

Reproductive effort of female bank voles in a risky environment

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Summary

In cyclically fluctuating vole populations, strong intraspecific competition and intense predation simultaneously or separately increase the costs of reproduction and so may set the framework for the optimal breeding tactic of voles. In a factorial experiment, we manipulated two factors in the breeding environment of bank vole (*Clethrionomys glareolus*) pairs, each with two treatment levels: no predation risk or high risk of specialist predators and low or high density of voles. In the manipulation, we used odours of conspecific voles and/or mustelid predators. Both over-wintered and young, summer-born, wild-caught bank vole females and males in breeding condition were used. Each female–male pair of voles was placed in a cage and the cages were distributed in large outdoor enclosures. All animals were fed *ad libitum*. Under predation risk, both old and young females suppressed breeding significantly. The density of conspecific voles did not affect overall breeding. However, there was some evidence that population density stimulated breeding of old females but suppressed breeding of young ones. Both risk factors appeared to increase litter sizes of those individuals who ‘decided’ to breed. Our results indicate that the risk of predation may be an important factor determining reproductive tactics of bank vole females. In risky environments, females seemed to choose between two totally opposite tactics: they suppressed breeding, which may increase their own survival to the next breeding event, or they continued to breed in spite of expected high survival costs. Females seemed to compensate the latter costs with a higher effort to the current and probably the last reproduction.

Keywords: breeding tactics; competition; microtine cycles; predation risk; reproductive costs; reproductive effort

Introduction

If reproduction is costly, an iteroparous organism always has two decisions to make: should it breed or not breed, and how much energy should be allocated to a current breeding event (Roff, 1992). An optimal decision of parental animals depends on two traits: (1) parental survival during current and future breeding, and (2) present and later survivorship of the young (Tuomi, 1990). Thus breeding tactics should mostly be determined by the predictability of breeding success over time.

In cyclically fluctuating vole populations, two risk factors – strong intraspecific competition and intense predation – simultaneously or separately increase the costs of reproduction or decrease the possibility of breeding. A high density of conspecifics decreases reproductive success in the bank vole, *Clethrionomys glareolus*, because of 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). Specialist predators – least weasel *Mustela nivalis* and stoat *Mustela erminea* – cause high survival costs for breeding females because they use

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

What is an optimal reproductive effort in an environment where costs of reproduction increase temporally to a high level, but soon after that dramatically decrease, as is the case in the cyclic biotic environment of microtines in Fennoscandia (Henttonen *et al.*, 1987; Hansson and Henttonen, 1988; Korpimäki *et al.*, 1991; Hanski *et al.*, 1993)? Previous experiments in the laboratory (Ylönen and Ronkainen, 1994; Koskela and Ylönen, 1995) have indicated that voles suppress their breeding under risk of predation. The present study was conducted in a more natural environment where we simulated two risk factors of bank vole females. We only used cues for risk factors (odours of conspecifics and/or predators) and fed the study animals *ad libitum*. The present experimental procedure allowed us to determine how a female bank vole 'chooses' between breeding tactics purely according to environmental cues (and the female's own characteristics, e.g. age and physiological condition). Thus the female's tactics do not depend on the direct effects of competition (exploitation or interference) or indirect effects of predation risk due to decreased feeding (see, e.g. Koskela and Ylönen, 1995).

We wondered what kind of breeding tactic a female will choose towards the end of the breeding season. Does she breed if the breeding environment cues indicate a high cost of reproduction (high population density of conspecifics and/or high risk of predation) and, if she breeds, how large are the litters she produces? Furthermore, how does the age of a female affect her breeding tactics?

Materials and methods

Study site and experimental animals

The study was carried out at Konnevesi Research Station, central Finland (62°37' N, 26°20' E). All experimental animals were caught in central Finland, where bank vole populations fluctuate in 3–4 year cycles (Ylönen *et al.*, 1988), a cycle length about 1 year shorter than in Northern Fennoscandia (Hanski *et al.*, 1991). Populations of small mustelids, least weasel *Mustela nivalis* and stoat *Mustela erminea*, follow vole abundances with a 0.5–1 year time lag in central Finland (Korpimäki *et al.*, 1991).

We used a total of 100 vole pairs consisting of both over-wintered ($n = 44$) and young, summer-born ($n = 56$) bank vole females in breeding condition. Wild-caught voles, and the female young of their first litter, were used in the experiment. Females were regarded as mature if they had an open vagina. Over-wintered females had given birth once prior to the experiment. Summer-born young females did not have any litters before the experiment. The males were over-wintered and their maturity was determined by the size of their testes.

Experimental design

In a 2×2 factorial 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. One hundred female–male pairs of mature, non-breeding bank voles were each placed in a $35 \times 20 \times 20$ cm wiremesh cage, where they had visual and olfactory contact with the surrounding environment. The numbers of replicates for each treatment are shown in Table 1. All animals were fed with sunflower seeds, oats, carrots and water *ad libitum*. The cages for the four different treatments were distributed in four large (0.5 hectare) outdoor enclosures. The habitat of the enclosures was an old field with homogeneous tall grass vegetation (Mappes *et al.*, 1995). In each experimental set, the cages were distributed at least 15 m from each other to ensure independence of replicates.

Table 1. Proportion of pregnant females in each treatment after the experiment^a

Population density	Summer-born females			Over-wintered females			All females		
	Predation risk		Total	Predation risk		Total	Predation risk		Total
	Low	High		Low	High		Low	High	
Low	58.3 (12)	37.5 (16)	46.4	55.6 (9)	22.2 (9)	38.9	57.1 (21)	32.0 (25)	43.5
High	37.5 (16)	25.5 (12)	32.1	58.3 (12)	35.5 (14)	46.2	46.4 (28)	30.8 (26)	38.9
Total	46.4	32.1		57.1	30.4		51.0	31.4	

^a Total percentages show the effect of each factor separately. Total numbers of vole pairs shown in parentheses.

Increased risk by specialist predators was simulated by spraying the close vegetation surrounding the cages with the odour of captive stoats, *Mustela erminea*. We placed the cages outdoors inside high grass vegetation and under natural light, and sprayed only the surrounding vegetation to study the predator effect in a more natural situation than used in previous experiments by Ylönen and Ronkainen (1994) and Koskela and Ylönen (1995). We did not spray the cages and feeding areas of voles with odours, which could have caused decreased feeding and weight changes among the experimental animals, as in earlier studies. In the present study, we did not observe the behaviour of the pairs, but in previous experiments we found no crucial changes in the social or mating behaviour of caged bank voles (Ronkainen and Ylönen, 1994; E. Koskela *et al.*, unpublished data). A high population density of voles was produced by spraying the vegetation surrounding the cages with the odour of captive bank voles (both those of mature females and males). The density effect was strengthened by a free-living population of 80–100 bank voles in both 0.5 ha enclosures surrounding the treatment cages. This is the same maximum density observed by Mappes *et al.* (1995). The odour of stoats and voles was produced as a weak solution of water and captive animals' faeces and urine. About 5 ml of this solution was sprayed around each cage once a day. The control treatment (no predation and no competition) was subjected to the same routine as the others with the exception that the spraying was conducted 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 to September, simulating the last breeding events of the year. The manipulations of each replicate lasted 3 weeks. At the end of the experiment, the voles were killed, weighed and dissected to determine their reproductive stage and the number of embryos.

Results

The simulated predation risk decreased the proportion of breeding females; only 31% bred under stoat odour compared to 51% in the control group (Table 1). Using linear logit analysis (Dobson, 1990), the simple model with predation as the only defining factor fitted the data satisfactorily (scaled deviance = 0.562, d.f. = 2, $P = 0.755$) and the predation effect was significant ($G^2 = 4.161$, d.f. = 1, $P = 0.041$). The females of both age categories reacted similarly to stoat odour (the joint effect of age and predation risk: $G^2 = 0.306$, d.f. = 1, $P = 0.580$). The density of conspecific voles did not affect overall breeding (density effect: $G^2 = 0.363$, d.f. = 1, $P = 0.547$; Table 1), as young and old females seemed to respond differently to the high level of competition. There was a slight tendency for the high population density to suppress breeding in summer-born females (from 46.4 to 32.1%), but to stimulate breeding in over-wintered females (from 38.9 to

Table 2. Analysis of covariance for the effects of treatments on the final weights of the females when initial weight was used as a covariate^a

Source of variation	d.f.	MS	F	P
Predation	1	24.66	2.13	0.148
Density	1	0.14	0.01	0.914
Predation × density	1	24.19	2.09	0.152
Breeding	1	348.46	30.08	0.000
Error	94	11.58		
Total	99	24.33		

^a The initial weight did not deviate between the experimental groups (see Table 2).

50.0%). The division into two age categories decreased the size of the groups with the result that the joint effect of age and population density was not statistically significant ($G^2 = 1.702$, d.f. = 1, $P = 0.192$). Unexpectedly, predation risk and population density did not have a joint effect on reproduction ($G^2 = 0.199$, d.f. = 1, $P = 0.656$).

Neither the weight of females (Table 2) nor the breeding condition of males was affected by predation risk or population density: testis weights did not deviate between experimental groups at the end of the experiment (two-way ANOVA, predation effect $P = 0.556$, and density effect $P = 0.407$). Females breeding under high population density had larger litter sizes than under low population density (Fig. 1, Table 3). The same tendency was found for females under predation risk. Female age did not affect litter size (ANCOVA, $F = 0.016$, d.f. = 1, $P = 0.899$), but the weight of the females at the beginning of the experiment correlated significantly with litter size (regression $y = 1.494 + 0.184x$, $r^2 = 0.394$, $P = 0.0001$; Table 3). Neither age nor weight correlated with the experimental factors (Table 3). Time of replicates did not significantly affect the characteristics of reproduction ($P > 0.2$ in all cases).

Discussion

Our results support the hypothesis that female bank voles may delay breeding at least over short unfavourable periods (Ylönen, 1989; Heikkilä *et al.*, 1993; Norrdahl, 1993; Korpimäki *et al.*, 1994; Ylönen and Ronkainen, 1994). It would appear that only females change their mating behaviour according to environmental cues signalling future breeding success and survival. It is probable that polygynous males without parental care do not incur significant costs of mating behaviour under high population densities or predation risk, and consequently they do not respond as strongly behaviourally to risky situations as females do (Ronkainen and Ylönen, 1994).

Earlier laboratory studies (Ylönen, 1989; Ylönen and Ronkainen, 1994) indicated that predation risk decreases the weight of voles during experiments, probably due to decreased foraging (Koskela and Ylönen, 1995). This had been suggested to be the probable cause of observed breeding suppression. However, our results do not support this hypothesis. The level of manipulation was probably significantly lower in our experiment, where the cages of voles were distributed outdoors. We did not spray either the odours of predators or conspecifics in the foraging areas of voles, as in previous studies.

Phenotypic plasticity in breeding behaviour should be possible if the period of time for risky reproduction is short enough to be encountered during an individual's lifespan (Stearns, 1976). In the present study, female bank voles were faced with a choice: Should they breed at the end of the breeding season or should they delay breeding over the winter? So, from the point of view of the

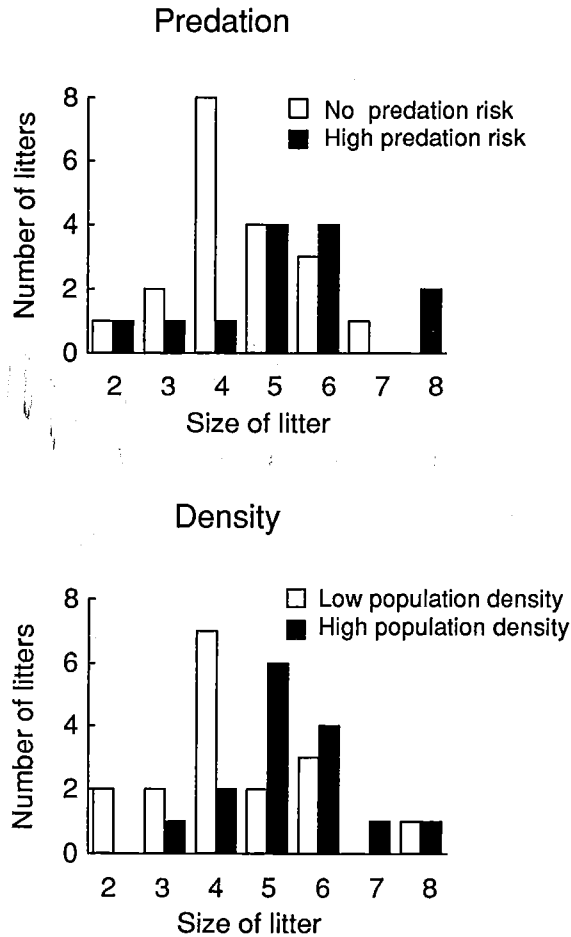


Figure 1. Distribution of litter sizes under different levels of predation risk and population density. The factors did not have a joint effect (Table 2), which permits a separate examination of the effects.

Table 3. Analysis of covariance for the effects of predation risk and population density on litter size^a

Source of variation	d.f.	MS	F	P
Predation	1	4.12	3.92	0.058
Density	1	6.64	6.32	0.018
Predation × density	1	0.01	0.01	0.931
Initial weight	1	26.35	25.08	0.000
Error	27	1.05		
Total	31	2.16		

^a The females were divided into two age categories, over-wintered and young females. The weight of females at the beginning of the experiment was used as a covariate. This initial weight did not deviate between the experimental groups (one-way ANOVA, $F = 0.96$, $P = 0.417$).

optimal tactic, the crucial question is: What is the likelihood that the risk factors – high population density and/or predation risk – which result in a high survival cost for breeding females and their young, will decrease during the following winter?

Densities of bank voles and their main predators (weasels and stoats) fluctuate cyclically and synchronously in central Finland (Korpimäki *et al.*, 1991). It would appear that populations of mustelids follow the abundances of bank voles with a 0.5–1 year time lag. In the present study, the high density of conspecifics and mustelids did not have a joint effect on breeding tactics of bank voles. This indicates that an increase in bank vole densities may not predict precisely an increase in predator densities, as 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.

Density-dependent breeding tactics

In the study area in central Finland, population densities of bank voles usually increase to high levels (over 100 individuals per ha) about every third autumn and then they crash (to one or two individuals per ha) during the following winter and early spring (Ylönen *et al.*, 1988). However, high autumn densities do not always predict very low spring densities and there may also be a decline during the following summer (Hansson and Henttonen, 1988). This unpredictability of population crashes might prevent female bank voles from adapting to cyclic density changes.

Under high breeding densities of bank voles, one can expect that breeding success of young summer-born females is very low. This is caused by social suppression of breeding by over-wintered females, which decreases their breeding success or prevents it altogether (Bujalska, 1985; Kawata, 1987). In the present study, a delay in breeding was slightly more common among young females. However, the evidence is limited and it is the task of future work to determine if some age categories of females respond differently to density variation.

Breeding tactics under predation risk

Populations of small mustelids track vole densities and reach high densities about every 3 years (Korpimäki *et al.*, 1991). The high autumn densities of mustelids seem to predict quite well their crashes during the following winter (four times out of six in weasels and three out of four in stoats, estimated from the results of Korpimäki *et al.*, 1991). The evidence of predictability is limited, but supports the existence of breeding adaptations described in the present paper.

Under a high risk of mustelid predation, both over-wintered and young summer-born females suppressed reproduction, although they had different life-time expectancies (Magnhagen, 1990). There is, however, some evidence 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 a high benefit of delayed breeding under high predation risk.

Reproductive investments and cyclic environment

It is to be expected (Stearns, 1976) that the delay in breeding might be profitable if (1) the physiological condition of individuals during mating and/or pregnancy or the mating behaviour itself increases vulnerability to predation (Cushing, 1985), (2) mortality of the young is very high during the current breeding season, or (3) the delay in breeding improves the individuals' survival to the next opportunity for reproduction (better physiological condition for overwintering; Clutton-Brock *et al.*, 1982). Accordingly, in a risky environment, a female vole appears to select

between two breeding tactics, which differ greatly in energy allocation and the probability of a 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 female bank voles may indicate an unstable equilibrium point in the trade-off curve between reproductive effort and adult survival (Schaffer, 1974; Stearns, 1976; Bell, 1980).

Besides the ecological benefits of delayed breeding (lower predation risk or population density in the next breeding season), there will also be 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.

In conclusion, we suggest that female voles are able to vary their reproductive effort if the environmental cues indicate the costs of reproduction. In cyclic vole populations, the crash of predator populations may be short enough to be encountered in a female's lifespan. An adaptation like breeding suppression could give a surviving individual a great selective advantage during the next breeding season when breeding success is significantly better.

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