

Infanticide in the bank vole (*Clethrionomys glareolus*): occurrence and the effect of familiarity on female infanticide

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We studied infanticide in the bank vole (*Clethrionomys glareolus*), in a species whose social organization is characterized by strict female territoriality during the breeding season. One possible origin of female territoriality could be to protect the nest site and pups from potentially infanticidal conspecifics. However, direct evidence of the occurrence of infanticide, and thus of its possible role in territorial behaviour of the bank vole females, is totally lacking. Observations in the laboratory, but also in the field and small enclosures yielded a proportion of 30% or more of infanticidal cases of both females and males intruding a strange nest. If an individual of either sex was infanticidal it killed all the pups in the nest. In 36 trials in eight 25-m² enclosures we tested the occurrence of infanticidal behaviour in voles from three female categories: mutually familiar females with neighbouring “territories” and mutually unfamiliar “stranger” females either breeding or non-breeding. In “stranger” females the proportion of infanticidal individuals was 25% in non-breeding and 42% in breeding ones. Mutual familiarity between neighbours decreased the frequency of infanticide significantly to only 6%. In a control group of adult non-familiar males the proportion of infanticide individuals was 67%. Thus, both sexual selection (males) and resource competitions (females) infanticide was observed for the first time in the bank vole or in general in *Clethrionomys* spp. Territoriality in the bank vole may function to deter potentially infanticide intruders from entering the nesting area and killing pups. It might be that in a breeding system of philopatric females, mutual familiarity between neighbouring females would decrease the frequency of infanticide. This would be reflected in higher survival of young in a breeding population of philopatric females with a high degree of kinship and/or familiarity.

1. Introduction

Killing of conspecific pups or juveniles has been discussed in a wide range of mammalian taxa, including a number of rodent species (for reviews see Hausfater & Hrdy 1984, vom Saal 1984, Agrell 1998). In many species this phenomenon accounts for high mortality of juveniles (e.g. up to 50% in a colony breeding black-tailed prairie dogs, *Cynomys ludovicianus* — Hoogland 1985). Infanticide initially was considered a result of reproductive competition in males as the most striking observations of pup-killing by strange males came from large predators like lions (Bertram 1975, Natoli 1990) and from primates (Chapman & Hausfater 1979, Hausfater *et al.* 1982). However, infanticide subsequently has been reported as a rather wide-spread reproductive strategy — considered to be adaptive in both males and females (Labov *et al.* 1985, Wolff 1989, Cicirello & Wolff 1990, for review see Agrell 1998).

Hrdy (1979) proposed five hypotheses for the occurrence and evolution of infanticide, of which two, resource competition and sexual selection, have been most often studied. Infanticide by males would increase their mating opportunities by shortening the time to the next ovulation in the female whose pups have been killed. Female infanticide, too, can be considered a reproductive strategy if it gives the infanticidal individual access to a new territory or to enlargement of the old one (Sherman 1981). In rodents, most cases of infanticide behaviour can be attributed to benefits either in terms of resources or mating opportunities, although exploitation as nutrition also has been reported (Hrdy 1979).

The bank vole (*Clethrionomys glareolus*) is a common rodent of boreal and central European forests. The social system in the bank vole is characterized by strict female territoriality during the breeding season (Bujalska 1973, Ylönen *et al.* 1988). Female territoriality may be based on food competition (e.g. Ostfeld 1985) or active defense of pups and nest sites against infanticidal intruders (Wolff 1993). In the bank vole, occupation of own territory is a prerequisite for maturation and breeding (Bujalska 1973) and the ability to have a large territory may be associated with increased reproductive success (Mappes *et al.* 1995). Behaviour of bank vole females towards conspecific females is characterized by a rather low level of

severe aggressiveness during a random encounter in a female's home range but fierce attacks in direct vicinity of nest with pups (H. Ylönen, unpubl.). Further, along the breeding cycle from the non-breeding state through pregnancy to lactation, the relative proportion of attacks against an intruder increases significantly (Rozenfeld & Denoel 1994, Koskela *et al.* 1997). Nothing is known of the occurrence of direct aggression of adult bank voles against juveniles or on infanticide on conspecific pups.

We monitored occurrence of infanticide in the bank vole in the field and in the laboratory colony. Further, we studied experimentally infanticide in different groups of the bank vole: in breeding and non-breeding females and in males which had not mated recently. We tested the effect of familiarity between neighbouring breeding females on the possible infanticide behaviour when having the possibility to intrude each others' territory. If a female already has a territory, the fitness gain in trying to exclude the neighbouring female by killing its pups should be rather low compared with an unsettled intruder female who needs to establish a territory in order to breed. It has been shown that mutual familiarity between individual voles decreases aggressiveness between them (Ferkin 1988). Obviously territory neighbours can get mutually familiar by means of direct contacts and olfactory cues (Viitala & Hoffmeyer 1985) but whether this has an effect on the occurrence of infanticide is unknown. Further, we studied if in bank voles, as in other rodent species studied in this respect, non-mated males would be the group most prone to commit infanticide (Cicirello & Wolff 1990).

2. Methods

2.1. Occurrence of infanticide

2.1.1. Study site and field observations

The study was conducted at the Konnevesi Research Station of the University of Jyväskylä, in Central Finland, during the summers of 1995 and 1996. To study the occurrence of infanticide in free-living bank vole populations we used three one-hectare field grids, where the populations were monitored by livetrapping throughout the summer. The habitat of all grids was mixed spruce forest with about 30% deciduous trees, a favoured habitat of the bank vole (e.g.

Ylönen *et al.* 1988). All individuals on the grids had been marked during the trapping periods preceding the infanticide trials.

Occurrence of infanticide was monitored with wooden nest boxes, placed in frequently visited trapping points of the grids after a recent livetrapping period for determining vole movements. Each nest box of $25 \times 25 \times 15$ cm was provided with two Ugglan livetraps, which served as entrance and exit holes of the nest box (see Wolff & Cicirello 1989). The entrance trap was the original trap from the permanent trapping grid and thus familiar for the local voles around the trapping point. In total, 25 trials were conducted, of which 21 were successful. However, five times already-captured individuals were caught for the second time. A single pup from the laboratory colony was placed late in the evening into the nest box in a nest made of cotton thread. The exit trap of the nest box was closed. Next morning the exit trap was checked and if there was a vole inside, its identity, sex and sexual status were determined. The condition of the pup in the nest box was checked and in non-infanticide cases the pup was returned to her mother.

2.1.2. Laboratory trials

In the laboratory we tested the frequency of infanticide in 36 trials with individuals in breeding condition (H. Ylönen & T. Horne unpubl.). The trials were made in a dark room using an arena of 50×50 -cm bottom area and 12-cm height, with attached entrance and exit tubes of $40 \times 10 \times 7$ cm in two diagonal corners of the arena. A nest box of $12 \times 12 \times 12$ cm made of wiremesh and filled with thread was placed in one corner between the entrance and exit openings. The nest was provided with two entrance/exit tubes of 7-cm length, also made of wiremesh. The whole arena was covered with a Plexiglas roof and infrared sensitive video equipment attached above the roof. Infanticide behaviour was monitored in the next room on the video monitor.

One pup of 2–3 days' age from the laboratory stock was placed into the nest and covered with thread and an adult target individual was placed inside an Uggland life trap into the entrance tube. After five minutes' acclimatization time, the one-way gate to the arena was opened. Each tested individual was allowed to enter the arena and the nest with a single unguarded pup. Its behaviour was observed from the video screen and after maximally five minutes' observation the exit gate was opened and the vole had the possibility to leave the arena. After that it was captured in the exit trap. The condition of the pup was determined after the trial and when uninjured was returned to the mother (H. Ylönen & T. Horne unpubl.).

2.1.3. Enclosure trials on the effect of female familiarity on infanticide

To test the frequency of infanticide in more natural conditions than in the laboratory we used eight 25-m² outdoor

enclosures. Each 5 × 5-m enclosure had a metal fence of 0.5 metres above and under the ground. Vegetation in the enclosures was old field vegetation with several grasses *Poa-ceae* sp., *Phleum pratense*, *Filipendula ulmaria*, *Urtica dioica*, *Epilobium angustifolium*, *Geranium* sp. and saplings of *Salix* sp. and *Rubus idaeus*. Each enclosure had in its centre a similar wooden nest box as used in our field grid observations. When we wanted to capture the vole present in the enclosure, we closed the exit trap and within a few hours it had passed through the nest and was found in the exit trap. Each nest box was provided with wood shavings and dry hay as nest material. Nest box and traps were covered with a plastic container of 40×50 cm to protect them from rain. One feeder, made from a 1-litre plastic bottle, and containing commercial mouse pellets (Labfor®), was placed in two diagonally opposite corners of the enclosure. The feeders were protected from rain with a wooden roof of 30×30 cm. Sunflower seeds were provided at one fence of the enclosure (see next paragraph) and potatoes and cabbage at the nest box.

The eight enclosures formed four pairs which were connected pairwise with an opening of 1.20 m in length and 5 cm in height, situated on the ground level at the joint fence of the enclosures. This pair of enclosures simulated neighbouring core areas of female home ranges and the opening formed the joint border between the two territories. The opening was covered with wire mesh, which allowed olfactory and tactile contacts between the pair of voles. The opening was further covered on both enclosure sides with a wooden plate which formed a tunnel of 1.5 m in length and 10 cm height on both sides of the wire mesh. In the tunnel we offered the neighbouring voles sunflower seeds. Feeding in the tunnel promoted vole movements beside the fence and thus promoted contacts between neighbouring females. In later experiments, the wire mesh was removed to let the two females freely move in both "territories".

All females used in the experiment were either wild-born, or laboratory-born first descendants of wild-born females. All males used were kept in the laboratory for at least two months before the study. In total, 55 females and 13 males, were used in the experiments.

Females, who became the territory owners, were paired with mature males in the laboratory and the males were removed from the females' cages after pregnancy was evident. After approximately 10 days' pregnancy, females were moved to the enclosures and released in the nest boxes. Nest exit holes were closed for one hour to allow females to familiarize themselves with the nest. Females easily accepted the nest box as a nest site. Females were weighed daily until delivery.

During the first sets of experiments, we introduced the females into the neighbouring enclosures at about the same phase of pregnancy. We conducted the infanticide experiments during days 2–6 after the birth of the young. During the experiment, we removed the mother from her enclosure and let the focal vole enter the enclosure. In the first trials we left the entire litter in the nest box. However, after we

documented three cases of infanticidal behaviour, in which all pups were killed, we left only one or two of the young in the nest box in subsequent trials. The remaining pups were kept in a special nest made of hay and cotton wool during the experiment. Pups were released together with their mother back to their original nest immediately after the experiment.

The following combinations were tested:

1. Mutually familiar breeding neighbours with own pups having access to neighbour's nest with pups (two different experimental combinations)
2. Unfamiliar breeding females having access to the nest with strange pups
3. Unfamiliar non-breeding females entering the nest area with strange pups.

Additionally, as a "control" only one category of males was tested, the most prone cohort to commit infanticide, that of adult non-breeding males (Wolff & Cicirello 1989).

Each pair of two connected enclosures simulated a pair of mutually familiar neighbouring females. Unfamiliar breeding females were living in the same-sized enclosures but they had no connection to the female whose nest/litter was used in the trial. Unfamiliar and non-breeding females were kept three–four days before being used in the experiments in similar enclosures to the breeding ones. Before that they lived in the same laboratory stock as the breeding ones but they were not paired to males before the experiments. Each female unfamiliar to the target female was captured in the enclosure and released in the experimental enclosure.

Each trial was regarded as successful when the focal vole had gone through the nest box and was found in the exit trap of the nest box or inside the nest box (c.f. Wolff & Cicirello 1989). The exit traps and the condition of the pups were examined 15 minutes from the beginning of the experiment and after that every hour. If the focal vole did not enter the nest box, the trial was stopped after five hours. This, however, was very exceptional. Each animal in the

Table 1. Proportion of infanticide observed in the bank vole (*Clethrionomys glareolus*): percentage of animals having killed an unguarded pup in the nestbox when visiting it either in the field, in the laboratory or in small enclosures. (The number of observations is given in parentheses.)

	Females	Males
In the field	37% (8)	37% (8)
In the laboratory	33% (22)	28% (14)
In small enclosures	33% (24)*	67% (12)*

* The female value in small enclosures does not include the group of mutually familiar females. The male group consists of only adult non-breeding individuals. See the text.

groups of voles unfamiliar to the nest owner was used only once in the experiment. In the neighbour combination trial, each female was tested separately against the litter of her neighbour. We observed the following variables of the voles' behaviour: average time until voles had entered the nest box (if the nest box could not be checked every hour the case was excluded), pups killed or not, location of bites in killed pups, pups eaten or not.

3. Results

3.1. Occurrence of infanticide

From the small sample size of 16, 37.5% of both females and males were found to be infanticidal in the field population (Table 1). All the individuals were in breeding condition, females either lactating or pregnant, males with scrotal testes. It seemed that infanticidal females were heavier than the non-infanticide ones ($W_{\text{infa}} = 33.7 \pm 5.3$ g, $W_{\text{non}} = 23.8 \pm 6.6$ g, $U = 14.5$, two-tailed $p = 0.036$, in males $W_{\text{infa}} = 29.8 \pm 3.1$ g, $W_{\text{non}} = 24.8 \pm 3.6$ g, $U = 13.0$, two-tailed $p = 0.142$).

In the laboratory trials, the order of magnitude of infanticide occurrence was the same as in the field: in females 33.3%, in males 28.6% (Table 1). In the laboratory, too, the infanticidal females seemed to be heavier than the non-infanticidal ones ($W_{\text{infa}} = 19.8 \pm 1.8$ g, $W_{\text{non}} = 16.9 \pm 3.0$ g, $U = 77.5$, $p = 0.030$; in males $W_{\text{infa}} = 25.9 \pm 8.0$ g, $W_{\text{non}} = 24.9 \pm 5.6$ g, $U = 20.5$, $p = 0.528$, both two-tailed).

In the small enclosure experiments, the frequency of female infanticide was the same as in the field and in the laboratory, with 33% infanticidal individuals, when the familiarized females were excluded. From the only tested male category, non-breeding adult males, 67% were infanticidal (Fig. 1). Neither in female weights between infanticidal and non-infanticidal individuals ($W_{\text{infa}} = 26.3 \pm 3.9$ g, $W_{\text{non}} = 24.7 \pm 4.4$ g, $U = 51.0$, two-tailed $p = 0.664$) nor in male weights ($W_{\text{infa}} = 22.6 \pm 2.6$ g, $W_{\text{non}} = 23.4 \pm 2.6$ g, $U = 18.5$, two-tailed $p = 0.720$) were any differences found.

3.2. Effect of territory neighbourhood on female infanticide

Nine females out of 42 (21.4%) individuals which entered the nest box with the pups, were infanti-

cidal. When infanticide occurred, without exception, all pups in the nest box were killed. Forty-two percent of unfamiliar breeding females ($n = 12$) and 25% of unfamiliar non-breeders ($n = 12$) were infanticidal, whereas only one (6%) of familiar neighbouring females ($n = 18$) were infanticidal (Fig. 1, difference between familiar and non-familiar breeding females, Fisher's exact Test, $p = 0.026$).

There was no difference in the frequency of infanticide in unfamiliar females, regardless of whether the female was breeding or not (Fisher's exact, $p = 0.667$). In the unfamiliar, non-breeding voles, there was a slight tendency that females would commit less infanticide than males (Fisher's exact Test, $p = 0.0995$).

The breeding status of a female seemed to affect its motivation to enter a strange nest. Both neighbouring and strange females with litters were found in the exit trap within one hour (Mean = 1.1 h, range 0.25–2.0 in the familiar females, $N = 4$; 1.3 h, range 1.0–2.5 in the unfamiliar ones, $N = 8$). The pooled average entering time of breeding females was significantly shorter than the entering time of non-breeding ones (Mean = 2.9 h, range 1.2–6.5, $N = 9$, Mann-Whitney $U = 96.0$, $p = 0.003$). Males of the enclosure experiments entered the nest in 2.1 h on average (range 0.5–2.5, $N = 11$).

In total, 40 pups were killed during the enclosure experiments. Almost all of the pups were killed by one or a few bites in the head (in females 91%, in males 100%), especially in the mouth region. Only a single intruding female ate any part of the pups, and two males ate one pup each of the two in the nest during that trial. Thus, the idea of infanticide committed for nutritional gains (Hrdy 1979, cf. Agrell *et al.* 1998) was not supported.

4. Discussion

4.1. Occurrence of infanticide

Infanticide has been shown to cause considerable mortality in field populations of some mammalian species (e.g. Hoogland 1985, 1995). In the present study, when infanticide occurred in bank voles (*Clethrionomys glareolus*) all the pups in

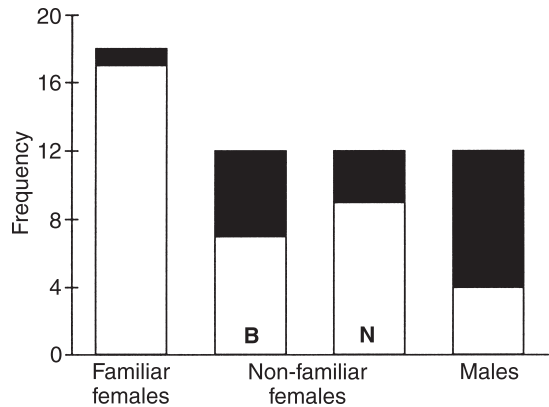


Fig. 1. Occurrence of infanticide in different test groups of bank voles in small-enclosure experiments: in breeding familiar neighbouring females, in non-familiar breeding females (B) and in non-familiar, non-breeding adult females (N) and in non-breeding adult males. The proportion of infanticidal individuals is shaded.

the nest were lost. This is a substantial cost, especially for short-lived animals, such as most rodents. Also, infanticidal behaviour was observed in about one third of the individuals in the field population and in laboratory trials, and in all tested groups of both sexes in the enclosure experiments. In a laboratory study with white-footed mice (*Peromyscus leucopus*), Cicirello and Wolff (1990) observed that approximately 50% of wild-caught mice committed infanticide regardless of whether they had been paired or kept isolated with no possibility of mating. In a field study with the same species, 100% of male mice committed infanticide (Wolff & Cicirello 1989). Also in the present study infanticide committed by unfamiliar non-mated males was high (67% infanticidal cases). These high frequencies probably result from so far unnatural situations that the mother of the pups was kept absent from the vicinity of the nest during the trials (H. Ylönen & T. Horne unpubl.). The mother's presence seems to provide an effective protection from intruding conspecifics (Wolff 1985, Xia & Millar 1988, Wilson *et al.* 1993). In the field, however, the existence of even low proportions of infanticidal traits among the different population cohorts could pose a considerable risk for the pups when a female leaves the nest unprotected, such as during foraging or for mating during post-partum oestrus (Horne & Ylönen 1996).

No data are available concerning infanticidal behaviour or the role of infanticide in the juvenile mortality of the bank vole. Also in other species it has been shown that infanticide occurs mainly before pups emerge from the nest, i.e. when vole pups are less than ten days old. In the case of the prairie dog, Hoogland (1995) suggested that the reason for this could be that the marauding female can be sure not to kill her own pups (see also Cicirello & Wolff 1990).

It seemed from the field and laboratory data that the infanticidal individuals are among the heaviest in the population (laboratory stock). This is plausible from theoretical considerations: especially heavy breeding females should be able to gain space/resources when eliminating other females' pups (see Hoogland 1995).

4.2. Effect of mutual familiarity between females on infanticide

The bank vole exhibits social system involving a high degree of philopatry (Bujalska 1973, Ylönen *et al.* 1988). During low and moderate densities, daughters of the first-born cohort fill the vacant space around the natal territory (Ylönen *et al.* 1995). When populations are high and there is no space to breed around the natal area, the risks of leaving the natal territory might be high (Wolff 1995) and young individuals might remain sexually immature in their mother's home range. In both cases, females are likely to be surrounded by breeding kin. If breeding in close proximity to relatives brings advantages in terms of survival (Wolff 1985, Mappes *et al.* 1995), philopatry of daughters in the bank vole could have evolved through kin selection and dispersal of sons to avoid inbreeding (Wolff 1992).

Because all the females used in the present study were unrelated to each other, the study indicates that familiarity *per se* is sufficient to decrease frequency of infanticidal acts against young of neighbouring females. However, its evolutionary origin could be kin selection. In an experiment on the impact of kinship and familiarity on population growth and survival of young, Ylönen *et al.* (1990) and Mappes *et al.* (1995) found a higher growth rate in kin populations. They suggested that the reason was because of a "lower

level of aggression between kin individuals", but no direct observations on causes of juvenile mortality could be made. If infanticide is a reproductive strategy, killing related pups should not increase an infanticidal individual's inclusive fitness, with the exception of some colonially breeding species (Hoogland 1985). It has also been shown that familiarization between non-kin microtines has the same effect of decreasing aggression as in a case where the individuals would be close kin (e.g. Ferkin 1988, Ylönen *et al.* 1993).

4.3. Infanticide and social structure of populations

In field populations of bank voles, we have observed relatively low rates of mortality among the young compared with the high frequencies of infanticide reported herein. Thus, there must exist mechanisms to control for such high rates of infanticide as observed in other experimental studies, too (Cicirello & Wolff 1985, 1990). Philopatry of daughters, maintenance of kin-clusters and territoriality towards unrelated females could act as a counter adaptation to female infanticide (Agréll *et al.* 1998). That territory ownership of a female is essential for the survival of her young was indirectly evidenced during other experiments where, during spring breeding, we brought females from field populations at the end of the pregnancy to the laboratory to give birth (J. Eccard & H. Ylönen, unpubl.). When returning them back to their home ranges after delivery, the loss of pups due to infanticide was strong — as probably another female had meanwhile taken over the vacant territory.

In the present study, too, the frequency of infanticide by non-mated unfamiliar males was the highest of all tested cohorts (see also Wolff & Cicirello 1989, Palanza & Parmigiani 1991). We don't know anything about the infanticidal behaviour of mated resident males (c.f. Elwood & Ostermeyer 1984). However, the evidence presented by Cicirello and Wolff (1990) on the inhibitive impact of mating on male infanticide may be valid in the bank vole, too. In conclusion, female territoriality would function against infanticide committed by strange females, and kinship or mutual familiarity would decrease infanticide between

neighbouring females. The role of male hierarchy and a probable promiscuous mating pattern (cf. Agrell *et al.* 1998) in females needs still to be studied in the bank vole.

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