Jyväskylän yliopiston julkaisuarkisto
Jyväskylä University Digital Archive

UNIVERSITY OF JYVÄSKYLÄ

This is an electronic reprint of the original article.
This reprint *may differ* from the original in pagination and typographic detail.

Author(s): Hakkarainen, H.; Korpimäki, E.; Mappes, T.; Palokangas, P.

Title: Kestrel hunting behaviour towards solitary and grouped Microtus agrestis and M. epiroticus — a laboratory experiment

Year: 1992

Version:

Please cite the original version:

Hakkarainen, H., Mappes, T., Palokangas, P. & Korpimäki, E. (1992). Kestrel hunting behaviour towards solitary and grouped microtus agrestis and m. epiroticus - a laboratory experiment. Annales Zoologici Fennici, 29, 279-284.

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

Ann. Zool. Fennici 29:279–284
Helsinki 23 December 1992

ISSN 0003-455X
© 1992 Finnish Zoological Publishing Board

Kestrel hunting behaviour towards solitary and grouped *Microtus agrestis* and *M. epiroticus* — a laboratory experiment

Harri Hakkarainen, Erkki Korpimäki, Tapio Mappes & Päivi Palokangas

Hakkarainen, H., Korpimäki, E. & Palokangas, P., Laboratory of Ecological Zoology, Department of Biology, University of Turku, SF-20500 Turku, Finland
Mappes, T., Department of Biology, University of Jyväskylä, Konnevesi Research Station, SF-44300 Konnevesi, Finland

Received 20 March 1992, accepted 19 September 1992

Extensive field data show that avian and mammalian predators take more *Microtus epiroticus* than coexisting *Microtus agrestis* voles. The different vulnerability of these vole species may arise from prey selection or susceptibility differences between the two vole species. We studied the prey selection and hunting behaviour of the kestrel *Falco tinnunculus* on two *Microtus* voles, in addition to how behaviour and group structure in voles affect their vulnerability. The main results were that 1) kestrels do not select either of these species, but 2) susceptibility of the vole species deviates significantly. Falcons were more successful in catching *M. epiroticus* than *M. agrestis*, indicating that the latter is better in escaping avian predators and thus may have a lower cost of predation. During the experiment *M. epiroticus* aggregated more than *M. agrestis* but group size did not significantly explain capture success. However, solitary *M. epiroticus* seemed to be predated faster than those in groups. Although our results suggest that the high density of conspecifics may provide protection for vulnerable *M. epiroticus*, the aggregative distribution in the field and the preference for an open uncovered habitat may expose them to patch-searching predators.

1. Introduction

Predation may affect prey species both directly (through removal of prey animals) and indirectly (through the effects of predators on prey behaviour). Many field studies in northern temperate areas show that the mortality of microtine rodents due to avian and mammalian predators is high (e.g. Erlinge et al. 1983, 1984, Korpimäki & Norrdahl 1989, 1991a, Korpimäki et al. 1991). Therefore, selection may promote the anti-predatory behaviour of microtine rodents. This may be important especially among northern cyclic vole species, because the individuals surviv-

ing over the crash phase of the vole cycle are the founders of the next peak population and thus may gain fitness. Captive vole experiments have revealed that the presence of predators may alter, for example, the foraging behaviour, activity time, space use and reproductive effort of the rodent prey (e.g. Kotler 1985, Brown et al. 1988, Ylönen 1989, Jędrzejewska & Jędrzejewski 1990, Gerkema & Verhulst 1990, Longland & Price 1991, Kotler et al. 1991, Ylönen et al. 1992).

Two similar *Microtus* voles (*M. agrestis* and *M. epiroticus*) coexist in open country in western Finland. *M. agrestis* is the native microtine rodent on grassland, but *M. epiroticus* was introduced to the area in the 1940s (Sulkava & Sulkava 1967). The density of these voles fluctuates in 3–4-year cycles from 10 to 100 fold during a cycle (Korpimäki & Norrdahl 1991b). *Microtus* voles are the main prey of avian and mammalian predators in this area (Korpimäki 1988a, Korpimäki & Norrdahl 1991a,b, Korpimäki et al. 1990, 1991). Norrdahl & Korpimäki (1992) studied factors affecting the coexistence of two *Microtus* voles and concluded that the relative importance of predation and interspecific competition varied in the course of the vole cycle. Competition was more important in the increase phase of the cycle and predation in turn in the crash phase. *M. epiroticus* was superior in competition for space due to its smaller and overlapping home ranges, but suffered more from predation than *M. agrestis*, possibly because *M. epiroticus* aggregations were exposed to patch-searching predators (Norrdahl & Korpimäki 1992). However, it is also possible that predators selectively hunt *M. epiroticus*, or that there are susceptibility differences between the vole species.

Here we report on the results of a captive vole experiment constructed for the purpose of studying whether *M. epiroticus* is more exposed to avian predators than *M. agrestis* and how the group size of these two *Microtus* voles affects the risk of avian predation. We used kestrels, *Falco tinnunculus,* as the predators because they are the most important enemies of voles among open-country predatory birds in western Finland (Korpimäki & Norrdahl 1991a, b). On the basis of the field data obtained by Norrdahl & Korpimäki (1992) we predicted that there are interspecific differences in the behaviour of the two *Microtus* voles: *M. epiroticus* should be more social and more exposed to kestrel predation than *M. agrestis*.

2. Material and methods

We trapped kestrels in the late breeding season of 1990 in the Kauhava and Seinäjoki regions (62°40′–63°10′N, 22°40′–23°15′E), in western Finland (see Korpimäki 1988b for methods). The falcons were held in captivity at Konnevesi Research Station with the permission of the Finnish Ministry of the Environment. A total of 6 adult males, 7 adult females and 14 juveniles were used in the experiments. The *Microtus* voles used in the experiments were caught in early October 1990 in the Kauhava region using Ugglan live-traps.

We conducted laboratory experiments in October 1990 at Konnevesi Research Station in a room of dimensions 5 × 4 × 2.5 m. In each replicate we used 5 *M. agrestis* and 5 *M. epiroticus* voles. Body weight in the two species did not differ significantly (*M. agrestis*: mean = 31 g, $SD = 11$, $n = 14$; *M. epiroticus*: mean = 26 g, $SD = 5$, $n = 20$, *t*-test, $T = 1.69$, $df = 32$, $P > 0.1$). The voles were introduced into four equal sized (2 × 2 × 0.8 m) uncovered enclosures located symmetrically around the perch of the hunting kestrel. The voles were randomly placed as follows: one *M. agrestis* and *M. epiroticus* vole in two enclosures and four individuals of the same species in two other enclosures. After this, a falcon was released on to the perch of the experimental room. We carried out a total of 47 replicates. In the experiment, kestrels and voles were used more than once, due to the fact that we had a total of 27 falcons and 56 voles. However, kestrels always chose new voles, confirming that the replicates were independent of each other.

The hunting behaviour of kestrels was observed over 60 minutes continuous recording (Martin & Bateson 1986). The following characteristics of hunting performance were recorded:

1) the "scan", where a falcon scanned a certain vole or voles, bobbing its head almost continuously to estimate the distance to the prey before a strike;

2) the "capture attempt", where the kestrel launched itself from the perch and struck at the vole;
3) the "hunting time", the period between the start of the replicate and the successful hunting attempt.

"Capture success" was estimated by the proportion of successful attacks. It was classified into two categories:

1) "high success", if falcons caught voles during the first capture attempt and
2) "low success", if falcons needed more than one attempt to catch prey or did not succeed at all.

We studied the effects of vole species and group size on capture success by using linear logit analyses. These two parameters were added to the model together and one by one. The value 0.5 was added to each observed cell, because the value of one cell was zero. The analyses were performed with SPSS-X statistical software.

Vole behaviour was recorded during the 60 minutes from the start of the replicate. The behaviour of the voles was observed when the kestrels started to hunt. "Staying" meant that voles avoided moving. By contrast, some voles tried to make holes in the enclosure walls. This was called "fleeing". Short-distance movements in the enclosure, e.g. from one corner to another, were classified as "running". Sociality was estimated by aggregating behaviour in which individuals settled peacefully in the same corner. "Squeaking" was also classified as social behaviour. Antagonistic behaviour of voles was estimated by the number of fights. All statistical tests are two-tailed.

3. Results

There were no species-related differences in the number of capture attempts made by perching kestrels, though *M. epiroticus* seemed to be the preferred hunting object (Wilcoxon signed rank test, $z = 0.99$, $P = 0.32$, see also Table 1). A total of eight solitary *M. epiroticus*, three group *M. epiroticus*, three solitary *M. agrestis* and six group *M. agrestis* were caught by kestrels in the experiment. However, a susceptibility difference was found between the species, as during the first hunting attempts kestrels succeeded in catching *M. agrestis* in 2 out of 8 cases and 9 out of 12 cases in *M. epiroticus*. In the logit analyses on the capture success of kestrels, two models provided a statistically adequate explanation of the data ($P > 0.05$, Table 2): model (2) including vole species and group size, and model (3) in which species explained the capture success. No significant relationship was found between the interactions of group size and vole species (model 1: $\chi^2 = 2.23$, $P = 0.14$, Table 2). We chose the simpler model (3), because the effect of group size was not statistically significant ($\chi^2 = 1.22$, $df = 1$, $P > 0.10$). Accordingly, kestrels succeeded better at catching *M. epiroticus* than *M. agrestis* (Fig. 1). Instead, group size did not affect capture success: 50% ($n = 12$) of solitary voles and 63% ($n = 8$) of group voles were caught during the first capture attempt (see Table 2; model 4 did not fit the data).

The time elapsed in hunting different prey categories indicates that solitary *M. epiroticus* were more vulnerable to predation than group *M. epiroticus* (Fig. 2): the hunting time of the former

Table 1. The mean (±*SD*) number of scans and capture attempts made by perching kestrels per replicate ($n = 47$) on solitary and grouped individuals of *M. epiroticus* and *M. agrestis*.

		Scans		Capture attempts	
M. epiroticus	solitary	2.1	2.4	0.53	2.22
	grouped	4.7	6.7	0.38	0.92
M. agrestis	solitary	2.4	3.9	0.26	0.85
	grouped	4.1	5.0	0.28	0.58

Table 2. Details of the logit models. Capture success in kestrels was explained by the vole species and group size of voles. ScD = scaled deviance.

Model	ScD	*df*	*P*
(1) species + group size + species x group size	0.00	0	1.00
(2) species + group size	2.23	1	0.14
(3) species	3.45	2	0.18
(4) group size	8.18	2	0.02
(5) constant	8.48	3	0.04

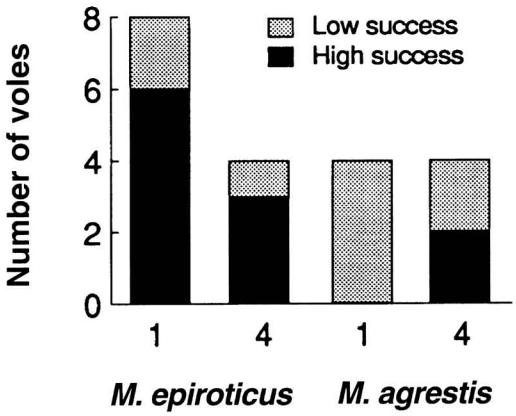

Fig. 1. The proportion of low and high capture success within different treatments (1 = capture success of solitary voles, 4 = the same, but for grouped voles).

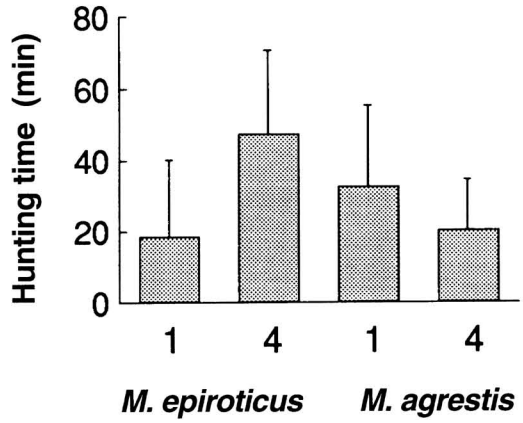

Fig. 2. The mean (±*SD*) hunting time (min.) for individual *Microtus epiroticus* 1 ($n = 8$), group *M. epiroticus* 4 ($n = 4$), individual *M. agrestis* 1 ($n = 4$) and group *M. agrestis* 4 ($n = 6$). The difference between the four treatments is nearly significant (Kruskal-Wallis test, $H = 5.65$, one-tailed $P = 0.07$).

tended to be shorter than that of the latter (Mann-Whitney *U*-test, $U = 5.0$, $P = 0.08$). Perching kestrels scanned vole groups significantly more than solitary voles (Wilcoxon matched-pairs signed ranks test, $T = 2.81$, $P = 0.005$ for *M. epiroticus*, and $T = 2.52$, $P = 0.012$ for *M. agrestis*) (Table 1). This was mainly due to young falcons: these focused on vole groups more than adults ($z = 3.31$, $P = 0.001$ for *M. epiroticus* and $z = 2.25$, $P = 0.02$ for *M. agrestis*).

M. agrestis seemed to fight more than did *M. epiroticus*, but the result was insignificant ($T = 1.27$, $P = 0.20$, Table 3). Indeed, the degree of aggregation differed significantly between the species: *M. epiroticus* aggregated more than *M. agrestis* ($T = 1.92$, $P = 0.03$), suggesting that the former species is more social than the latter one.

The vole group or solitary voles being scanned often responded to predation risk by running, as there were positive correlations between the number of scans and amount of running in each treatment (Spearman rank correlation, $r_s = 0.47$, $n = 47$, $P < 0.01$ for solitary *M. epiroticus*, $r_s = 0.26$, $P < 0.10$ for *M. epiroticus* groups, $r_s = 0.31$, $P < 0.05$ for solitary *M. agrestis*, and $r_s = 0.50$, $P < 0.001$ for *M. agrestis* groups). However, voles not being scanned did not respond to predation risk by running (r_s from 0.04 to 0.19 for different

Table 3. The behaviour of solitary and grouped voles of two *Microtus* species in 47 replicates in the presence of a kestrel. The figures show the mean number (±*SD*) of different kinds of behaviour per replicate.

	M. epiroticus		*M. agrestis*	
	Solitary	Grouped	Solitary	Grouped
Running	0.62 ± 2.09	0.77 ± 1.17	0.34 ± 0.56	0.98 ± 2.13
Squeaking	0.02 ± 0.15	0.32 ± 1.11	0.02 ± 0.15	0.30 ± 0.69
Fighting		0.04 ± 0.20		0.26 ± 0.99
Aggregating		0.79 ± 2.80		0.32 ± 1.08
Staying	0.83 ± 1.01	0.64 ± 0.76	0.91 ± 1.14	0.72 ± 0.83
Fleeing	0.30 ± 0.83	0.38 ± 1.10	0.09 ± 0.35	0.30 ± 1.10

treatments). Solitary *M. agrestis* tended to flee less than *M. epiroticus* (T = 1.60, P = 0.06). Vole groups of both species tended to run and squeak more than solitary voles (Table 3), but this may be simply because groups include more voles.

4. Discussion

No differences were found in catching attempts between the vole species, indicating that the high predation impact on *M. epiroticus* in the field (Norrdahl & Korpimäki 1992) obviously is not due to prey choice of avian predators. Instead, there were susceptibility differences between the vole species as hunting success in *M. epiroticus* was better than that of *M. agrestis*. Accordingly, the latter species seems to be better at escaping avian predators at the moment of catching. This was not due to prey size, because individuals of both species selected in this experiment were of the same size. For example, Kotler et el. (1988) have shown that predatory risk increases with rodent body size.

Kestrels, especially young ones, scanned vole groups more than individual voles, probably because a crowd of prey items is more conspicuous than a single item. Despite this, solitary *M. epiroticus* seemed to be killed faster than individuals of the same species in the group. Accordingly, the aggregative behaviour of *M. epiroticus* may decrease the avian predation risk. This may be because "the more eyes, the better the detection of a predator", a generally suggested advantage of group-living (see Bertram 1978 for a review). For example, in *M. arvalis* groups exposed to a kestrel model, neighbouring conspecifics which were unable to see the model also escaped provided they could see fleeing voles (Gerkema & Verhulst 1990). Also, several potential prey animals in the group may confuse the predator so that the predator is less able to concentrate on a certain prey item (Bertram 1987). It seems that aggregating behaviour of *M. epiroticus* may compensate for the high predation impact on this species although in this study group size did not affect hunting success. We did not observe aggregating behaviour of voles in the absence of a predator, which makes it impossible to tell whether aggregating behaviour of *M. epiroticus* was a response to the high predation risk.

In the field, there are at least two additional reasons which increase the predation impact on *M. epiroticus* compared with *M. agrestis*. First, the aggregative distribution of *M. epiroticus* with overlapping home ranges exposes them to patch-searching predators (Norrdahl & Korpimäki 1992), whereas solitariness and territoriality are a normal way of life in *M. agrestis* (e.g. Myllymäki 1977, Norrdahl & Korpimäki 1992). Second, open uncovered habitat may also make *M. epiroticus* vulnerable to avian predators. In the wild, *M. epiroticus* mainly occupies intensely cultivated fields with high predation risk, whereas *M. agrestis* favours high-grass vegetation, for example hay fields [(Norrdahl & Korpimäki (1992); for southern Finland see Myllymäki (1977), *M. epiroticus* was misidentified as *M. arvalis*)].

The finding that *M. epiroticus* aggregated more than *M. agrestis* is consistent with the field data from western Finland showing that the home ranges of *M. epiroticus* are smaller and overlap more than those of *M. agrestis* (Norrdahl & Korpimäki 1992). We thus conclude that *M. epiroticus* is more social than *M. agrestis*. Again, the close relative of *M. epiroticus*, *M. arvalis*, living in central and western Europe, is more gregarious than the sympatric *M. agrestis* (de Jonge 1983).

Finally, we would like to stress that the rodent enclosure experiments are hampered by unusually high predator densities that probably never occur in the field. Thus, the results of enclosure experiments do not necessarily reveal much about the predation rate in the field. As crepuscular or nocturnal activity of small rodents is difficult to observe in the field, we suggest that the best approach to the studies on their predator-prey interactions in the wild is most likely the combination of long-term field observations, field experiments and enclosure trials. Without detailed background data in the field, captive experiments may be too robust: predators visit the experimental enclosure too often, they perch too close to the prey, and prey densities are unnaturally high. In particular, this is true for the studies on avian and mammalian predator-vole prey interactions setting out to explain the causes of vole cycles in northern temperate areas (see e.g. Finerty 1980, Hestbeck 1987 for reviews).

Acknowledgements. We are grateful to Mikko Hänninen, Sakari Ikola and Jussi Ryssy for assistance in trapping voles and kestrels, and to Jussi Viitala and Antti Sirkka for good working facilities at Konnevesi Research Station. For valuable comments on the manuscript we thank Bogumila Jędrzejewska, Burt P. Kotler, Mikael Sandell and Hannu Ylönen. Antti Penttinen and Jukka Jokela helped with statistical analyses. H.H. was supported by the Finnish Cultural Foundation, E.K. by the Academy of Finland, T.M. by the Jenny and Antti Wihuri Foundation and H.H., T.M. and P.P. by the Alfred Kordelin Foundation.

References

Bertram, B. C. R. 1978: Living in groups: predators and prey. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural Ecology: 64–96. Blackwell Scientific Publications, Oxford.

Brown, J. S., Kotler, B. P., Smith, R. J. & Wirtz II, W. O. 1988: The effects of owl predation on the foraging behaviour of heteromyid rodents. — Oecologia 76:408–415.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., v. Schantz, T. & Sylvén, M. 1983: Predation as a regulating factor in small rodent populations in southern Sweden. — Oikos 40:36–52.

Erlinge, S., Göransson, G., Högstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I. N., v. Schantz, T. & Sylvén, M. 1984: Can vertebrate predators regulate their prey? — Amer. Nat. 123:125–133.

Finerty, J. P. 1980: The population ecology of cycles in small mammals. Mathematical theory and biological fact. — Yale University Press, New Haven and London. 230 pp.

Gerkema, M. P. & Verhulst, S. 1990: Warning against unseen predator: a functional aspect of synchronous feeding in the common vole, Microtus arvalis. — Anim. Behav. 40:1169–1178.

Hestbeck, J. B. 1987: Multiple regulation states in populations of small mammals: a state-transition model. — Amer. Nat. 129:520–532.

Jędrzejewska, B. & Jędrzejewski, W. 1990: Antipredatory behaviour of bank voles and prey choice of weasels — enclosure experiments. — Ann. Zool. Fennici 27:321–328.

de Jonge, G. 1983: Aggression and group formation in the voles Microtus agrestis, M. arvalis and Clethrionomys glareolus in relation to intra- and interspecific competition. — Behaviour 84:1–73.

Korpimäki, E. 1988a: Diet of breeding Tengmalm's Owls Aegolius funereus: long-term changes and year-to-year variation under cyclic food conditions. — Ornis Fennica 65:21–30.

— 1988b: Factors promoting polygyny in European birds of prey – a hypothesis. — Oecologia 77:278–285.

Korpimäki, E. & Norrdahl, K. 1989: Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of voles. — Oikos 54:154–164.

— 1991a: Do breeding nomadic avian predators dampen population fluctuations of small mammals? — Oikos 62:195–208.

— 1991b: Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. — Ecology 72:814–826.

Korpimäki, E., Huhtala, K. & Sulkava, S. 1990: Does the year-to-year variation in the diet of eagle and Ural owls support the alternative prey hypothesis? — Oikos 58:47–54.

Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. 1991: Responses of stoats and least weasels to fluctuating vole abundances: is the low phase of the vole cycle due to mustelid predation? — Oecologia 88:552–561.

Kotler, B. P. 1985: Owl predation on desert rodents which differ in morphology and behaviour. — J. Mammal. 66:824–828.

Kotler, B. P., Brown, J. S., Rosemary, S. J. & William, W. O. 1988: The effects of morphology and body size on rates of owl predation on desert rodents. — Oikos 53:145–152.

Kotler, B. P., Brown, J. L. & Hasson, O. 1991: Factors affecting gerbil foraging behavior and rates of owl predation. — Ecology 72:2249–2260.

Longland, W. S. & Price, M. V. 1991: Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? — Ecology 72:2261–2273.

Martin, P. & Bateson, P. 1986: Measuring behaviour. An introductory guide. — Cambridge University Press, Cambridge. 193 pp.

Myllymäki, A. 1977: Interactions between the field vole Microtus agrestis and its microtine competitors in Central-Scandinavian populations. — Oikos 29:570–580.

Norrdahl, K. & Korpimäki, E. 1992: Predation and interspecific competition in two Microtus voles. — Oikos (in press).

Sulkava, S. & Sulkava, P. 1967: On the small-mammal fauna of Southern Ostrobothnia. — Aquilo, Ser. Zool. 5:18–29.

Ylönen, H. 1989: Weasels Mustela nivalis suppress reproduction in cyclic bank voles Clethrionomys glareolus. — Oikos 55:138–140.

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.