

Different microhabitat preferences of field and bank voles under manipulated predation risk from an alien predator

Karen Fey¹, Peter B. Banks² & Erkki Korpimäki¹

¹) Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland (e-mails: karen.fey@utu.fi, erkki.korpimaki@utu.fi)

²) School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia (e-mail: p.banks@unsw.edu.au)

Received 4 Aug. 2005, revised version received 14 Nov. 2005, accepted 20 Nov. 2005

Fey, K., Banks, P. B. & Korpimäki, E. 2006: Different microhabitat preferences of field and bank voles under manipulated predation risk from an alien predator. — *Ann. Zool. Fennici* 43: 9–16.

Avoiding predators spatially or selecting safer habitats can improve survival prospects of potential prey animals. However, in the case of introduced predators, prey populations might lack the behavioural traits to escape predation. We studied responses of native voles to removal of an alien predator, the American mink (*Mustela vison*), on small islands in the outer archipelago of the Baltic Sea, SW Finland. Voles were live-trapped on 10 manipulation and 10 control islands in a grid of 50 traps per island. Microhabitat characteristics around trap locations were classified to four types reflecting risks of mink predation and suitability for foraging: grassy patches, juniper bushes, berries and open habitats. Microhabitat use of voles was analysed in relation to microhabitat availability. Field voles (*Microtus agrestis*) responded to the presence of mink with a microhabitat shift from open grassy habitats to juniper bushes. Bank voles (*Clethrionomys glareolus*), however, avoided juniper in the presence of mink and were significantly more often captured in juniper in removal areas. Use of open habitats by bank voles was also affected by their own density on islands. These divergent results may reflect species-specific differences in the social system, diet selection and escape behaviour of voles, but provide novel evidence for a microhabitat shift of native prey animals induced by an alien predator.

Introduction

Around the world, alien predators have typically had a devastating impact on native prey. Indeed, predation by introduced predators is listed in Diamond's evil quartet of extinction forces contributing to worldwide biodiversity declines (Diamond 1984). Their impact is also often rapid, with some prey species disappearing within just a few years of alien predator arrival.

In island ecosystems where re-colonisation is slow, the overall impact of alien predators is worst with islands having suffered the highest extinction rates for vertebrate animals, primarily caused by introduced predators (Courchamp *et al.* 2003). Prey naiveté to the novel predator is often cited as a primary factor in acute vulnerability of native species (Banks 1998, Short *et al.* 2002). Because adaptations to avoid predation risk, so called anti-predatory behaviours, derive

from long-term co-evolution between predator and prey, native prey are usually not adapted to the hunting strategies of introduced predators (Dickman 1996). However, there has been little experimental testing of this general hypothesis.

In co-evolved predator-prey systems, the mere risk of predation may induce behavioural changes in potential prey which are assumed to reduce risks of predation. These include changes in activity patterns, use of home ranges and habitats, foraging and even reproduction patterns (Lima & Dill 1990, Kats & Dill 1998). Avoidance of open microhabitats is a particularly common trait among many prey and has been suggested as an innate behaviour for some groups because the risk of successful attack from avian predators in open space seems universal (Banks & Powell 2004). But decision theory (Charnov 1976) predicts that risk avoidance is not without costs in terms of missed foraging and social opportunities, and so many prey tailor their behaviour to the level of risk posed by different sources of predation hazard (Brown & Kotler 2004). Thus many of these predation sensitive behaviours may be forsaken when the risk comes from an unknown source of predation risk such as from alien predators (Dickman 1992).

Among mammals, anti-predatory behaviour has been most extensively studied in rodents.

Particular attention has been paid to the study of voles and their mustelid predators in the search for the causes of vole cycles, including laboratory studies (Jedrzejewski *et al.* 1993, Korpimäki *et al.* 1996, Koivisto & Puseenius 2003, Sundell & Ylönen 2004), enclosure experiments (Erlinge *et al.* 1974, Jedrzejewska & Jedrzejewski 1990, Ylönen *et al.* 1992, Sundell *et al.* 2003), as well as field experiments (Korpimäki *et al.* 1994, Norrdahl & Korpimäki 1998, Jacob & Brown 2000, Banks *et al.* 2002, Carter & Bright 2003, Fülling & Halle 2004). Responses of voles to risk have been variable, including changes in habitat use, shifting of activity time and delaying maturation, particularly in response to indirect cues to predation risk such as predator odours. Voles also appear to recognise differing levels of risk associated with the odours of different predators, and respond accordingly (Jedrzejewski *et al.* 1993). Dickman (1992) showed that mice used more structurally complex habitats

when predation risk from alien, but co-existing predators (foxes and cats) was simulated to be high by adding predator odours.

But recent research examining large scale (enclosure-based) responses to odour manipulations have rejected earlier laboratory studies, showing that odour cues do not lead to the changes in mobility (Jönsson *et al.* 2000), habitat use (Wolff & Davis-Born 1997) and delays in breeding (Mappes *et al.* 1998) as expected. Similarly, the many correlative studies which have assumed that rodents typically avoid open microhabitats because the risks of predation from certain predators are higher there (for review see Lima & Dill 1990) have not measured or manipulated risk. Indeed, the responses of any mammals to manipulations of direct predation risk, via reduction of their predators, have rarely been studied (but see Norrdahl & Korpimäki 1998, Banks *et al.* 1999).

In this study we examine anti-predator behavioural responses of vole populations in the outer archipelagos of the Baltic Sea where they have had no resident mammalian predators in recent history while on the mainland of North Europe, small and medium sized predators, such as the polecat (*Mustela putorius*), stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*), exert considerable predation pressure on vole populations (Korpimäki & Norrdahl 1998, Korpimäki *et al.* 2002). But 20 years ago, American mink (*Mustela vison*; hereafter mink), a North American mustelid, began to invade the archipelagos of the Baltic Sea. Mink have continually escaped from Fennoscandian fur farms for more than 60 years and are now resident along the coastlines of the Baltic Sea and in the archipelago (Kauhala 1996). Mink have a diverse diet comprising mainly of fish and migratory birds, but they also feed on small rodents as a supplemental component of their diet (Niemimaa & Pokki 1990). During its invasion, mink had no natural competitors or enemies in the archipelago. The European mink (*Mustela lutreola*), which is morphologically similar to American Mink, never occupied archipelago areas. The native top predator in the archipelago, the white-tailed sea eagle (*Haliaeetus albicilla*), was practically absent when mink invaded the outer archipelago and is only now returning to the area due to

effective conservation programmes (Stjernberg *et al.* 2001). Thus contact between mink and voles in these systems has been limited so that selection for adaptations against mink has probably been less.

We focus on the effect of predation risk from mink on the habitat selection of field voles (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*) which are native occupants of outer archipelagos (Kostian 1970, Pokki 1981). We manipulated predation risk by removing mink from groups of small islands in the outer archipelago of the Baltic Sea and tested whether voles select different microhabitats in predator absence or presence. If voles are sensitive to risks of predation from mink, we predict that voles on islands with mink should prefer safer, denser microhabitats, i.e. habitats offering more shelter and facilities to escape, than voles on islands without mink.

Materials and methods

Study area and species

The study was conducted in the outer archipelago of the Baltic Sea (59°N, 21°E), which forms part of the Archipelago National Park in south-western Finland, approx. 80 km southwest of Turku. The area is characterised by small, exposed rocky islands and skerries, of which 75% are smaller than 2 ha. Vegetation on the islands is sparse and typically dominated by grasses (mainly *Festuca* spp.), low juniper bushes (*Juniperus communis*), bog bilberry (*Vaccinium uliginosum*) and crowberry (*Empetrum nigrum*) (see Nordström *et al.* 2002, 2003, Nordström & Korpimäki 2004 for additional details).

In the archipelago, two native vole species are found: the field vole, which is the most common herbivorous small mammal in the archipelago, and the bank vole, which is more patchily distributed and generally more abundant closer to the mainland (Kostian 1970, Ebenhard 1988) but does occur also in remote areas (Banks *et al.* 2004). They are preyed upon by birds and black adders (*Vipera berus*), but American mink (*Mustela vison*), a North American mustelid, is essentially the only terrestrial mammalian pred-

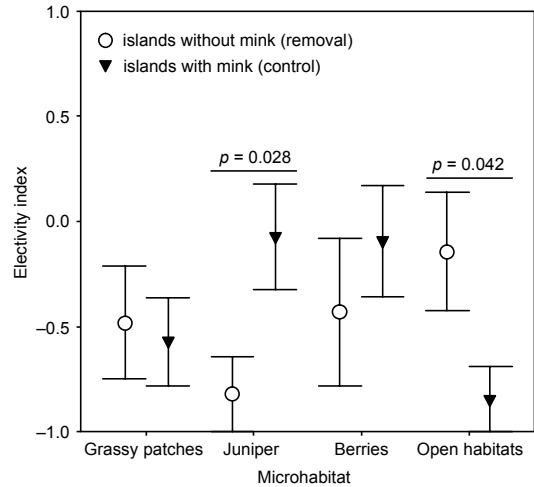


Fig. 1. Mean electivity indices (means \pm SD) for habitat selection of field voles in predator removal and control areas. A higher electivity index indicates stronger preference for a certain microhabitat type. Field voles showed significant different preferences for juniper and open habitats on mink removal and mink islands (Table 1).

tor in the study area. Other predators, such as red fox (*Vulpes vulpes*) and raccoon dog (*Nyctereutes procyonoides*), are extremely rare on islands of the outer archipelago (Nordström *et al.* 2002, 2003), and we did not observe any signs of mammalian predators other than mink during the study.

We studied mink impact on vole behaviour using a large-scale predator removal experiment. Since autumn 1992, mink have been consistently removed by gamekeepers during spring and autumn from 60 islands in a 72 km² area (R1) in Trunsö near Nauvo (59°49'N, 21°48'E). A control area with mink present (C1) of 77 islands across 90 km² was established > 10 km east in Vänö near Dragsfjärd (59°48'N, 22°11'E) (see Nordström *et al.* 2002, see 2003 for methods of removing mink and annual numbers removed and Banks *et al.* 2004: fig. 1, for a map of the study area).

Data collection

For each vole survey, 25 Ugglan multiple capture live-traps baited with standard laboratory mouse pellets were set on 10 islands of the control area

and 10 islands of the removal area. Islands were chosen to be as similar as possible in size and vegetation cover to support voles. Traps were set in 5 lines (10 m between lines) of 5 traps (20 m between traps) in vegetated areas avoiding bare rocks, and checked twice a day for four days. After two days traps were moved 10 m along the line to increase sampling of different microhabitats, thereby effecting a 10 m trap distance as typical for vole studies (Norrdahl & Korpimäki 1993, Prévot-Julliard *et al.* 1999, Klemola *et al.* 2000). All trapped individuals within each island group were individually marked both with an island code and a unique individual identifier.

To test our hypothesis under direct manipulation of predator numbers, the microhabitat characteristics in a 1 m radius around each trap location were recorded in 1999. The dominant vegetation was recorded and then classified to four broad microhabitat types which reflect a combination of structural complexity (and predation risk) and suitability for foraging: (1) grassy patches where voles feed and have their runways, (2) juniper, providing a dense covering but often with an open ground layer, and offering little in terms of foraging opportunities, (3) berries (comprising crowberries *Empetrum nigrum*, bog bilberries *Vaccinium uliginosum*, and raspberries *Rubus idaeus*), which offer sparse foraging opportunities, and some protection from predation risk, and (4) open habitats (comprising swamps, lichens, mosses, fern, heather *Calluna vulgaris*, tall reeds and bare rock) where foraging opportunities are sparse and which are most dangerous for voles due to the lack of structural complexity that would facilitate escape.

Statistical analyses

Islands were originally chosen because they generally contained suitable habitat for voles but showed small differences in vegetation and hence microhabitat availability, reflecting larger scale phenomena associated with their position in the archipelago landscape (*see* Banks *et al.* 2004). Therefore, to assess microhabitat use of voles in relation to microhabitat availability on an island, we calculated the Ivlev's Electivity Index E (Krebs 1989) for each habitat type on

each island using the following equation:

$$E = \frac{\text{success} - \text{availability}}{\text{success} + \text{availability}}$$

where

$$\text{success} = \frac{\text{number of successful traps within a habitat type}}{\text{number of successful traps on the whole island}}$$

and

$$\text{availability} = \frac{\text{number of traps within a habitat type}}{\text{number of traps on the whole island}}$$

A trap was only considered successful when an individual vole was trapped there for the first time; repeated captures were not taken into account and islands where no voles were trapped were excluded from the analysis.

We tested for mink removal effects on electivity index of voles for each microhabitat type separately. We used general linear models with treatment as a factor, and island as a nested factor within treatment. The factor island had no influence on electivity of voles, so we excluded it from the analyses (Underwood 1990) and assume that individual voles showed independent responses to mink presence. Mink removal did not influence vole densities in 1999 (Banks *et al.* 2004), thus density of voles on each island could be used as a covariate in the model (Underwood 1990). We also tested for possible effects of inter-specific competition, because both islands with only one vole species and both species were included in the study. But presence of the other species had no effect on electivity of voles and was excluded from the analyses.

All analyses were conducted with SPSS 11.5.

Results

During the study, 38 field voles were captured on 13 islands (seven islands with mink, six mink removal islands), and 58 bank voles on nine islands (four islands with mink, five mink removal islands). Of the 20 study islands eight were inhabited by field voles, four by bank voles, five by both vole species, and three islands were unoccupied.

Microhabitat selection of both vole species was influenced by the presence of mink. We

found significant differences in microhabitat selection in both field and bank voles (Table 1). Field voles on mink islands were significantly more often trapped under juniper bushes than field voles on mink removal islands. Field voles more often used open habitats on mink removal islands than on islands with mink (Table 1 and Fig. 1). Bank voles, on the other hand, preferred juniper bushes on mink removal islands but avoided them on islands with mink. The use of open habitats was influenced by bank vole density. Bank voles used open habitats only, when their density was high (Table 1 and Fig. 2). Both vole species showed no obvious differences between mink islands and removal islands in the selection of grass- and berry-dominated habitats.

Discussion

Our results show that voles in the outer archipelago differ in their microhabitat use when mink is present or absent. All habitat types that we pooled into the category open habitats provided minimal foraging opportunities and little protection from avian and mammalian predators, and should thus be avoided by voles. Field voles clearly avoided these open habitats in the presence of mink, but were occasionally trapped in such habitats on mink-free island. Bank voles were trapped only in open habitats where their density was high. The inter-specific difference might relate to their social systems. Bank vole females, in contrast to field voles, are strongly territorial during the breeding season (Myllymäki 1977, Koskela *et*

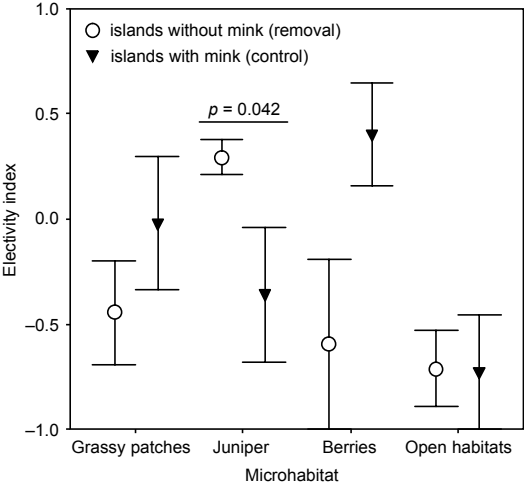


Fig. 2. Mean electivity indices (means \pm SD) for habitat selection of bank voles in mink removal and control areas. A higher electivity index indicates stronger preference for a certain microhabitat type. Bank voles showed significant different preferences for juniper on mink removal and mink islands (Table 1).

al. 1997). Thus, under high-density conditions, a proportion of female bank voles probably has to elude from already occupied areas to unfavoured areas.

Surprisingly, bank voles avoided juniper in the presence of mink. Juniper bushes do not offer much in terms of foraging but should afford protection for bank voles in terms of shelter and structural complexity to facilitate escape from predators because their most efficient escape tactic is climbing on trees and bushes (Jedrzejewska & Jedrzejewski 1990), whereas field voles mostly take refuge in tunnels

Table 1. ANCOVA on the effects of mink removal and voles' density on voles' preference of certain habitat types.

Habitat type	Source of variation	d.f.	Field voles		Bank voles	
			<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Grassy patches	treatment	1	0.037	0.851	0.691	0.438
	density	1	3.114	0.108	0.008	0.932
Juniper	treatment	1	6.642	0.028	6.615	0.042
	density	1	2.404	0.152	0.346	0.578
Berries	treatment	1	0.518	0.490	3.659	0.152
	density	1	0.005	0.943	1.049	0.381
Open habitats	treatment	1	5.407	0.042	4.793	0.071
	density	1	2.395	0.153	29.029	0.002

(Erlinge *et al.* 1974). However, juniper provides probably better shelter against avian predation than against mammalian predation, especially from mustelids which can hunt in small narrow spaces. Moreover, as there is much open space under these bushes, and remains of prey items of mink were often found under juniper (M. Nordström pers. comm.) during former studies on the islands (Nordström *et al.* 2002, 2003, Nordström & Korpimäki 2004), we assume that mink itself prefers juniper as shelter against predators such as sea eagle to explain the avoidance of these areas by bank voles in the presence of mink.

Field voles, in contrast, showed some preference for juniper on mink islands and might not be able to perceive predation risk there from sheltering mink. Bank voles are able to recognize and avoid the scent of American mink, as well as that of their native predators (Ylönen *et al.* 1992), but it remains unclear whether field voles are able to recognize mink in this way. (Carter & Bright 2003) showed e.g., that water voles *Arvicola terrestris* in the UK lack this behavioural mechanism to combat predation by non-native mink.

However, avoidance of open habitats in mink presence and different selection of juniper as habitat on mink islands and mink removal islands, though contrary to the behaviour of bank voles, suggest that field voles are also able to recognize predation risk by mink. It seems that they respond to predation risk by mink with tactics against avian predation, which has been, except for predation by black adders, the only form of predation risk in the archipelago for a long time. Snake predation risk might have less effect than avian predation risk on behavioural changes in small mammal prey. Kotler *et al.* (1992) found that gerbils confronted with predation risk from both owls and snakes seemed to perceive owls to be a greater threat than snakes. It is generally assumed that field voles are more vulnerable to predation than bank voles (Henttonen *et al.* 1977, Hanski & Henttonen 1996) because of their larger size, clumsiness and inferior escape tactics. Our results suggest also that adaptation to a new predator is faster proceeding in bank voles than in field voles.

Theory predicts that restricted access to foraging induced by mink presence could have

sub-lethal effects on vole populations (Hik 1995, Banks *et al.* 1999) and add to the lethal effects of mink predation on the voles (Banks *et al.* 2004). But mink presence had no impact on selection for habitats offering the most foraging opportunities, grass- and berry-dominated trap sites. It seems that voles are not necessarily trading safety for loss of foraging, and this may exacerbate the lethal effects of mink if risk of predation from mink in these places is higher. It is also possible that these patterns reflect differing level of predation in different habitats, such that we only measured the distribution of survivors not their behaviours. This scenario is not likely as small mammals are highly mobile and can typically invade empty space within a few days of vacancy after death of territory holders (Krebs *et al.* 1976).

Overall, our results indicate that voles perceive risks posed by mink, even though it is an alien predator and voles have had less than 50 years of exposure to predation pressure. Evolution of a trait depends upon many factors, including the strength of selective pressure, duration of exposure and costs of exhibiting the trait. In Australia, 3000 years of co-existence appears insufficient for native bush rats (*Rattus fuscipes*) to recognise and avoid odours of wild dogs (*Canis lupus dingo*) (Banks *et al.* 2003) which are an opportunistic predator of these rodents (Mitchell & Banks 2005). Similar naiveté has been reported in response of bush rats to foxes (*Vulpes vulpes*) after 150 years of exposure, and tammar wallaby (*Macropus eugenii*) responses to both wild dog and fox (Blumstein *et al.* 2002). In turn, Dickman (1992) also showed that insular alien house mice (*Mus domesticus*) do not recognise native marsupial quoll (*Dasyurus maculates*) odours despite 200 years of co-existence, but maintained avoidance of the odours from cats (*Felis catus*) and foxes without any exposure in the last 200 years. In our system, the vole's apparent rapid adaptation to risk from mink might have been facilitated by historic co-evolution on the mainland with other mustelids such as weasels and stoats. Mustelids share similarities in hunting techniques and chemical components of their odours which may aid in a general mustelids avoidance strategy (Nolte *et al.* 1994).

Acknowledgements

We thank Jayne Tipping and William Velmala for field assistance, and students of the Ph.D. seminar of the Section of Ecology, University of Turku for comments on the draft manuscript. The study was financially supported by the Maj and Tor Nessling Foundation.

References

- Banks, P. B. 1998: Responses of Australian bush rats, *Rattus fuscipes*, to the odor of introduced *Vulpes vulpes*. — *Journal of Mammalogy* 79: 1260–1264.
- Banks, P. B. & Powell, F. 2004: Does maternal condition or predation risk influence small mammal population dynamics? — *Oikos* 106: 176–184.
- Banks, P. B., Hughes, N. K. & Rose, T. R. 2003: Do native Australian small mammals avoid faeces of domestic dogs? Response of *Rattus fuscipes* and *Antechinus stuartii*. — *Australian Zoologist* 32: 406–409.
- Banks, P. B., Hume, I. D. & Crowe, O. 1999: Behavioural, morphological and dietary response of rabbits to predation risk from foxes. — *Oikos* 85: 247–256.
- Banks, P. B., Norrdahl, K. & Korpimäki, E. 2002: Mobility decisions and the predation risks of reintroduction. — *Biological Conservation* 103: 133–138.
- Banks, P. B., Norrdahl, K., Nordström, M. & Korpimäki, E. 2004: Dynamic impacts of feral mink predation on vole metapopulations in the outer archipelago of the Baltic Sea. — *Oikos* 105: 79–88.
- Blumstein, D. T., Mari, M., Daniel, J. C., Ardron, J. G., Griffin, A. S. & Evans, C. S. 2002: Olfactory predator recognition: wallabies may have to learn to be wary. — *Animal Conservation* 5: 87–93.
- Brown, J. S. & Kotler, B. P. 2004: Hazardous duty pay and the foraging cost of predation. — *Ecology Letters* 7: 999–1014.
- Carter, S. P. & Bright, P. W. 2003: Reedbeds as refuges for water voles (*Arvicola terrestris*) from predation by introduced mink (*Mustela vison*). — *Biological Conservation* 111: 371–376.
- Charnov, E. L. 1976: Optimal foraging, marginal value theorem. — *Theoretical Population Biology* 9: 129–136.
- Courchamp, F., Chapuis, J. L. & Pascal, M. 2003: Mammal invaders on islands: impact, control and control impact. — *Biological Reviews* 78: 347–383.
- Diamond, J. M. 1984: Normal extinctions of isolated populations. — In: Nitecki, M. H. (ed.), *Extinctions*: 191–246. Chicago University Press.
- Dickman, C. R. 1992: Predation and habitat shift in the house mouse, *Mus domesticus*. — *Ecology* 73: 313–322.
- Dickman, C. R. 1996: Impact of exotic generalist predators on the native fauna of Australia. — *Wildlife Biology* 2: 185–195.
- Ebenhard, T. 1988: Demography and island colonization of experimentally introduced and natural vole populations. — *Acta Univ. Uppsala* 141: 1–28.
- Erlinge, S., Bergsten, B. & Kristiansson, H. 1974: Hermelin och dess byte — jaktbeteende och flyktreaktioner. — *Fauna och Flora* 69: 203–211.
- Fülling, O. & Halle, S. 2004: Breeding suppression in free-ranging grey-sided voles under the influence of predator odour. — *Oecologia* 138: 151–159.
- Hanski, I. & Henttonen, H. 1996: Predation on competing rodent species: a simple explanation of complex patterns. — *J. Anim. Ecol.* 65: 220–232.
- Henttonen, H., Kaikusalo, A., Tast, J. & Viitala, J. 1977: Interspecific competition between small rodents in subarctic and boreal ecosystems. — *Oikos* 29: 581–590.
- Hik, D. S. 1995: Does risk of predation influence population dynamics — evidence from the cyclic decline of snowshoe hares. — *Wildlife Research* 22: 115–129.
- Jacob, J. & Brown, J. S. 2000: Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. — *Oikos* 91: 131–138.
- Jedrzejewska, B. & Jedrzejewski, W. 1990: Antipredatory behaviour of bank voles and prey choice of weasels — enclosure experiments. — *Ann. Zool. Fennici* 27: 321–328.
- Jedrzejewski, W., Rychlik, L. & Jedrzejewska, B. 1993: Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator–vole relationships. — *Oikos* 68: 251–257.
- Jönsson, P., Koskela, E. & Mappes, T. 2000: Does risk of predation by mammalian predators affect the spacing behaviour of rodents? Two large-scale experiments. — *Oecologia* 122: 487–492.
- Kats, L. B. & Dill, L. M. 1998: The scent of death: Chemosensory assessment of predation risk by prey animals. — *Ecoscience* 5: 361–394.
- Kauhala, K. 1996: Distributional history of the American mink (*Mustela vison*) in Finland with special reference to the trends in otter (*Lutra lutra*) populations. — *Ann. Zool. Fennici* 33: 283–291.
- Klemola, T., Koivula, M., Korpimäki, E. & Norrdahl, K. 2000: Experimental tests of predation and food hypotheses for population cycles of voles. — *Proc. R. Soc. London B* 267: 351–356.
- Koivisto, E. & Puseenius, J. 2003: Effects of temporal variation in the risk of predation by least weasel (*Mustela nivalis*) on feeding behavior of field vole (*Microtus agrestis*). — *Evol. Ecol.* 17: 477–489.
- Korpimäki, E. & Norrdahl, K. 1998: Experimental reduction of predators reverses the crash phase of small-rodent cycles. — *Ecology* 79: 2448–2455.
- Korpimäki, E., Koivunen, V. & Hakkarainen, H. 1996: Microhabitat use and behavior of voles under weasel and raptor predation risk: Predator facilitation? — *Behav. Ecol.* 7: 30–34.
- Korpimäki, E., Norrdahl, K. & Valkama, J. 1994: Reproductive investment under fluctuating predation risk — microtine rodents and small mustelids. — *Evol. Ecol.* 8: 357–368.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N. C. 2002: Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. — *Proc. Roy. Soc. London B* 269: 991–997.

- Koskela, E., Mappes, T. & Ylönen, H. 1997: Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. — *J. Anim. Ecol.* 66: 341–349.
- Kostian, E. 1970: Habitat requirements and breeding biology of the root vole, *Microtus oeconomus* (Pallas), on shore meadows in the Gulf of Bothnia, Finland. — *Ann. Zool. Fennici* 7: 329–340.
- Kotler, B. P., Blaustein, L. & Brown, J. S. 1992: Predator facilitation — the combined effect of snakes and owls on the foraging behaviour of gerbils. — *Ann. Zool. Fennici* 29: 199–206.
- Krebs, C. J., Wingate, I., Leduc, J., Redfield, J. A., Taitt, M. & Hilborn, R. 1976: *Microtus* population biology — dispersal in fluctuating populations of *Microtus townsendii*. — *Can. J. Zool.* 54: 79–95.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation — a review and prospectus. — *Can. J. Zool.* 68: 619–640.
- Mappes, T., Koskela, E. & Ylönen, H. 1998: Breeding suppression in voles under predation risk of small mustelids: laboratory or methodological artifact? — *Oikos* 82: 365–369.
- Mitchell, B. D. & Banks, P. B. 2005: Do wild dogs exclude foxes? Evidence from dietary and spatial overlaps. — *Austral Ecology* 30: 581–591.
- Myllymäki, A. 1977: Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. — *Oikos* 29: 553–569.
- Niemimaa, J. & Pokki, J. 1990: Minkin ravinnosta Suomenlahden ulkosaaristossa. — *Suomen Riista* 36: 18–36.
- Nolte, D. L., Mason, J. R., Eppler, G., Aronov, E. & Campbell, D. L. 1994: Why are predator urines aversive to prey. — *J. Chem. Ecol.* 20: 1505–1516.
- Nordström, M. & Korpimäki, E. 2004: Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. — *J. Anim. Ecol.* 73: 424–433.
- Nordström, M., Högmänder, J., Nummelin, J., Laine, J., Laanetu, N. & Korpimäki, E. 2002: Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. — *Ecography* 25: 385–394.
- Nordström, M., Högmänder, J., Laine, J., Nummelin, J., Laanetu, N. & Korpimäki, E. 2003: Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. — *Biological Conservation* 109: 359–368.
- Norrdahl, K. & Korpimäki, E. 1993: Predation and inter-specific competition in 2 *Microtus* voles. — *Oikos* 67: 149–158.
- Norrdahl, K. & Korpimäki, E. 1998: Does mobility or sex of voles affect risk of predation by mammalian predators? — *Ecology* 79: 226–232.
- Pokki, J. 1981: Distribution, demography and dispersal of the field vole, *Microtus agrestis* (L.), in the Tvärminne archipelago, Finland. — *Acta Zool. Fennica* 164: 1–48.
- Prévot-Julliard, A. C., Henttonen, H., Yoccoz, N. G. & Stenseth, N. C. 1999: Delayed maturation in female bank voles: optimal decision or social constraint? — *J. Anim. Ecol.* 68: 684–697.
- Short, J., Kinnear, J. E. & Robley, A. 2002: Surplus killing by introduced predators in Australia — evidence for ineffective anti-predator adaptations in native prey species? — *Biological Conservation* 103: 283–301.
- Stjernberg, T., Koivusaari, J. & Lehtonen, J. 2001: Population size, nesting success and protection status of nesting sites of the Whitetailed Sea Eagle *Haliaeetus albicilla* in Finland in 1999–2000. — *Yearbook of Linnéan magazine* 2000: 20–28.
- Sundell, J. & Ylönen, H. 2004: Behaviour and choice of refuge by voles under predation risk. — *Behav. Ecol. Sociobiol.* 56: 263–269.
- Sundell, J., Eccard, J. A., Tiilikainen, R. & Ylönen, H. 2003: Predation rate, prey preference and predator switching: experiments on voles and weasels. — *Oikos* 101: 615–623.
- Underwood, A. J. 1990: Experiments in ecology and management — their logics, functions and interpretations. — *Australian Journal of Ecology* 15: 365–389.
- Wolff, J. O. & Davis-Born, R. 1997: Response of gray-tailed voles to odours of a mustelid predator: A field test. — *Oikos* 79: 543–548.
- Ylönen, H., Jedrzejewska, B., Jedrzejewski, W. & Heikkilä, J. 1992: Antipredatory behaviour of *Clethrionomys* voles — ‘David and Goliath’ arms race. — *Ann. Zool. Fennici* 29: 207–216.