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Tapio Mappes

Breeding Tactics and
Reproductive Success
in the Bank Vole

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1995

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ABSTRACT

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The aim of this thesis was to study what kinds of breeding tactics bank vole *Clethrionomys glareolus* females will adopt in relation to the particular ecological environments where they live. We also studied how successful the adopted tactics were and what were the main mechanisms which determined the success. The determinants of optimal litter size were studied by manipulating litter size. Nursing different sized litters affected the success of the present reproduction, only. Increased litter size did not cause survival or fecundity costs for breeding females. Further, home range size seemed to determine the initial litter size of females, but the females did not compensate for the enlarged demand of effort by changing their space use. This may indicate that litter size is regulated by space competition of territorial females in the saturated breeding populations. Territorial behaviour was examined in relation to female reproductive state. Home range overlap decreased and territory size increased from non-pregnancy to nursing, though home range size did not change. Attacks against intruder females increased and amicable behaviour decreased as the time for delivery got closer. The territorial behaviour also seemed to correlate positively with home range and territory size of females. These results indicate that competition for space is most intensive in the late part of breeding, especially during nursing. The effects of kinship on spacing behaviour, breeding success and survival were studied with experimental populations established by related (R) and unrelated females (UR). The R populations grew twice as fast as the UR ones. The breeding success of UR females decreased with distance to the nearest neighbour. The home ranges of UR females overlapped less and were smaller if they were situated close to each other. Further, juveniles seemed to avoid territories of adult females and their survival declined with dispersal distance from the natal territory in the UR populations. These results indicate that space competition is more intense among UR females decreasing their reproductive success. Infanticide towards UR nestlings and juveniles is one possible mechanism causing lower recruitment of young in this study. In an experiment where predation risk and the density of voles were manipulated, under high predation risk both old and young females suppressed breeding, while density did not affect overall breeding. Both risk factors appeared to increase litter sizes. In risky environments females seemed to choose between two opposite tactics: They suppressed breeding, which may increase their own survival to the next breeding or they continued to breed in spite of expected higher survival costs. Females seemed to compensate for the increased survival costs with a higher effort to the current reproduction.

Key words: Bank vole; breeding tactics; cost of reproduction; intraspecific competition; kinship; litter size; territoriality; predation risk; reproductive effort.

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List of original publications

This thesis is based on the following articles, which are referred to by their Roman numerals in the text:

- I Mappes, T., Koskela, E. & Ylönen, H.: Reproductive costs and litter size in the bank vole. - Proc. R. Soc. Lond. B (1995) 261, 19-24.
- II Koskela, E., Mappes, T. & Ylönen, H.: Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. - Journal of Animal Ecology 1997, 66,341-349.
- III Ylönen, H., Mappes, T. & Viitala, J. 1990: Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*. - Oecologia 83: 333-337.
- IV Mappes, T. Ylönen, H. & Viitala, J. 1995: Higher reproductive success among kin groups of bank voles *Clethrionomys glareolus*. - Ecology (in press).
- V Mappes, T. & Ylönen, H.: Reproductive effort of bank vole females in a risky environment - Evolutionary Ecology, 1997, 11, 591-598.

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1 INTRODUCTION

1.1 General introduction

Breeding success and survival of an individual is a function of the particular ecological environment where it lives. The ecological constraints, e.g. intraspecific competition and risk of predation, generally limit the utilization of reproductive resources or affect survival costs for breeding individuals. Thus, if reproduction is costly or constrained, an iteroparous organism is always faced with two decisions: Should it breed or not, and further, how much energy should it allocate to the current breeding event. To maximize life-time reproductive success each female has to tradeoff her current reproductive effort (e.g. the number and quality of offspring) against her own performance and survival to the next breeding attempt (Williams 1966, Bell & Koufopanou 1986). Furthermore, some life-history traits like offspring and parental survival may change as a function of each other, which makes estimation of the optimal breeding tactic even more complicated (Tuomi 1990).

In this thesis I estimated the breeding success of bank vole *Clethrionomys glareolus* females, and further, tried to determine the reproductive costs and mechanisms which constrain breeding success in this species. Earlier studies indicate that at least two factors may greatly affect the reproductive success in this species, and thus, may cause selection pressure for phenotypic plasticity in breeding tactics. The first assumption is that reproductive resources are limited by other breeding females in the population. Indeed, there is evidence that the breeding success of females decreases when the density of the breeding population increases (Nakata 1984). One way to secure a sufficient quantity and quality of reproductive resources is to defend them (e.g. to be territorial) (Ostfeld 1985). The second assumption is that predators cause survival costs for breeding females or offspring (Cushing 1985). These

costs could be minimised by varying the breeding effort temporally (Ylönen 1989).

1.2 Reproductive costs and optimal litter size

Life history theory predicts that reproduction involves costs in terms of present and future breeding success. Reznick (1985) divided the measurements of these costs to four types: (i) Unmanipulated phenotypic correlations, (ii) manipulated phenotypic correlations, (iii) genetic correlations, and (iv) selection experiments. He argued, that the latter two methods only may verify the reproductive costs in the evolutionary meaningful sense. However, many other researchers have justified the use of manipulated phenotypic correlations as a good method in field studies (e.g. Gustafsson & Sutherland 1988, Sinervo et al. 1992). For example, in most vertebrates measurements of genetic correlations or long-term selection experiments have been considered impossible.

In vertebrates reproductive costs have most often been estimated by manipulating clutch sizes in birds (see review by Roff 1992). In many studies the manipulation have been found to affect the present breeding success; e.g. clutch enlargements have decreased nestling survival and juvenile survival to the next breeding season. Some studies have also indicated that clutch enlargement may decrease parent survival and/or the clutch size in the future. However, a trade-off between the number of offspring and parental fitness seems to be far less common than a trade-off between offspring number and survival (Linden & Møller 1989).

In mammals measurements of reproductive costs and optimal litter size are based only on unmanipulated phenotypic correlations in field or on few litter manipulations in laboratory (see review by Roff 1992). There are obvious biases that are difficult to control in the analyses of non-experimental studies (Reznick 1986). For example, there is often a positive correlation between natural litter size and the quality of mother, which may obscure possible reproductive costs (Högstedt 1980). On the other hand, some reproductive costs may be difficult to detect in laboratory studies, where the environmental circumstances, e.g. nutritional level, physical environment or intraspecific interactions, differ from the situation in the field (Stearns 1992).

In the first study (I) we examined potential reproductive costs by manipulating litter size in free ranging bank voles. We determined the consequences of nursing different number of offspring for both the offspring and the mothers. We were also able to investigate if home range size of females will correlate with their litter size and how females will change their space use in relation to the manipulation.

1.3 Territoriality of breeding females

Territoriality in breeding female mammals is generally suggested to be based on intraspecific competition for food resources (Ostfeld 1985). According to the

resource defence hypothesis availability of food limits the reproductive success of females, and thus food distribution and abundance should determine the spacing patterns of females. Another benefit of territoriality has been suggested to be the prevention of infanticide (Wolff 1993), since it might be advantageous for a female to kill strange pups or young that will compete with their own offspring for resources. This hypothesis predicts that females defend their home ranges, particularly near the nest and during nursing when pups are most likely to be killed. However, the predictions of these two hypotheses of territoriality are not exclusive and both predict highest level of defence during the nursing period.

In the present study (II) we determined how female home range size, home range overlap and territory defending behaviour change during the reproductive cycle. We also studied if the above-mentioned factors correlate with the reproductive effort (litter size) and the breeding success of females.

1.4 Kin interactions

According to the kin-selection theory (Hamilton 1963, 1964), a high degree of kinship between individuals may decrease the level of competition. However, the characteristics of a social system should greatly determine how an individual can utilize interactions with relatives. For example, altruistic and cooperative sharing of space and other resources may appear as reduced size and/or increased overlap of home ranges of related neighbours. On the contrary, space competition should be more intense and infanticide more common between non-relatives.

In the third study (III) we investigated if the demography of bank vole populations differs according to the degree of relatedness. In the next study (IV) we analysed the mechanisms behind the observed different population growth patterns of the experimental populations. We studied if (i) size and distribution of territories differ between related and unrelated groups, whether (ii) the spatial organization of related and unrelated females is connected to their breeding success, and if (iii) breeding females influence the spacing behaviour and trappability of juveniles indicating avoidance of territorial females.

1.5 Breeding tactics and predictable reproductive costs

In cyclically fluctuating vole populations two risk factors, strong intraspecific competition and intense predation, simultaneously or separately increase the costs of reproduction. High density of conspecifics decreases reproductive success in the bank vole due to strict female territoriality and social suppression of breeding. In particular, young females do not mature during the summer of their birth if the density of breeding females is high (Bujalska 1985, Ylönen et al. 1988). The main predators of bank voles, the least weasel *Mustela nivalis* and the stoat *M. erminea*, cause high mortality among breeding females because they

use odour tracks of oestrous females as hunting cues (Cushing 1985). These costs should be independent of the age of breeding females.

What is an optimal breeding tactic in an environment where costs of reproduction increase temporally to a high level, but decrease dramatically soon after, as is the case in the cyclic biotic environment of microtines in Fennoscandia (Hanski et al. 1993)? In the fifth study (V) we hypothesized that reproductive effort of experimental females should be depended on the expected success of the present breeding event and the prospects for future reproduction. We tested what kind of a breeding tactic a female bank vole will "choose" towards the end of the breeding season: (i) Does she breed or not if the breeding environment cues indicate a high cost of reproduction (high population density and/or high risk of predation), and if she breeds (ii) how large are the litters she produces? We also tested (iii) if the age of a female affects her breeding tactics?

2 METHODS

2.1 Study area and study species

All the studies were carried out at Konnevesi Research Station, in central Finland (62°37' N, 26°20' E). The experiments were performed in four 0.5 ha (III-V) or eight 0.25 ha (I and II) outdoor enclosures, that were founded on a homogeneous abandoned field. The vegetation in enclosures is typical for old fields: grasses (e.g. *Alopecurus pratensis*, *Phleum pratense*, *Elymus repens*, *Deschampsia* spp., *Poa* spp.) and herbs (e.g. *Ranunculus acris*, *Hypericum maculatum*, *Geum rivale*, *Alchemilla* spp., *Trifolium* spp.) dominate the field layer.

All experimental animals were caught in central Finland, where females produce 3-4 litters of 2-9 young from May to September (T. Mappes et al. unpublished data). In central Finland bank vole populations fluctuate in 3-4 year cycles (M. Halonen, T. Mappes, T. Meri and J. Suhonen, in prep.). Populations of the main predators, the least weasel and the stoat follow vole abundances with a 0.5 to 1-year time lag (Korpimäki et al. 1991).

2.2 Monitoring of individuals

For monitoring the populations we used 100 Ugglan Special multiple-capture live traps per hectare with 10 meters between the trapping stations. During the trapping periods traps were usually checked 10 times at 6-9 h intervals. Trap location, sex, weight, and reproductive status for each capture of each individual were recorded. Home range size was measured by the inclusive boundary strip method (Stickel 1954). Percentile home range overlap was estimated as the proportion of total trap sites in the home range of each female visited also by other females (Ims 1987). The size of exclusive space (territory)

was calculated as the number of trap sites (one site = 100 m²) which only the territory owner visited. Home range centre was calculated as the mean point of each individual's capture coordinates. Nearest neighbour distance was calculated from distances between the home range centres of the nearest neighbours. Trappability of voles is a percentage expressing the number of times an individual was captured in relation to the number of possibilities to enter a trap during the trapping period.

2.3 Litter size manipulation (I)

We used wild-caught, non-gravid, over-wintered females, which had given birth once in the early summer before the experiment. Forty females (five per enclosure) were randomly released to the eight enclosures at the beginning of July. At this density (20 individuals/ha) all females have an opportunity to gain a territory and breed (T. Mappes et al., unpublished data). Females were allowed one week to accustomize themselves with the available resource environment and to establish their territories. After that three males were released to each enclosure. All females were captured just before parturition and they gave birth within 2-3 days in a laboratory. Manipulation was carried out when pups were one to two days old. We randomly divided the litters from each original litter size category (range 4 - 9) to three treatment groups: Reduced litters (- 2 pups, N = 15), enlarged litters (+ 2 pups, N = 13), and control litters (N = 12) where the original litter size remained unchanged, but two pups were exchanged with another litter. After the manipulation females with their pups were simultaneously released to the activity centres of their home ranges. Females were captured again just before the second parturition in order to determine the size of second litters, and after that the females and second litters were released back to the enclosures.

Four trapping periods were carried out during the study: (i) Before the first parturitions and the litter manipulation, (ii) during nursing about one week after the parturitions, (iii) after weaning of the manipulated litters before the birth of second litters, and (iii) after weaning of the second litters.

The effect of weanling weight on the probability of maturation was analysed from the data of an earlier study (IV), where we investigated the effects of kin interactions on breeding success. Kin manipulation did not affect the maturation probability of juveniles and, thus, we were able to analyse maturation data in that study. All weanlings were weighed at the same age (one month) as in the present study, and we estimated if this weight will predict their maturation during the summer of the birth.

2.4 Territorial behaviour (II)

Over-wintered female bank voles at the same reproductive status (mature, non-gravid but having given birth once in the early summer) were used in the study. Five females and three males were randomly assigned to each of the

seven enclosures. For monitoring the populations there were five trapping periods at different stages of the reproductive females: (i) When non-gravid, (ii) in the early pregnancy, (iii) in the late pregnancy, (iv) when nursing and (v) when weanlings were recruited to the population. After the third trapping period all females were removed from the enclosures to a laboratory where they gave birth. After that females and their litters were returned to the activity centres of their home ranges.

The behaviour of owner females against intruder females was determined five times, once during the last two days of each trapping period. Behavioural trials lasted 10 minutes and were carried out in small arenas, which were placed directly on the ground at the trap station nearest to the activity centre of territory owner. Behaviour of females was described by following variables: approaching, amicable behaviour, attacks, threats, freezing, avoidance and fleeing.

2.5 Kin and non-kin groups of bank voles (III and IV)

Two "Related" populations were formed from a mother with four daughters and two "Unrelated" populations from five unrelated females. The compositions (the number, ages and weights) of the two non-kin female groups were similar to the Related populations. Number of births was estimated by mass loss of pregnant females. Reproductive success of each female was determined by number of juveniles recruited into her territory per number of births during the experiment. The juveniles were trapped within their natal home range when they were 2.5- 3 weeks old before dispersing.

2.6 Predation risk and population density (V)

Both over-wintered and summer-born bank vole females in breeding condition were used in the experiment. All males were over-wintered and their maturity was determined by the size of testes. In a 2 x 2 factor experiment, two factors were manipulated each with two treatment levels: No predation risk or high risk of mustelid predators and low or high density of voles. Female-male pairs were placed in cages, which were evenly distributed in four large (0.5 hectare) outdoor enclosures. All animals were fed *ad libitum*. Predator risk was simulated by spraying the vegetation surrounding the cages with the odour of stoats. A high population density of voles was produced by a free living population of 80 - 100 individuals of bank voles in both the enclosures surrounding the cages of density treatments. The density effect was strengthened by spraying the vegetation surrounding the cages with the odour of captive bank voles. The control treatment (no predation and no competition) was subjected to the same disturbance as the other ones but was sprayed with distilled water. There were no free-living bank voles around the control cages.

The experiment was carried out during the latter part of the breeding season between July and September simulating the last breeding events of the

year. The manipulations of each replicate lasted for three weeks during which the odours were sprayed once a day. At the end of the experiment the voles were killed, weighed, and dissected in order to determine their reproductive stage and the number of embryos.

3 RESULTS AND DISCUSSION

3.1 Cost of reproduction and offspring survival (I)

The cost of nursing an enlarged litters appeared in the nestling survival and weight of juvenile after weaning. No negative correlations existed between the degree of manipulation and parental survival or success of subsequent breeding. It seemed that the original litter size produced a maximum number of high quality offspring, which supports the individual optimization hypothesis (Pettifor et al. 1988).

The result that females did not tradeoff their condition against the quality of offspring, could be explained in at least two ways. (i) Females do not invest more to enlarged litters, because the higher investment could decrease their own survival during the present breeding event. This hypothesis suggests that juvenile survival changes as a function of mother survival. So, mothers should maximize their current breeding success by decreasing the cost of nursing and thus avoiding the risk of complete reproductive failure (Tuomi 1990). Moreover, controlling the reproductive investment can be advantageous for a mother, if allocation to survival and to the next breeding attempt maximizes her life-time reproductive success (Williams 1966). Secondly, it is possible that (ii) females can not increase their breeding effort, because other individuals constrain the utilization of reproductive resources (Cooke et al 1990).

We supposed that the size of home range correlates quite accurately with the amount of available food resources in the relatively homogenous environment of the enclosures. The range size before the manipulation correlated significantly with the number of pups produced. Further, the home range size of females seemed to be related to their weight and ability to defend their own exclusive area (territory) (II). Thus, the amount of available reproductive resources is suggested to depend on female dominance rank in

the breeding population. Under these circumstances manipulation did not affect the size of territories. This may indicate, that females with enlarged litters were not able to compensate for the higher nursing costs by increasing the amount of resources in the saturated breeding populations (Cooke et al. 1990). This seems quite obvious, because bank vole females defend their territories, especially during nursing, and their territories overlap very little during that breeding phase (II). Thus, as Cooke et al. (1990) proposed selection may act upon both the litter size and some behavioural component that correlates with territory quality in the bank vole.

Increased number of offspring during the lactation period seemed to decrease the weight of weanlings, which agrees with the few experiments in laboratory (Machin & Page 1973, Fleming & Rauscher 1978, Kaufman & Kaufman 1987). In these studies, however, the effects of weight at weaning on later survival or breeding success of juveniles were not investigated in natural circumstances. In our study weight at weaning did not affect survival during the experiment. However, we suggest that phenotypic selection may act upon the weight of juveniles in at least two ways. Firstly, the probability of maturation and breeding may depend on their weight at weaning. In the present study the juveniles were not able to breed during the summer of their birth. However, the data from the earlier study (IV) indicates that the probability of maturation and breeding increases with the weight at weaning. Another advantage of higher weight, especially just before winter, could be a higher survival probability to spring. Unfortunately, we were not able to estimate this possible advantage in the present study.

3.2 Strict territoriality during nursing (II)

In the present study female aggression towards other females increased significantly and amicable behaviour decreased as the time of parturition got closer. These results agree with an earlier laboratory experiment with the bank vole (Rozenfeld & Denoël 1994) and the general finding that aggressiveness increases at the onset of lactation in microtines (e.g. Mallory & Brooks 1980). At the same time the degree of overlap of home ranges decreased and the size of exclusive space (territory) increased although the size of home range did not change. Clearly, the spacing pattern of females developed towards strict breeding territoriality. Our results indicate that changes in spacing patterns during reproductive cycle are a direct consequence of interactions between breeding females rather than phenotypic plasticity in simultaneously changing environmental conditions.

3.3 Higher breeding success among kin groups (III and IV)

The "Related" populations grew significantly faster than the "Unrelated". This was mostly caused by a higher number of recruits and their better survival among the Related as the density of breeding females did not differ between

the treatments. The reproductive success of females is related to their space use if the neighbouring breeding females are non-kin. The home range sizes of unrelated neighbours decreased when the ranges were near to each other. However, the distance to the territory of the neighbour was the only factor which affected their breeding success, not the size of home ranges. This may indicate that the lower breeding success of unrelated females was not directly caused by intraspecific competition for food resources.

Some of the unrelated females, especially the lighter ones, had their territories close to each other although that obviously decreased their reproductive success. A possible explanation is that dominant females forced the lighter unrelated females to live close to each other in the fenced enclosures where space is rather limited and dispersal impossible. We also found that the costs of having overlapping ranges with related females seemed to be insignificant or very small as indicated by their reproductive success. If low, such costs could be outweighed by the possible benefits (e.g. higher inclusive fitness) of space sharing among relatives. Lower quality of habitat may, instead, induce more "selfish" behaviour between close relatives (Brown & Brown 1993).

Altruistic and/or cooperative space sharing may result in dense groups of breeding females. In the present study there seemed to be enough space for the founder females to breed in both Related and Unrelated treatments. So, space sharing might only increase the maturation possibilities of juvenile females. However, in spite of a greater tolerance of kin-neighbours and their offspring, we did not find a higher number of juveniles matured in Related populations. The density of breeding females seemed to be saturated at 10-12 voles/ha regardless of kinship. Breeding females allowed related young females to use their home range but, still, they may suppress their breeding (even their own daughters). This parent-offspring -conflict force young females either to stay and delay breeding (Bujalska 1985), or to disperse from their mothers' home range in order to find a vacant territory to breed (Gliwicz 1989).

We found that survival of three to four weeks old Unrelated juveniles declined when they moved further away from their mother's territory. Furthermore, trappability of juveniles declined significantly near the territories of unrelated females, which indicates avoidance of traps scented by unrelated breeding females. Trap avoidance was also more common among the lighter juveniles. These results indicate agonistic behaviour (even infanticide, c.f. Wolff 1993) towards non-kin young, especially towards the smaller ones.

3.4 Two opposite breeding tactics in a risky environment (V)

The simulated predation risk suppressed breeding of bank vole females which supports the hypothesis that females might delay breeding at least over short unfavourable periods (Ylönen 1989). The density of conspecifics did not affect overall breeding as young and old females seemed to respond differently to the high level of competition. There was a slight tendency that the high population density would suppress breeding in summer-born females but on the other

hand, it stimulated breeding of over-wintered females. Under high breeding densities of bank voles one can expect that breeding success of young summer-born females to be very low. This is caused by social suppression of breeding by over-wintered females which decreases breeding success of young or prevents it totally (Bujalska 1985, Kawata 1987, Ylönen et al. 1988). Under a high risk of mustelid predation both over-wintered and young summer-born females suppressed reproduction although they have different life-time expectations (Magnhagen 1990). There are, however, some observations that female bank voles may survive over the second winter and breed again during the next breeding season (T. Mappes et al. unpublished data). Nevertheless, breeding suppression of over-wintered females indicates a very high survival cost of reproduction and significant benefits from delayed breeding under high predation risk.

Unexpectedly, the two risk factors, high density of conspecifics and mustelids, did not have a joint effect on breeding tactics of the bank voles. This result indicates that the increase in bank vole densities does not predict precisely the increase in predator densities, as also observed by Korpimäki et al. (1991). This unpredictability, and the time lag between the density variations, may prevent female bank voles from adapting their breeding tactics to different risks at the same time.

Females breeding under high population density produced larger litters than under low density. The same tendency existed for females under predation risk. It seems that, in a risky environment a female vole selects between two breeding tactics, which differ greatly in energy allocation and the probability of the female's own survivorship. A female can adopt a costly current breeding tactic with larger litters or she can invest in her own survival by delaying breeding. This dimorphism in breeding tactics of bank vole females may indicate an unstable equilibrium point in trade-off curve between reproductive effort and adult survival (Schaffer 1974, Stearns 1976, Bell 1980). For example, Bell's (1980) model predicts that if a trade-off curve is concave, the optimal tactic would be either delayed breeding or high investment, but not between them. We suggest that the trade-off curve should be concave, if the shape of the curve is largely determined by survival costs caused by oestrus (Cushing 1985). The survival of females would decrease instantly when they become oestrus, but the slope of the survival curve is less steep if females increase reproductive investment (e.g. produce more pups). Besides the ecological benefits of delayed breeding (lower predation risk or population density in the next breeding season), there will be also physiological benefits: Breeding is energetically costly and pregnant or lactating females are not able to moult to produce winter fur when lactating or breeding (Koponen 1970). Females, therefore, choose either to continue breeding or to invest in winter survival.

4 CONCLUSIONS

In this thesis I studied the reproductive tactics of bank vole females and the mechanisms which determine the reproductive success in this species. The main findings are summarized in Table 1. Possible reproductive costs were assessed by manipulating reproductive effort of bank vole females during lactation. Enlargement of litter size decreased the success of the current breeding, but did not cause survival or fecundity costs for the breeding female. Bank vole females seemed to adapt their litter size to their breeding environment (home range size), and this original litter size seemed to be the most successful one for producing the highest number of good quality offspring. Possibilities to increase reproductive effort with a number of offspring may be limited in saturated breeding populations of bank voles. Furthermore, controlling the reproductive effort can also be advantageous for females, if increased allocation to survival and future breeding attempts maximizes their life-time reproductive success.

The spacing behaviour of bank vole females was clearly dependent on their reproductive state, so that females were strictly territorial only during the late part of the breeding. Intense competition for space during nursing can be a crucial factor in determining litter size and limiting parental effort to offspring (see above).

Kinship between females increased the size and the overlap of home ranges, and further, tolerance of juveniles. Decreased competition for reproductive resources and/or reduced risk of infanticide might increase breeding success of related females, indicating that kin selection may act in the social system of the bank vole.

Risk of mustelid predation changed female breeding tactics. The optimality of a tactic may be related to predictable changes in predation risk. However, the results did not support the hypothesis that delayed breeding is a response to long term cyclic changes in densities of voles and their main predators. We predict that optimality of the two opposite tactics, high effort

breeding and delayed breeding, is determined by the shape of the trade-off curve between survival of females and their reproductive effort.

TABLE 1. Possible reproductive costs or constraints of breeding success (A) and adaptive responses to them (B), and verifications of A and B in the thesis.

A. Reproductive costs or constraints of breeding success	B. Adaptations	Verifications of A and B
Nursing of young (lactation)	Adapting litter size to breeding environment	A. (i) Nursing of enlarged litters decreased the survival and quality of offspring (I) (ii) However, manipulated reproductive effort did not cause survival or fecundity costs for the mothers (I) B. Possible; the original litter size seemed to produce maximum number of high quality offspring
Intraspecific competition	Occupation and defence of food territory	A. (i) Size of home ranges and breeding success decreased with nearest neighbour distance (IV) (ii) Defence of home ranges (space competition) was most intensive during the most critical breeding states (late pregnancy and nursing) (II) B. (i) Litter size increased with size of home range (I) (ii) However, size of defended area did correlate with breeding success (II)
Intraspecific competition	Nepotism or tolerance of relatives	A. See above B. Home ranges overlapped more and breeding success was better if nearest neighbour was related (IV)
Risk of intraspecific competition	Temporal variation in reproductive effort	A. Not studied B. Not verified (V)

TABLE 1. (Continued)

A. Reproductive costs or constraints of breeding success	B. Adaptations	Verifications of A and B
Infanticide	Defence of nest (exclusive home range)	A. Only indirect evidence: (i) Breeding success decreased with nearest neighbour distance (IV) (ii) young juveniles avoided strange breeding females (IV) B. Not verified: size of defended area or defending behaviour did not correlate with breeding success (II)
Survival risk caused by predation	Temporal variation in reproductive effort	A. Not studied B. Possible: Females delayed their breeding or increased reproductive effort, but the success of these tactics was not determined (V)

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YHTEENVETO

Metsämyyrän lisääntymistaktiikat ja -menestys

Elinkiertoteorian keskeinen oletus on, että lisääntyminen aiheuttaa yksilölle kustannuksia (Williams 1966). Kustannushypoteesin mukaan panostus nykyiseen lisääntymiseen voi vaikuttaa yksilön myöhempään lisääntymismenestykseen. Tämän lisäksi lisääntymistaktiikoiden optimaalisuutta säätelevät kompromissit (engl. trade-offs) eri elinkierto-parametrien välillä, sekä yksilön sisäiset (esim. fysiologiset) ja ulkoiset rajoitteet (esim. kilpailu muiden yksilöiden kanssa ja predaatoririski) (Stearns 1976, Roff 1992). Näiden kustannusten, kompromissien ja rajoitteiden oletetaan säätelevän iteroparisen yksilön lisääntymistaktiikoiden valintaa, esim. maturoitumisikää, lisääntymiskertojen määrää ja lisääntymispanostusta. Väitöskirjani osatutkimuksissa olen kokeellisesti selvittänyt, miten erilaiset, lähinnä ulkoiset rajoitteet ja kustannukset vaikuttavat metsämyyränaaraan *Clethrionomys glareolus* lisääntymistaktiikoiden valintaan. Lisäksi olen pyrkinyt selvittämään, onko valittu taktiikka ollut optimaalinen siinä ympäristössä, missä se on valittu.

Poikuekoon vaihtelun ja lisääntymiskustannusten välistä suhdetta tutkimme kokeellisesti manipuloimalla naaraiden poikuekokoa. Naaraan alkuperäistä poikuekokoa joko kasvatettiin kahdella ("lisätyt") tai vähennettiin kahdella ("vähennetyt"), ja sen lisäksi osa naaraiden poikueista jätettiin ennalleen ("kontrolli"). Poikuekoon kasvattaminen ei nostanut tuotettujen rekryyttien määrää, vaan lisätyt poikueet olivat kuukauden iässä keskimäärin yhtä suuria kuin kontrollipoikueet. Manipulointi vaikutti poikasten painonkehitykseen siten, että lisätyt olivat merkittävästi kevyempiä ja vähennetyt painavampia kuin kontrollipoikaset. Nuorten painoerot eri koeryhmien välillä tasoittuivat syksyä kohti, mutta olivat tilastollisesti merkittäviä vielä kahden kuukauden iässä. Manipulaatio ei vaikuttanut poikasten säilyvyyteen vieroitusiästä syksyyn. Poikuemanipulaatio ei myöskään näyttänyt aiheuttavan kustannuksia emoille. Esimerkiksi emojen paino ja säilyvyys sekä myöhemmin tuotetun poikueen koko ja menestys eivät eronneet eri koeryhmien välillä. Naaraan liikkuma-alan koko korreloi positiivisesti sen synnyttämän poikasmäärän kanssa. Tämä voi viitata siihen, että naaraan valloittaman territorion koko korreloi positiivisesti myös lisääntymiseen tarvittavan ravinnon määrän kanssa. Naaraat eivät kuitenkaan muuttaneet liikkuma-alansa kokoa suhteessa poikuekoon keinotekoiseen muutokseen. Ilmeisesti naaraat synnyttävät sen määrän poikasia, minkä pystyvät parhaiten kasvattamaan siinä ympäristössä, missä ne elävät. Tiukka tilakilpailu lisääntyvien naaraiden välillä saattaa olla se mekanismi, joka rajoittaa naaraiden kykyä lisätä panostusta poikuekoon muuttuessa.

Metsämyyränaaraan lisääntymismenestykseen vaikuttaa olennaisesti lajin sisäinen tilakilpailu. Naaraan valtaama territorio on olennainen

lisääntymisresurssi joka turvaa riittävän ravinnon saannin (Ostfeld 1985) ja/tai suojaa poikasia toisilta naarailta, jotka saattavat tappaa poikasia (Wolff 1993). Naaraiden tilankäyttöä ja territoriaalisuutta tutkimme lisääntymissyklin eri vaiheissa, ennen tiineyttä, tiineyden alussa, tiineyden lopulla sekä imetyksen aikana. Lisäksi selvitimme, miten tilankäyttö ja -puolustus vaikutti naaraiden lisääntymisnestykseen. Tilankäyttöä selvitimme elävänäpyynneillä ja tilanpuolustusta käytöskokeilla. Kokeissa havainnoitiin naaraan käyttäytymistä vierasta lisääntymiskuntoista naarasta kohtaan, joka tuodaan keskelle sen territoriaa. Tulokset osoittivat, että naaraiden liikkuma-alojen päällekkäisyys laski ja territorion koko (alue, joka oli ainoastaan naaraan omassa käytössä, engl. exclusive space) kasvoi lisääntymisen loppua kohti. Naaraat suhtautuivat myös aggressiivisemmin vieraita naaraita kohtaan tiineyden loppuvaiheessa ja imetyksen aikana. Alueen puolustus näytti myös korreloivan naaraan territorion koon kanssa. Naaraat muuttuivat siis selvästi territoriaalisiksi vasta lisääntymisyklinsä loppuvaiheessa. Tämä voi olla edullista sekä riittävän ravinnon turvaamisen että poikasten suojaamisen kannalta. Naaraiden käytöksen ei kuitenkaan voitu osoittaa korreloivan selkeästi niiden lisääntymismenestyksen, esimerkiksi pesästä lähteneiden poikasten määrän kanssa.

Yksilöiden väliset sukulaissuhteet voivat olennaisesti vaikuttaa yksilöiden väliseen kilpailusuhteeseen (Hamilton 1963, 1964). Sukulaisvalintateorian mukaan resurssien jakamista (uhrautumista ja/tai yhteistyötä) edesauttavat geenit voivat yleistyä nimenomaan sukulaisryhmissä. Tutkimme kokeellisesti sukulaissuhteiden vaikutusta metsämyyränaaraiden väliseen tilakilpailuun ja edelleen naaraiden lisääntymismenestykseen. Koepopulaatioissa, jotka koostuivat toisilleen vieraista naaraista, lisääntyvien naaraiden liikkuma-alat olivat merkitsevästi vähemmän päällekkäin kuin vastaavissa sukulaispopulaatioissa. Ei-sukulaisnaaraiden liikkuma-alat olivat myös pienemmät ja niiden lisääntymismenestys huonompi, mikäli niiden liikkuma-alat sijaitsivat lähellä toisiaan. Menestys korreloi kuitenkin merkitsevästi vain liikkuma-alojen läheisyyden, ei liikkuma-alojen koon kanssa. Tämä havainto ei tue hypoteesia siitä, että lisääntymismenestystä laskee nimenomaan kilpailu ravintoresursseista. Sen sijaan poikasten tappaminen saattoi olla yleisempää ei-sukulaisnaaraiden välillä. Tätä tukevat myös tulokset siitä, että juuri pesästä lähteneet nuoret välttelivät vanhoja ei-sukua olevia naaraita ja niiden liikkuma-aloja.

Myyrien elinympäristö Keski- ja Pohjois-Fennoskandiassa vaihtelee säännöllisen syklisesti. Myyräyksilön säilymiseen ja lisääntymiseen ratkaisevasti vaikuttavat tekijät, mm. saalistuksen voimakkuus ja kilpailu, sekä lajin sisäinen että ulkoinen, vaihtelevat ennustettavasti 3-4 vuoden sykleissä. Varsinkin myyräsykleihin liittyvän kannan huipun ja romahduksen aikaan predaatoririski ja/tai kilpailu saattavat aiheuttaa merkittäviä kustannuksia tai rajoitteita lisääntyville yksilöille. Pyrimme faktorikokeella selvittämään kahden metsämyyrän ympäristössä keskeisesti vaihtelevan riskitekijän, spesialisimaapetojen saalistuksen ja lajin sisäisen kilpailun vaikutusta yksilöiden lisääntymistaktiikoihin. Molempia riskitekijöitä manipuloimme epäsuorasti karpän ja/tai myyrän hajulla. Predaatoririski laski lisääntyvien myyrien osuutta merkitsevästi. Sen sijaan populaatiotiheydellä ei ollut vaikutusta lisäänty-

miseen. Nuoret naaraat näyttivät kyllä lisääntyvän korkean tiheyden aikana hiukan heikommin kuin talvehtineet. Naaraan iällä ei sen sijaan ollut vaikutusta sen reaktioon predaatoriskiin. Predaatoriskillä ja populaatiotiheydellä ei ollut myöskään yhteisvaikutusta. Kummatkaan koetekijät eivät vaikuttaneet koiraiden sukupuoliseen kuntoon. Korkean populaatiotiheyden aikana lisääntyneillä naarailla poikueet olivat suurempia kuin alhaisen tiheyden aikana lisääntyneillä. Myös predaatoriski näytti suurentavan poikuekokoa. Naaraan paino korreloi positiivisesti poikueen koon kanssa, sen sijaan ikä ei vaikuttanut poikasten määrään. Naaraat näyttivät siis "valitsevan" riskiympäristössä lisääntymispanostuksen kannalta kahden vastakkaisen taktiikan välillä; ne joko jättivät lisääntymättä tai tuottivat suuria poikueita. Tämä taktiikoiden valinta voi selittyä sillä, että lisääntymispanostuksen ja säilyvyyden välinen trade-off käyrä on kovera (ks. yksityiskohtat osajulkaisu V). Tulokset tukevat myös hypoteesia siitä (Ylönen 1989), että metsämyyränaaraat saattavat yrittää siirtää lisääntymistään lyhyiden ennustettavasti ohi menevien riskikausien yli. Havaittujen lisääntymistaktiikoiden optimaalisuutta, esimerkiksi taktiikan vaikutusta naaraan säilyvyyteen tai myöhempään lisääntymismenestykseen, emme voineet kokeessa kuitenkaan testata.

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ORIGINAL PAPERS

I

Reproductive costs and litter size in the bank vole

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II

**Territorial behaviour and reproductive success of bank vole
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III

Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*

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IV

**Higher reproductive success among kin groups of bank voles
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V

Reproductive effort of bank vole females in a risky environment

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