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On the evolutionary stability of female infanticide

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Abstract Territoriality among female rodents may have evolved as an adaptation to intraspecific competition for resources or, alternatively, to defend pups against infanticide. In order to evaluate the latter, we analyse the conditions that allow an infanticidal strategy to invade a population of non-infanticidal females, and the circumstances under which infanticide may become an evolutionarily stable strategy (ESS). Our game theoretical analyses indicate that infanticide has to be associated with some direct (cannibalism) or indirect (reduced competition) resource benefits in order to invade a non-infanticidal population. We also expect that females will primarily kill litters of nearby neighbors, thereby removing the closest competitors while keeping costs at a low level. However, once established in a population, infanticide may be an ESS, even if females do not gain any resource benefits. This is theoretically possible if a female through infanticide can reduce the possibility that other, potentially infanticidal, females establish and/or stay close to her nest. While behavioral data indicate that these special circumstances sometimes occur, they may be too specific to apply generally to small rodents. Therefore, we expect that the evolutionary stability of infanticide often requires resource benefits, and that female infanticide in small rodents may, in fact, be a consequence rather than a cause of territoriality.

Key words Evolutionary stability · Female behavior · Game theory · Infanticide · Small rodents

Introduction

Two major hypotheses have been proposed to explain female territoriality in small rodents. First, territoriality may have evolved as an adaptation to intraspecific exploitative competition, if females are defending resources required for successful reproduction (Ostfeld 1985, 1990). Second, female territoriality may have evolved as a counter-adaptation to infanticide, if females are defending their nests against conspecifics that may kill their litters (Wolff 1985a, 1993). Although infanticide in small rodent species is seldom directly observed in the field (Cockburn 1988), available data suggest that female infanticide has a significant impact on juvenile survival (Boonstra 1978; Caley and Boutin 1985; Hoo-gland 1985; see also review by Brooks 1984) and is, therefore, expected to have evolutionary consequences for female spacing behavior.

However, one may suspect that, in order to evolve and to be evolutionarily stable, infanticide has to provide some resource benefits to infanticidal females. For instance, females may gain nutritionally from the consumption of killed pups (Elwood 1992). They may improve access to food or nest sites (Sherman 1981; Wolff and Cicirello 1989), or eliminate potential competitors for themselves or their offspring (Hrady and Hausfater 1984). Such benefits may allow infanticidal females and their descendants to invade a population of non-infanticidal females. However, it is not entirely obvious what may happen when most females are infanticidal. Infanticide will be evolutionarily stable only if non-infanticidal females cannot invade the population of infanticidal females. In other words, infanticidal females should have some advantage over non-infanticidal females. Can infanticide be an evolutionarily stable

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strategy (ESS) in such situations without providing any resource benefits?

Below we analyse, following Glass et al. (1985), evolutionary stability of female infanticide in a simple game-theoretical context. We suggest that, in general, resource benefits will improve the evolutionary stability of female infanticide and that such benefits, together with the energetic costs of the behavior, determine the optimal level of infanticide. Still, infanticide may sometimes be evolutionarily stable without any resource benefits. In our model, this is possible if the litter of an infanticidal female has a better chance to escape from being exposed to infanticide, as compared to the litter of a non-infanticidal female, when both females are associated with an infanticidal neighbor. After establishing these theoretical results, we discuss how well these circumstances may fit female behavior in small rodents.

A model of female infanticide

Strategies and payoffs

We assume two females, the player and her neighbor (the opponent), that are independently allowed to choose a pure strategy, either N or I (Fig. 1). N denotes the non-infanticidal strategy and I the infanticidal strategy (Table 1).

If both females adopt N, the player gains fitness W_0 . If the player is N and the neighbor is I, the player's litter will be exposed to infanticide with a risk s_0 of being attacked. When exposed to infanticide, the player will lose her entire litter and the consequent decrement in her fitness is d ($0 < d \leq W_0$). The frequency of I in the population is p and females associate randomly. Thus, the fitness of the non-infanticidal strategy will be

$$W_N = W_0 - s_0dp, \tag{1a}$$

which decreases, for $0 < s_0 \leq 1$, as the infanticidal type becomes more common. The risk-level s_0 is here supposed to indicate how effectively the non-infanticidal type is defending her nest. If $s_0 = 1$, nest defense is

		Neighbor	
		N	I
Player	N	W_0	$W_0 - s_0d$
	I	$W_0 - c + s_0b$	$W_0 - c + s_1b - s_2d$

Fig. 1 Payoffs to the player when she and the neighbor can choose two pure strategies, either to behave infanticidally (I) or not (N). For definitions of variables, see Table 1

minimal and the infanticidal neighbor will always succeed in killing the player's litter. In contrast, $s_0 = 0$ corresponds to maximal nest defense as the neighbor never succeeds in killing the player's litter.

If the player adopts I, she will invest time and energy into infanticide at a cost to her reproductive effort. This cost is denoted by c , which is assumed to be independent of the neighbor's strategy, and thus does not include changes in the level of nest defense of the infanticidal female. If the neighbor is N, the infanticidal player succeeds with probability s_0 in killing the neighbor's litter and by these means gains a fitness increment, b (Fig. 1). We consider b as a benefit that the female gains in reproductive success, either when her young experience reduced exploitative competition due to the death of the neighbor's litter (Hrdy and Hausfater 1984), or when she acquires more resources that she can invest in the young (Sherman 1981; Wolff and Cicirello 1989; Elwood 1992). Thus $b = 0$ would imply the absence of intraspecific competition, or that the young establish territories far from the mother's home range. In order to be conservative, we suppose that $0 \leq b < d$, i.e. the benefits gained due to the death of the neighbor's litter are always smaller than the fitness decrement due to the death of the player's own litter. If the neighbor has also adopted I, the infanticidal player gains b with probability s_1 or loses her litter with probability s_2 (Fig. 1). The fitness of the infanticidal strategy will thus be

$$W_I = W_0 - c + s_0b(1 - p) + (s_1b - s_2d)p, \tag{1b}$$

which decreases with p if $s_1b < s_0b + s_2d$.

Attack probabilities and nest defense

We show below that the evolutionary stability of the strategies depends, not only on the magnitude of the proposed fitness costs (c and d) and benefits (b), but also on the probabilities (s_0, s_1 , and s_2) that the player will be subject to the given fitness effects. In order to interpret the general results of the model, we have to introduce some rules that determine s_1 and s_2 when both females are infanticidal.

First, we define s as the probability that the neighbor succeeds in locating and killing the litter of an infanticidal female. If $s_0 < s$, infanticidal females will have weaker nest defense than non-infanticidal females. This situation will arise if infanticidal females spend time searching for and destroying other females' litters, and therefore leave their nests without protection more often than do non-infanticidal ones (e.g. Hoogland 1994, 1995). On the other hand, if $s_0 = s$, non-infanticidal and infanticidal females will have an equal level of nest defense. For instance, both types of females may remain close to their own nests during the time when young are vulnerable, and infanticidal females attack only those neighboring nests encountered within their own territories or home ranges.

Table 1 Basic mathematical terms and their definitions

Term	Definition
b	Fitness increment due to improved resource availability as a consequence of the death of the neighbor's litter (resource benefit)
c	Fitness decrement due to the energetic costs of infanticidal behavior
d	Fitness decrement due to the death of the female's own litter
I	Infanticidal strategy that attempts to kill the neighbor's litter
i_m	Level of infanticide for a rare mutant
i_p	Level of infanticide in a population of females which, with the probability i_p , will attack in order to kill the neighbor's litter
N	Non-infanticidal strategy that never kills
p	The frequency of the infanticidal strategy (I) in a population
s	Probability that an attack is successful against the nest of an infanticidal female
s_0	Probability that a non-infanticidal female loses her litter due to infanticide by the I-neighbor
s_1	Probability that an infanticidal female gains resource benefit, b
s_2	Probability that an infanticidal female will be subject to fitness loss, d
W_0	Baseline fitness
W_I	Fitness of infanticidal strategy (I)
W_N	Fitness of non-infanticidal strategy (N)
$W(i_m, i_p)$	Fitness of a rare mutant with infanticide level of i_m living in a population where other females attack with probability i_p

Second, when two infanticidal females are interacting with each other, we consider only a single attack-defense cycle where each female attacks at most once. The player is the first one to attack in half of the cases, while the neighbor will attack first in the other half. Because females thus have no earlier experience of each other, they have not adjusted their behavior to the neighbor's previous responses. Learning during repeated sequences of attack and defense would provide a more detailed, and presumably more realistic, picture of female behavior. A single attack-defense cycle, however, suffices as a simplified model of infanticidal interactions as far as learning can be neglected. This model generates two possibilities:

Case 1: *the neighbor will not attack if she loses her litter*. The infanticidal player will gain b with probability $(1/2)s$ if she attacks first and the neighbor fails in defending her nest, or with probability $(1/2)(1-s)s$ if the neighbor attacks first and the player attacks after defending successfully her own nest. Consequently, she will gain b with probability $s_1 = (1/2)s + (1/2)(1-s)s = (1/2)s(2-s)$. The infanticidal female will lose her litter and experience the fitness loss d with probability $(1/2)(1-s)s$ if she attacks first and the neighbor defends her nest successfully after which she will attack the player's nest who fails to defend her nest, or with probability $(1/2)s$ if the neighbor attacks first and the player fails to defend her nest. Therefore, the player experiences d with probability $s_2 = (1/2)s(2-s)$.

Case 2: *the neighbor attacks even if she loses her litter*. In this case, the order of attack is irrelevant so that $s_1 = s(1-s)$, i.e. the player will gain b if her attack against the neighbor's nest is successful while the neighbor's attack on the player's nest is not. On the other hand, the infanticidal female will lose her litter and experience the fitness loss d , whenever she fails to defend her nest regardless of who might attack first. Thus simply $s_2 = s$.

Consequently, $s_0 \leq s_2$ in case 2 as far as $s_0 \leq s$. In other words, the nests of infanticidal females are less well or at best equally well protected as compared to the nests of non-infanticidal females. In contrast, this need not always be true in case 1. If nest defense is inefficient enough, $s_2 < s_0$ is possible so that the nests of infanticidal females are less often exposed to infanticide than are the nests of non-infanticidal females (case 1a). The special requirement for this is that infanticidal females can eliminate attacks by the neighbor by killing the neighbor's litter. This is not possible in case 2 where infanticidal females will attack even when they have lost their litter, and in case 1 if efficient nest defense prevents other females from killing one's young (case 1b).

Below, we separately analyse the evolutionary stability of infanticide for "Defense gain by infanticide" (case 1a) and "No defense gain by infanticide" (cases 1b and 2). The energetic costs (c) of infanticide are, for simplicity, assumed to be the same in all cases.

Evolutionary stability

The functions presented in Eqs. 1a,b imply the following conditions for non-infanticidal (N) and infanticidal (I) strategies to be evolutionarily stable. N will be an ESS if, for $p \rightarrow 0$, $W_N > W_I$ or

$$s_0b < c. \quad (2a)$$

When this condition holds, the infanticidal strategy cannot invade a population dominated by non-infanticidal females. If, on the other hand, the inequality (2a) does not hold, the infanticidal strategy can invade. The result is important because it suggests that, in order to evolve in the first place, the infanticidal strategy has to be associated with some benefits ($b > 0$) if this behavior has any energetic costs ($c > 0$). The area in the c - b parameter space where the invasion of the infanticidal

Table 2 Resource benefits and evolutionary stability of infanticide in three cases which differ with respect to probabilities s_0 , s_1 , and s_2 defined in Table 1. Cases 1b and 2 yield qualitatively similar results, while case 1a allows infanticide to be an evolutionarily stable strategy (ESS) for $b = 0$

Response to the loss of litter	Defense gain by infanticide	Resource benefits (b) by infanticide
1. Female will not attack; $s_1 = s_2$	a. Yes; $s_2 < s_0$ b. No; $s_0 \leq s_2$	Infanticide can be an ESS for both $b = 0$ and $0 < b$ $0 < b$ is necessary for infanticide to be an ESS
2. Female will attack; $s_1 = s_2$	No; $s_0 \leq s_2$	$0 < b$ is necessary for infanticide to be an ESS

strategy is possible will decrease accordingly when s_0 approaches zero. This is so because, for small s_0 , the infanticidal females have to overcome better nest defense of non-infanticidal females and, therefore, less often succeed in killing the neighbor's litter.

The infanticidal strategy, I, will be an ESS if, for $p \rightarrow 1$, $W_I > W_N$ or

$$c < s_1 b + (s_0 - s_2)d. \tag{2a}$$

If this condition holds, the non-infanticidal strategy cannot invade a population dominated by infanticidal females. These conditions allow two qualitatively different scenarios depending on s_0 relative to s_2 (Table 2).

Defense gain by infanticide ($s_2 < s_0$; case 1a, Table 2) allows three possible outcomes: (a) N is a pure ESS, (b) I is a pure ESS, and (c) both strategies are ESSs (Fig. 2A). The last situation is especially interesting because it can be obtained even for $b \rightarrow 0$, provided that $0 < c < (s_0 - s_2)d$. In other words, once established in a population, infanticide can be an ESS even though it may yield no resource benefit for the infanticidal female. The reason why this is possible is that the non-infanticidal females are ineffective in their nest defense against infanticidal neighbors. The infanticidal females, on the other hand, may reduce the risk that their litters will be exposed to infanticide, if they themselves succeed in killing their neighbor's litters first and if, as a consequence, the neighbor loses her motivation to commit infanticide.

No defense gain by infanticide ($s_0 \leq s_2$; cases 1b and 2, Table 2) also leads to three possibilities: (a) N is a pure

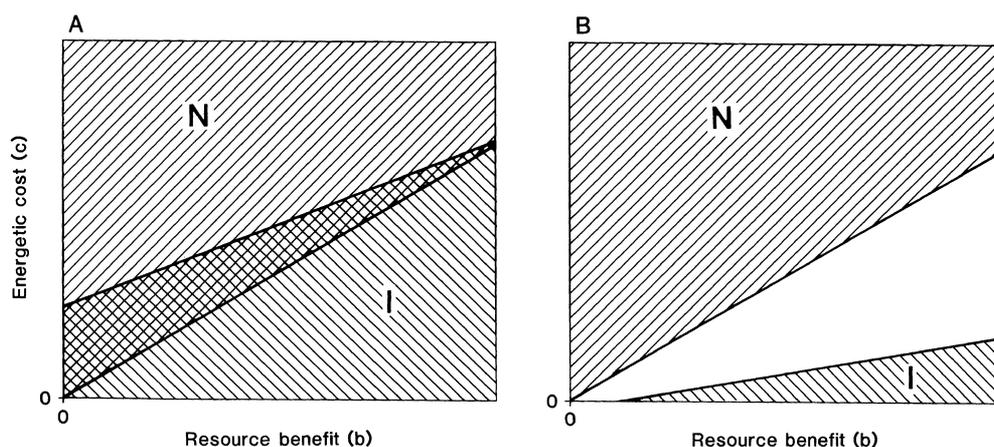
ESS, (b) I is a pure ESS, and (c) neither N nor I is an ESS (Fig. 2B). In the last situation, both types coexist in the population since both of them can invade but they cannot outcompete each other. As compared to case 1a (Fig. 2A), the evolutionary stability of infanticide has to meet stronger conditions when females cannot make any defense gain. Consequently, infanticide is an ESS over a much smaller parameter area, and it has to be associated with benefits in competition (i.e. $b > 0$ in Fig. 2B). Moreover, the costs of infanticide have to be relatively low, otherwise non-infanticidal females can invade, which will result either in stable polymorphism or infanticidal females being outcompeted by non-infanticidal females.

Optimal level of infanticide

Above, we have studied the evolutionary stability of infanticide when females have only two available choices, either to behave infanticidally or not. However, our analysis does not so far tell us anything about the level of infanticide that might be evolutionarily stable in a given situation. Therefore, we formulate case 2 (Table 2) in terms of continuous strategies by allowing females to choose a level of infanticide between 0 and 1. This level, say i , can be assumed to indicate attack rate or probability that a female will attack in order to kill the neighbor's litter.

For this purpose, we assume a population of females with a level of infanticide i_p and a rare mutant with a

Fig. 2A,B The parameter areas where the infanticidal (I) and the non-infanticidal (N) strategies are pure ESSs for two cases: **A** defense gain by infanticide ($s_2 < s_0$), and **B** no defense gain by infanticide ($s_0 \leq s_2$). In **A**, both strategies are ESSs in the *cross-hatched area*. In **B** there will be stable polymorphism when neither strategy is an ESS (*blank area*). Both figures assume $0 \leq b < d$



level of infanticide i_m . Probability that an attack is successful (s) is constant irrespective of i_p and i_m . Then we can express the fitness of the mutant as

$$W(i_m, i_p) = W_0 - c(i_m, i_p) - di_p s + bi_m s [1 - i_p + i_p(1 - s)], \quad (3)$$

where $c(i_m, i_p)$ indicates the energetic costs of infanticide for the mutant. d is the fitness decrement for the mutant due to the loss of her litter. This will happen with probability $i_p s$, i.e. that the neighbor attacks and the mutant fails to defend her nest. b is the gain that the mutant gets if the neighbor loses her litter. This requires that the mutant attacks and that the neighbor fails to defend her nest, as given by probability $i_m s$. It further requires that the mutant female does not lose her litter. This will occur with probability $1 - i_p$ (the neighbor does not attack) or $i_p(1 - s)$ (the neighbor attacks but the mutant defends her nest successfully).

The necessary condition of an ESS (e.g. Eshel 1983; Taylor 1989), simplifies in our case to

$$bs(1 - i_p s) = c' \quad (4)$$

where the partial derivative $c' = \partial c / \partial i_m$ is evaluated for $i_m = i_p$, and it indicates marginal costs or the rate of increase of energetic costs with increasing level of infanticide. The optimal level of infanticide satisfying Eq. 4 depends on the marginal costs, c' , and on the expected benefits of an attempted attack (i.e. the expression on the left hand side). Eq. 4 generates two possibilities for obtaining an increase in the optimal level of infanticide. First, it is advantageous to increase the level of infanticide if the potential resource benefits (b) are high (Fig. 3A). This will be so, for instance, if the neighbor's nest is close to the female's own nest. The same effects result from increasing the intensity of competition for food or space. Under severe resource limitation, the benefits should be higher and, accordingly, one could expect a higher propensity for infanticide. Second, it will be advantageous to increase the level of infanticide if the costs increase less steeply with an increase in the level of infanticide (Fig. 3B). Again this

could be true for the closest neighboring nests. Therefore, it may not be advantageous to devote time and energy to locate and attack nests far from the female's own nest.

The optimal level of infanticide also depends on s . This is most easily seen by assuming a linear cost function, say $c = ai_m$, with a constant marginal cost $c' = a$. Then Eq. 4 yields the following optimal level of infanticide

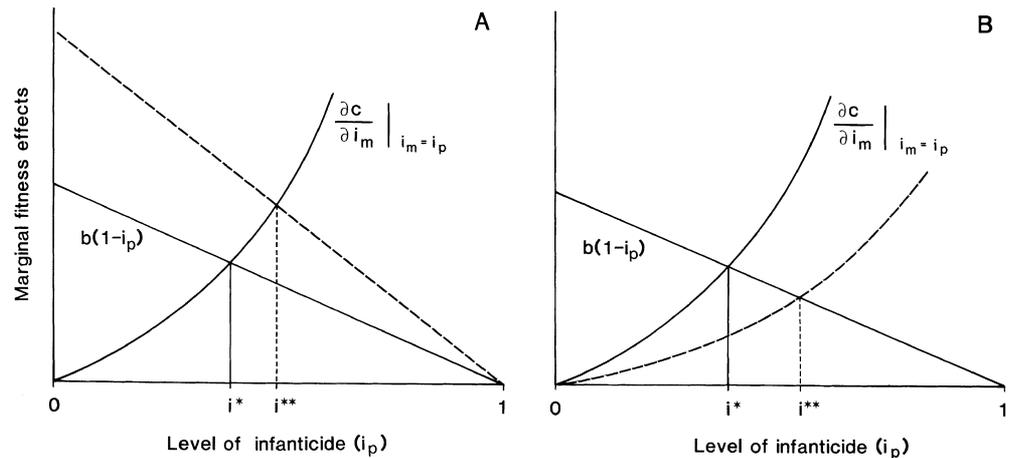
$$i^* = (1/s)(1 - a/b), \quad (5)$$

which is shown in Fig. 4 for selected values of a/b . For $b \leq a$, infanticide will not be advantageous and thus $i^* = 0$ for any s . But for $0 \leq a < b$, infanticide can evolve provided that s is high enough. For given values of a and b , the highest level of infanticide is obtained for $s = 2a/b$. If s is low, the attacks will seldom be successful and, hence, the female should not invest too much energy in locating the neighboring nests. When s is high, the female will more often succeed in her attacks. However, at the same time, there is an increasing risk that the neighbor succeeds in killing the female's own litter. Therefore, the optimal level of infanticide tends to decrease for very high values of s , i.e. $s > 2a/b$ (Fig. 4).

Discussion

The evolutionary stability of female infanticide is most easily obtained if infanticide is associated with resource benefits either directly through cannibalism or indirectly through reduced competition. This conclusion holds irrespective of whether infanticide is associated with defense gains or not, although the requirement is more definite if no defense gain can be achieved (Table 2). Moreover, some benefit of infanticidal behavior is needed otherwise infanticidal females cannot invade a population of non-infanticidal females. Consequently, there are good reasons to believe that the evolution of female infanticide is associated with direct or indirect resource benefits.

Fig. 3A, B The optimal level of infanticide according to Eq. 4 with minimal nest defense ($s = 1$). The optimal level of infanticide is obtained when the increasing curve (marginal cost) and the decreasing line (expected benefit of an attempted attack) intersect each other. **A** Optimal strategy for low (i^*) and high (i^{**}) resource benefits, and **B** for steep (i^*) and less steep (i^{**}) increase in the energetic costs with the level of infanticide



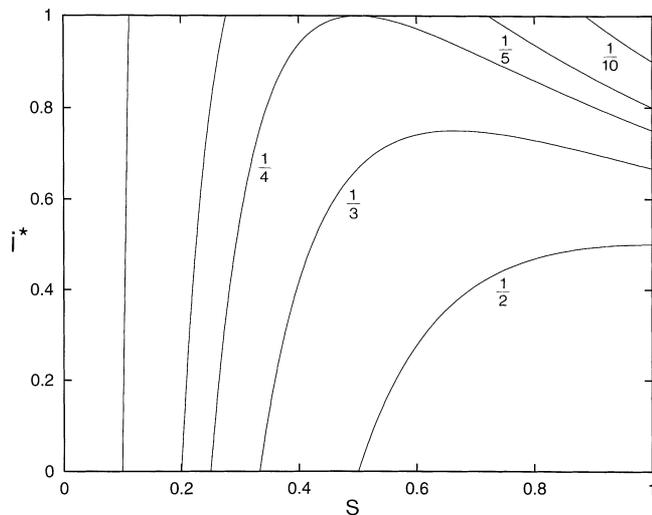


Fig. 4 The optimal level of infanticide (i^*) as a function of the probability that an attack will be successful (s). The curves are calculated from Eq. 5 for the ratios between marginal costs and resource benefits (a/b) which are shown below the curves

However, once established, infanticide may be evolutionarily stable without any substantial resource benefits. In our model, this is possible when the risk of losing the litter is higher for non-infanticidal than for infanticidal females (case 1a, Table 2; $b = 0$, Fig. 2A). In order to obtain such a situation infanticidal females must easily find the nests of non-infanticidal females (i.e. a low cost for infanticidal behavior) and defense of litters against infanticide must be limited. Although female aggression may be efficient in deterring infanticidal conspecifics when they are confronted (Wolff 1985b), these assumptions might work in some small rodents. First, since the role of olfactory cues play a central role in social interactions (see e.g. Wolff 1985c), the nest of a neighboring female is probably located quickly. In social species, visual cues can also make nests with live juveniles easy to locate (Hoogland 1995). Second, most microtine rodents inhabit cryptic habitats (Getz 1985) where the possibility of detecting an intruder is low (cf. Ims 1988; Boonstra et al. 1992; Nelson 1994).

A further requirement of case 1a is that somehow an infanticidal female should be able to reduce the risk that her own litter will be killed by infanticidal neighbors. In principle, this might work if the female manages to kill the neighbor's litter and if this reduces the risk for the female's own litter. We envisage two possibilities for this:

1. *Only reproductive females are infanticidal and they have only one breeding opportunity each season.* However, if the female starts a new litter more or less directly after losing the previous one, this mechanism would hardly work. Small rodents often produce consecutive litters, e.g. all microtine species (Seabloom 1985). Furthermore, the predisposition to female infanticidal behavior in many small rodents is

most pronounced during pregnancy and among non-reproducing females, whereas it is in general less common after parturition and during lactation (e.g. Elwood 1980; Elwood and Ostermeyer 1984; Cicirello and Wolff 1990; Soroker and Terkel 1988; but see Parmigiani et al. 1994). Consequently, if a female kills the neighbor's young, this could even result in an increased risk of infanticide for her own litter. This might happen if the neighbor's losing her young increases her disposition to infanticide or if she shows more movement activity than a lactating female. However, there are also contradictory examples. In California ground squirrels (*Spermophilus beecheyi*), only females that were themselves mothers killed other females' pups (Trulio 1996). Accordingly, female Belding's ground squirrels (*S. beldingi*) fail to become sexually receptive after losing their offspring (Sherman 1981). In black-tailed prairie dogs (*Cynomys ludovicianus*), lactating females kill offspring of close kin (Hoogland 1985). Recently, Hoogland (1994) suggested that one reason for this behavior may be that an infanticidal female thereby reduces the probability that her own young will be killed. He considers killing in this context as a secondary advantage that might explain the evolutionary maintenance of killing, but that cannot easily account for the evolutionary origin of infanticide (Hoogland 1995).

2. *Females move away after having failed to breed at one place.* This is a reasonable strategy for avoiding future infanticide. If the female loses her litter, there will be a high risk that the replacement litter will also be exposed to infanticide. Thus it might be beneficial to seek a new nest site with non-infanticidal neighbors. This possibility receives support from studies where females have been shown to abandon nests when their litters have been destroyed by infanticidal individuals (Sherman 1981; Wolff and Cicirello 1989). Vole females disturbed at their nest site commonly move their young away to establish elsewhere (J. Agrell, unpublished work). In some cases, infanticidal females have been observed to take over the nests of the females whose young they have killed (Errington 1963; Balfour 1983; Waterman 1984).

Nevertheless, if these special circumstances do not exist, some resource benefit is required for the evolutionary stability of infanticide. Then, it is reasonable to assume that a female will get the highest benefit from the removal of the nests of the closest competitors. As a consequence, the energetic balance between benefits and costs is highest for attacks in the vicinity of the female's own nest, while it may not be profitable to seek and attack nests farther away (Fig. 3). So far only a few studies have investigated this, but available data indicate that the behavior of female rodents is remarkably similar to our suggestion. In an experimental study on white-footed mice (*Peromyscus maniculatus*), resident females were found only to kill young if these were confronted within the borders of their own home ranges (Wolff and

Cicirello 1989), with 90% of all resident females being infanticidal within their home range (Wolff and Cicirello 1991). Also, in California ground squirrels 50% of the killings were directed towards the nearest litter of non-relatives (Trulio 1996), and, with few exceptions, prairie dog mothers victimize only nearby burrows in the home clan territory (Hoogland 1995). The non-overlapping female home ranges observed in many small rodent species (reviewed by Ostfeld 1985; Madison 1985; Cockburn 1988) also suggest that females usually do not engage in raids into other females' home ranges.

To conclude, infanticidal behavior among small rodent females is likely to have evolved because females killing neighboring females' young gained some resource benefits. If the benefits originate from reduced competition over food or nest sites, it would be more natural to consider infanticide as a consequence rather than a cause of female territoriality. That is, originally territoriality as such could have evolved as a resource defense strategy, and infanticide could have evolved later in this context.

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