a mechanism of reproductive suppression (Wasser & Barash 1983), infanticide by females seems to be a key element of a package of traits that make marmots, and perhaps some microtines, cooperative breeders (Solomon & Getz 1997; Blumstein & Armitage 1999). Reproduction in subordinate females is often suppressed in multifemale rodent societies (Solomon & Getz 1997; Wolff 1997; Blumstein & Armitage 1999). Infanticide by females would be predicted if and when a subordinate successfully reproduces. While infanticide by females is not reported in the more social golden or alpine marmots, subdominant females in groups without new male migrants are sometimes seen with swollen nipples (indicating lactation) yet litters are never seen to emerge above ground (D.T.B., pers. obs.). Agrell *et al.* (1998) predicted that infanticide by females leads to more complex mechanisms of reproductive suppression. While this is likely, data do not currently exist to test this hypothesis.

Does the risk of infanticide by females lead to female territoriality?

Female microtine rodents are more aggressive and territorial than males, especially during the breeding season (e.g., Webster & Brooks 1981; Wolff 1985). Sherman (1981) and particularly Wolff (1985, 1993, 1997) suggested that female territoriality in altricial mammals evolved in response to the risk of infanticide by females: the pup defense hypothesis (see also Digby, Chapter 17). Females of infanticidal species must defend their altricial young; one way to do this would be by defending a home territory from other females.

If infanticide was a key factor leading to the evolution of territorial behavior, infanticide by females should be an ancestral trait in territorial species that produce altricial young. In support of Wolff's hypothesis, infanticide by females seems to be an ancestral trait in muroid rodents. However, infanticide by females is a derived trait in sciurid rodents – all of whom are territorial (suggesting that female territoriality is ancestral in this lineage) and produce altricial young. Ebensperger (1998a), citing several conflicting case studies, suggested that the pattern of rodent territorial behavior did not support the pup defense hypothesis. To what extent female territorial behavior in other taxa can be explained solely by infanticide is a question that will be better answered when we have more data on the distribution of infanticide by females.

Conclusions

The evolution of infanticide in rodents

Rodents offer the unique opportunity for richly interdisciplinary studies of infanticide. Comparative studies suggest that infanticide has evolved at least three times in rodents. Detailed studies of the muroid and sciurid rodents did not support the hypothesis that infanticide in rodents evolved as a mechanism of sexual selection. Specifically, infanticide by males and by females was the ancestral state in muroid rodents, and there was no evidence that infanticide by males was associated with the evolution of male-induced pregnancy termination.

Independent evolution within the rodents provides at least three data points for understanding the larger question of how the interplay of ecological factors, developmental constraints, and physiological constraints influence the evolution of infanticide. Comparative analyses, like these, can be applied to other taxa and will eventually provide a better understanding of the evolution of infanticide.

Unfortunately, we simply need better data for future comparative studies. I believe much can be learned by systematically applying the standardized and humane techniques developed for laboratory studies (e.g., Elwood 1991) to species not typically maintained in the laboratory. For instance, it should be possible to introduce new males systematically to females and look for evidence of both Bruce effects (e.g., Stehn & Jannett 1981) and infanticidal aggression for many of the species in which infanticide is suspected from field observations. A considerable amount of information can also be learned by conducting captive (e.g., Stubbe &

Janke 1994) or semi-natural field cage experiments (e.g., Lidicker 1979) with new species.

Infanticidal sciurid rodents offer a particularly good opportunity for studies of social strategies that females use to avoid or reduce male infanticide. Female sciurids illustrate several potential anti-infanticide strategies such as multiple mating, and female territoriality, although it remains to be seen whether Bruce effects are common. In many ways, however, sciurid sociality is much less complex (Blumstein & Armitage 1997, 1998) than that found in many primates. Thus we may not expect to find highly complex relationships evolving to reduce the likelihood of male infanticide.

Conservation implications of rodent infanticide

Understanding the distribution and function of infanticide in nature has profound implications for the conservation and management of infanticidal species. For instance, human hunts of male brown bears (*Ursus arctos*) increase the likelihood of sexually selected infanticide by increasing the frequency with which females with vulnerable young interact with novel males (Swenson *et al.* 1997). Planned hunts as a means of population control may therefore have a greater than anticipated effect on bear population size. More generally, sexually selected infanticide influences a population's effective population size, and thus affects the likelihood that a population will persist over time (Anthony & Blumstein 2000). Wildlife managers must be aware of the pattern of infanticide in nature.

The Vancouver Island marmot (*Marmota vancouverensis*) is one of the rarest mammals in the world (Bryant & Janz 1996). Current management plans include captive breeding to build up population sizes followed by the reintroduction of captively bred animals to their formally occupied range (A. Bryant, pers. comm.). Even though there is no evidence of infanticide in Vancouver Island marmots, knowledge of infanticide in other marmots should influence planned rearing patterns. For instance, novel males should not be introduced to breeding females, and breeding females should probably be separated from other breeding females. Moreover, reintroducing or translocating males into pre-existing social groups may be risky. Managers and breeders of other rodent species can modify their behavior on the basis of knowledge of the distribution of infanticide.

We have made much progress in understanding infanticide since Hrdy (1974, 1979), Wilson (1975) and Sherman (1981) emphasized adaptive socioecological hypotheses for infanticide. The development of a comparative data base will surely make the future decades as exciting as the past decades for enriching our understanding of the causes and consequences of infanticide in nature.

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