

## Commentary

# Small mustelids and breeding suppression of cyclic microtines: adaptation or general sensitivity?

Hannu Ylönen, Esa Koskela & Mappes Tapio

*Ylönen, H., Koskela, E. & Mappes, T., Evolutionary Ecology Unit, Department of Biology and Environmental Science and Konnevesi Research Station, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä*

*Received 20 April 1994, accepted 30 November 1994*

## Summary

In this commentary we summarize mainly our own recent data on mating behaviour and reproduction in cyclic microtines, the bank vole *Clethrionomys glareolus* and the field vole *Microtus agrestis*, under increased predation risk by small mustelids. We suggest that breeding delay might be an adaptation to cyclically fluctuating predation risk, with fitness consequences for the individuals who chose the tactic of delayed reproduction during the population crash. This antipredatory adaptation should be stronger than, and possibly additive to the density-mediated behavioural differences between cyclic and non-cyclic voles. Further we suggest that the bank vole and the field vole, cycling synchronously in our study area and forming the main food resource for small mustelids, should exhibit similar behavioural responses to the presence of small mustelids.

## Introduction

We observed a strongly delayed onset of breeding in free-living bank vole females during a overwintering experiment in spring 1988 (Ylönen 1989). After that we have been able to show that

under laboratory conditions increased predation risk simulated by small mustelid odours suppresses or delays breeding both in bank voles and field voles originating from cyclic populations (Ylönen 1989, Ylönen et al. 1992, Ylönen & Ronkainen 1994, Koskela & Ylönen 1995). We have further observed the same effect under more natural conditions in large outdoor enclosures (Mappes & Ylönen, in prep.). Based on these similar results in all our experiments we suggest that in the delayed breeding we deal with a life historical adaptation with fitness consequences for the individuals living during the population crashes of vole cycles (Ylönen 1994). The two most common rodent species in cyclic study area, the bank vole and the field vole, have synchronous population fluctuations (see e.g. Henttonen et al. 1987) despite of their ecological divergence (see Table 1). Thus they face the same kind of biotic environment during different population phases. Characteristics of this environment include high intra- and interspecific competition and increasing predation pressure during the population peak, and strongest predation pressure — mainly by small mustelids — during the crash phase of the population. The early increase phase is characterized by only few conspecifics and other voles and almost total absence of small mustelid predators (e.g. Korpimäki et al. 1991). Small mustelids, especially the least

weasel, prefer *Microtus* voles before bank voles in their diet (reviewed by Henttonen et al. 1987, Korpimäki et al. 1991). Thus we suggest that *Microtus* voles should respond as strongly to small mustelid presence as *Clethrionomys* ones, or even stronger as suggested by Norrdahl (1993), and we should find the same kind of antipredatory adaptations to the increased predation risk by small mustelids in both prey species, the bank vole and the field vole.

### Sensitivity syndrom?

It has been shown in several studies on laboratory colonies (mainly on the bank vole) that voles

from cyclic populations react more sensitively to laboratory circumstances and possible density effects in the breeding colonies, than voles from non-cyclic populations (see Hansson 1990). As reviewed by Hansson (1995) this sensitivity can be seen in different behavioural parameters of cyclic voles in captivity, e.g. worse breeding, delayed maturation, greater aggressiveness, higher activity and stronger growth of individuals. Based on the number of differences between cyclic and non-cyclic voles Hansson (1995) suggests that a “general sensitivity syndrom” in cyclic voles, caused by high peak densities and crowding effects, could form the nature of cyclic voles’ stronger responses to the presence of small mustelid predators.

Table.1. Ecological characteristics of the bank vole *Clethrionomys glareolus* and the field vole *Microtus agrestis* in cyclic Fennoscandian populations and their responses to increased predation risk by small mustelids *Mustela nivalis* and *M. erminea*.

	Bank vole	Field vole
<b>Ecology and social behaviour</b>		
Preferred habitat	Forest, forest edges 1,2,3)	Fields, old fields, agricultural areas, clearcuts 1,2)
Habitat characteristics	Stable, unproductive 1)	Unstable, productive 1)
Food	Granivore – omnivore 4)	Folivore 4)
Social organization	Territoriality of breeding females 1,3)	Female clusters, and unstable territories 1,5)
Population cycles	Interspecific synchrony 6)	Interspecific synchrony 6)
<b>Predation and antipredatory responses</b>		
Role as food for small mustelids	Important 7,8)	Very important 7,8)
Breeding suppression in field under mustelid predation risk	Yes 9,10)	No significant change 10)
Breeding suppression in the laboratory	Yes 9,11,12)	Yes 13)
Changes in copulatory behaviour	Yes, less copulations 14)	Yes, less copulations 13)
Litter size under mustelid predation, in the laboratory	Increased 12, see also 11)	Not enough data 13)
Littersize under mustelid predation, in the field	Decreased 10)	No clear change 10)
Suppression of maturation under mustelid odour in the laboratory	Yes 15)	No data

1) Viitala & Hoffmeyer (1985), 2) Henttonen & Hansson 1984, 3) Ylönen et al. (1988), 4) Hansson (1985), 5) Pusenius & Viitala (1993), 6) Henttonen et al. (1987), 7) Erlinge (1975), 8) Korpimäki et al. 1991, 9) Ylönen (1989), 10) Korpimäki et al. (1994), 11) Ylönen & Ronkainen (1994), 12) Mappes & Ylönen (unpubl. data), 13) Koskela & Ylönen (1995), 14) Ronkainen & Ylönen (1994), 15) Heikkilä et al. (1993).

We have obtained breeding data from the control treatments of our experiments on the bank vole and the field vole (without any experimental manipulation, predator odour or conspecifics odour, and thus representing only the laboratory stock artifact). In every experiment we had far greater proportions of breeding females, than in Hansson's (1990, 1995) studies on the bank vole with only 20–30 % of the females from the cyclic populations breeding (see Table 2). In all of our experiments 50–100% of the wild-born control females bred. What we observed was a significant suppressive effect of small mustelid odour on breeding of experimental groups compared to “normally disturbed” voles of control groups: less than 17% of the females under mustelid odour bred, respectively (Ylönen 1989, Ylönen & Ronkainen 1994, Koskela & Ylönen 1995, Mappes & Ylönen, in prep.). Thus we did not observe the strong sensitivity in our cyclic voles to the laboratory environment artifact observed by Hansson (1990, 1995) and by Bondrup-Nielsen & Ims (1986). One explanation could be that we held the voles only for a short period, normally two weeks, in captivity before pairing them, compared to monogamous pairing of bank voles for longer than one year in Hansson's (1990) study. However, the different way of pairing cannot explain the significant differences between the experimental treatments. Further, in an experiment where we held bank vole pairs in cages in large outdoor enclosures with natural envi-

ronment, light and temperature conditions (= fresh air) (Mappes & Ylönen in prep.), we had a non-significant effect of conspecifics odour treatment (density effect) on breeding of the caged females at the same time as predator odour effect was significant. Thus our results indicate that the effect of small mustelid presence is different — and stronger — from those of density and crowding effects, which should cause the greater general sensitivity of individuals from cyclic populations (Hansson 1995). We suggest that the response to the mustelid odour could be additive to the other effects summarized by Hansson (1995) which should operate mainly in high-density populations, and thus the Former should have an adaptive character for the voles surviving the population crash. Adaptations operating during the population crash should be of far stronger selective advantage than those occurring during other phases of the cycle, as such a low number of individuals survive to the next breeding season (further discussed by Ylönen (1994)).

#### Do bank voles and field voles respond similarly to small mustelid presence?

Recently Korpimäki et al. (1994) studied with large unfenced study areas the effect of small mustelid presence and absence (= reduction) on reproduction of the voles inhabiting the study area. They found that the reduction of small mustelids increased the number of breeding bank vole females but not that of two “field” vole species, *M. agrestis* and *M. epiroticus* (= *M. roosiaemeridionalis*). In our experiments, however, we found about the same suppressive effect of mustelid odour on field vole and bank vole females: only 13% (n = 16) bred in the field vole and 18% (n = 34) in the bank vole Koskela & Ylönen 1995, Ylönen & Ronkainen 1994). Behavioural changes both in the bank vole and field vole females suggested that females under increased predation risk get some kind of copulatory inhibition and mating does take place more seldom than in the control group (Ronkainen & Ylönen 1994, Koskela & Ylönen 1995). Although laboratory and enclosure experiments have several restrictions in terms of generality, we believe that with a relatively great total number of caged pairs they allow us to draw a conclusion that the same

Table 2. Percentages of female bank voles and field voles reproducing in the control groups of our experiments, based on animals born in the field or in the laboratory. Wild-born individuals were held in average two weeks in captivity before pairing them.

Females	n	%	Reference
<b>FIELD-BORN</b>			
Bank vole	4	100	Ylönen (1989)
	6	50	Ylönen et al. (1992)
	34	67	Ylönen & Ronkainen (1994)
	9	55	Mappes & Ylönen unpubl. data
	11	81	Mappes et al. unpubl. data
Field vole	17	82	Koskela & Ylönen (1995)
<b>LAB-BORN</b>			
Bank vole	14	57	Mappes et al. unpubl. data

kind of adaptive delay of breeding occurs both in *Clethrionomys* and *Microtus* voles under increased risk of predation. This was expected according to the role of these both vole species in the diet of predators, and especially small specialist mustelids (reviewed by Henttonen et al. 1987).

## Conclusions

To conclude, results from several laboratory studies suggest that individual voles from cyclic populations can react differently and more sensitively to artificial laboratory conditions and crowding than do voles from non-cyclic populations. However, we believe that the strong response in breeding behaviour to the presence of small mustelids followed by breeding delay in females, is not primarily a same kind of sensitivity reaction, but an additive reaction to density effects with fitness consequences. In our sets of experiments ecologically different rodent species, the bank vole and the field vole, responded similarly to the indirect presence of small mustelids. This suggests the evolutionary origin of the phenomenon as individuals of the both species face the same selective environment during their synchronous population fluctuations (e.g. Henttonen et al. 1987). Already a delay of breeding of some months during the crash year summer should give the surviving individuals a great selective advantage, as the small mustelid populations decline strongly already during that summer (Korpimäki et al. 1991). Further the subsequent breeding season is characterized by low predation pressure resulting in a better survival of the young born during this phase of the cycle.

*Acknowledgements:* We thank Lennart Hansson and Erkki Korpimäki for comments on this note. Our studies were supported by the Finnish Academy.

## References

- Bondrup-Nielsen, S. & Ims, R. A. 1986: Reproduction and spacing behaviour of females in a peak density population of *Clethrionomys glareolus*. — *Holarctic Ecology* 9: 109–112.
- Erlinge, S. 1975: Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. — *Oikos* 26: 378–384.
- Hansson, L. 1985: The food of bank voles, wood mice and yellow-necked mice. — *Symp. zool. Soc. Lond.*: 55 141–168.
- 1990: Breeding of captive bank voles (*Clethrionomys glareolus*) related to dynamics of source populations. — *J. Reprod. Fert.* 89: 769–772.
- 1995: Is the indirect predator effect a special case of generalized reactions to density-related disturbances in cyclic rodent populations? — *Ann. Zool. Fennici* 32: 154–162.
- Heikkilä, J., Kaarsalo, K., Mustonen, O. & Pekkarinen, P. 1993: Influence of predation risk on early development and maturation in three species of *Clethrionomys* voles. — *Ann. Zool. Fennici* 30: 153–161.
- Henttonen, H. & Hansson, L. 1984: Interspecific relations between small rodents in European boreal and subarctic environments. — *Acta Zool. Fennica* 172: 61–65.
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukialmi, V. 1987: How much do weasels shape microtine cycles in the northern Fennoscandian taiga? — *Oikos* 50: 353–365.
- Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. 1991: Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? — *Oecologia* 88: 552–561.
- Korpimäki, E., Norrdahl, K. & Valkama, J. 1994: Reproductive investment under fluctuating predation risk: microtines and small mustelids. — *Evol. Ecology* 8: 357–368.
- Koskela, E. & Ylönen, H. 1995: Suppressed breeding in the field vole (*Microtus agrestis*): an adaptation to cyclically fluctuating predation risk. — *Behav. Ecol.* (in press).
- Norrdahl, K. 1993: Regulation of cyclic small mammal population by avian and mustelid predators. — PhD. Thesis, Department of Zoology, University of Helsinki.
- Pusenius, J. & Viitala, J. 1993: Varying spacing behaviour of breeding field voles, *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 143–152.
- Ronkainen, H. & Ylönen, H. 1994: Behaviour of cyclic bank voles under risk of mustelid predation: do females avoid copulations? — *Oecologia* 97: 377–381.
- Viitala, J. & Hoffmeyer, I. 1985: Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus*: Social odours, chemistry and biological effects. — *Ann. Zool. Fennici* 22: 359–371.
- Ylönen, H. 1989: Weasels *Mustela nivalis* suppress reproduction in cyclic bank voles *Clethrionomys glareolus*. — *Oikos* 55: 138–140.
- 1994: Vole cycles and antipredatory behaviour. — *Trends Ecol. Evol.* 9: 426–430.
- Ylönen, H. & Ronkainen, H. 1994: Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. — *Evol. Ecology* 8: 658–666.
- Ylönen, H., Kojola, T. & Viitala, J. 1988: Changing female spacing behaviour and demography in an enclosed breeding population of *Clethrionomys glareolus*. — *Holarct. Ecol.* 11: 286–292.
- Ylönen, H., Jędrzejewska, B., Jędrzejewski, W. & Heikkilä, J. 1992: Antipredatory behaviour of *Clethrionomys* voles — 'David and Goliath' arms race. — *Ann. Zool. Fennici* 29: 207–216.