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Does avian predation risk depress reproduction of voles?

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Abstract Reproductive output and the growth of captive voles were quantified under high and low avian predation risk in a semi-natural experiment. Voles were exposed to Eurasian kestrels (*Falco tinnunculus*), the main avian predator of vole species studied (*Clethrionomys glareolus*, *Microtus agrestis* and *M. rossiaemeridionalis*). Vole pairs were housed in cages settled under nest-boxes occupied by breeding kestrels or in control cages settled under empty nest-boxes for 2 weeks. The experiment was conducted in mid-summer when kestrels had half-grown nestlings, because in that time hunting adults and begging nestlings produce noise and scats which may indicate significant predation threat to voles housed underneath the nest-boxes. The risk of kestrel predation did not have any obvious impact on pregnancy rates, mean litter sizes, or growth rates of kestrel-exposed voles compared with control voles studied. These results indicate that the risk of avian predation does not depress the reproductive investment of voles.

Key words Avian predation risk · Indirect effects of predation · Reproductive investment · Breeding suppression · Voles

Introduction

Predation by birds of prey may be a substantial cause of mortality in small-rodent populations (e.g. Erlinge et al. 1983; Korpimäki and Norrdahl 1989, 1991a, b; Lin and Batzli 1995; Norrdahl and Korpimäki 1995a; Reid et al. 1997). Besides lowered survival, vole populations may also be indirectly affected by predators, if the mere risk of predation changes the behaviour of individual voles (Lima and Dill 1990). To date, most studies on indirect effects by avian predators have focused on changes in foraging behaviour, habitat selection and predator avoidance of voles (e.g. Desy et al. 1990; Gerkema and Verhulst 1990; Hakkarainen et al. 1992; Harper and Batzli 1996; Korpimäki et al. 1996), and other small mammals (e.g. Brown et al. 1988; Kotler et al. 1991, 1992; Longland and Price 1991; Boonstra et al. 1996; Rohner and Krebs 1996; Abramsky et al. 1997; Kotler 1997). However, the possible detrimental effects of avian predation risk on the reproductive output of prey have been highly ignored, although lowered productivity due to predation directly affects the demography of small mammal populations that are preyed upon (Korpimäki et al. 1994; Hik 1995; Klemola et al. 1997; Boonstra et al. 1998).

Theoretical models predict that prey animals will optimize their expected reproductive fitness by adjusting their behaviour to predation risk, and therefore their reproductive investment is supposed to vary according to predator densities (Ives and Dobson 1987). Varying predation risk is characteristic for vole populations fluctuating in a cyclic manner, because densities of their predators also fluctuate temporally (e.g. Henttonen et al. 1987; Korpimäki and Norrdahl 1989, 1991a; Korpimäki et al. 1991; Oksanen and Oksanen 1992; Korpimäki 1994). Individuals that have survived periods with the most intensive predation may have high fitness, because their descendants found the next peak population. Therefore, behavioural adaptations promoting survival of parents or their offspring during periods of high predation pressure should be highly advantageous. As reproductive activities may cause a greater risk of being eaten by a predator (Magnhagen 1991 and references therein), prey individuals may survive by refraining from breeding when predation risk is high.

To test the indirect effects of avian predators on the performance of voles, we conducted a semi-natural experiment exposing captive vole pairs to nesting Eurasian kestrels (*Falco tinnunculus*). In this experiment, we were particularly interested in knowing whether the presence

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of avian predators could depress the reproductive output and growth of voles.

Materials and methods

The experiment was carried out in the Alajoki study area covering 100 km^2 in western Finland (63°N, 23°E), where field voles (*Microtus agrestis*), sibling voles (*M. rossiaemeridionalis* syn. *M. epiroticus*) and bank voles (*Clethrionomys glareolus*) are the most abundant small rodents (Korpimäki and Norrdahl 1991b), and where the kestrel is the most important avian predator of these voles (Korpimäki and Norrdahl 1991a, b). The densities of vole species fluctuate up to 100-fold with a cycle length of 3 years (Norrdahl and Korpimäki 1995a), and the breeding density of kestrels is determined by the abundance of voles in early spring, at the time the kestrels settle on their territories (Korpimäki and Norrdahl 1991a; Korpimäki 1994).

Two hundred nest-boxes affixed to the walls of small barns are available for kestrels in the Alajoki study area (see Korpimäki and Norrdahl 1991a). In the experimental treatment, we used nest-boxes occupied by breeding kestrels to produce olfactory, auditory and visual stimuli for voles. These nest-boxes were randomly selected among all the boxes occupied by kestrels (31, 19, 24 and 32 nests in 1992–1995). Plastic vole cages (bottom 53 × 36 cm, height 30 cm) with half inch wire mesh cover were placed on ground under the nest-box. Each cage contained two sections: a sheltered part (*c*. 36 × 20 cm wide) with a plywood roof, and hay and straw as bedding and nesting material, and an open part with *ad libitum* food. The distance from the bottom of the cage to the nest of the kestrel was 4.5–5.0 m. For each experimental cage, a similar control cage was placed under an empty nest-box in a comparable site far (>500 m) from breeding kestrels.

We started the experiment with field and sibling voles (hereafter *Microtus* voles) in summer 1992, and continued with bank voles during 1993–1995. We used voles live-trapped from agricultural fields of the study area. Before the experiment, we weighed the voles to the nearest 0.5 g and checked their age, sex and breeding status. To ensure that female voles were not pregnant, they were individually housed for a week before the experiment. Thereafter, voles were randomly divided into experimental and control groups. One pair of voles was housed in each cage for 2 weeks. During the experimental period voles were given potatoes, carrots, oats and rat chow *ad lib* and fresh hay and dicotyledons (*Trifolium pratense*, *Stellaria media*, *Ranunculus acris* and *Taraxacum* sp.) every 3 day. After the experiment, we reweighed the voles, and sacrificed them in order to check their reproductive condition. We used the number of embryos as an estimate of the litter size of individual female voles. For pregnant *Microtus* females, we weighed the total mass of embryos, but for bank vole females, only lengths (to the nearest mm) of embryos were measured. Afterwards these lengths were converted to mass units according to the reference data by Ożdżeński and Mystkowska (1976), and subtracted from the final body mass of voles.

Voles were exposed to the breeding kestrels in late June to mid-July, when the nestlings were *c*. 2 weeks old. At that time, continuously hunting adult kestrels and their begging nestlings produce noise. In addition, droppings and pellets from the nest-box could cause olfactory disturbance and indicate a high predation risk to the experimental voles caged under the nest-boxes. No direct attacks by avian or mammalian predators towards vole cages were observed.

The data were analysed separately for bank and *Microtus* voles, and only voles surviving throughout the experiment were included. Breeding parameters (the proportion of pregnant females and the mean litter size) of females present underneath kestrel nests were compared with control females. The final body mass was tested by ANCOVA, using initial body mass as a covariate. Normalities of residuals of ANCOVAs were confirmed with Shapiro-Wilk's tests, and homoscedasticities of dependent variables were tested with Levene's tests. Statistical analyses used the SAS statistical package, version 6.10.

Results

There was no apparent between-treatment difference in the proportion of voles that become pregnant in the course of the 2-week experimental period. After the experiment, 27% of bank vole females exposed to kestrels were pregnant compared with 36% of control females (years pooled, Table 1). Respectively, half of *Microtus* vole females (species pooled) become pregnant during the experiment regardless of treatment (Table 1). The mean litter size (the mean number of embryos of females which had litters) did not differ significantly between experimental and control bank or *Microtus* voles (Table 1).

The final body mass of voles was unaffected by the experimental treatment (Fig. 1, Table 2). There were significant intersexual differences in the growth rate of

Table 1 The proportion of pregnant females (tested by Fisher's exact test) and the mean litter size (*t*-test) of experimental and control voles

Species	Experimental	Control	Two-tailed *P*
Pregnant females/(All females)			
Bank vole (1993–1995)			
Overwintered	3 (8)	3 (7)	1.00
Young of year	1 (7)	2 (7)	1.00
Pooled	4 (15)	5 (14)	0.70
Microtus voles (1992)			
Field vole	2 (4)	1 (2)	–[a]
Sibling vole	2 (3)	2 (4)	–[a]
Pooled	4 (7)	3 (6)	1.00
All species pooled	8 (22)	8 (20)	1.00 ($\chi^2 = 0.06$, $P = 0.81$)
Mean (±SE) litter size			
Bank vole (1993–1995)			
Overwintered	6.0 ± 0	5.3 ± 0.9	0.49
Young of year	5.0 ± –	5.5 ± 0.5	–[a]
Pooled	5.8 ± 0.3	5.4 ± 0.5	0.59
Microtus voles (1992)			
Field vole	5.0 ± 0	5.0 ± –	–[a]
Sibling vole	6.5 ± 0.5	3.5 ± 1.5	–[a]
Pooled	5.8 ± 0.5	4.0 ± 1.0	0.14

[a] Not tested

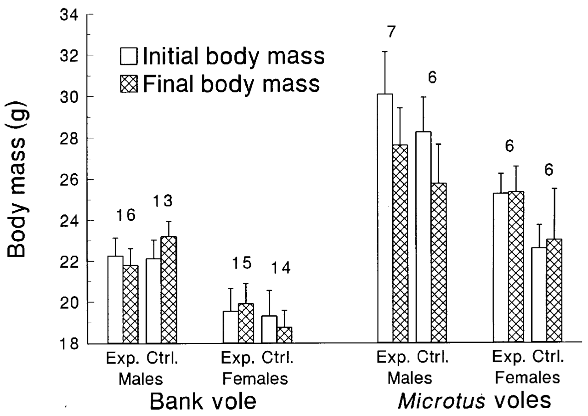

Fig. 1 Mean (+SE) body mass of bank and *Microtus* vole males and females in experimental (*Exp.*) and control (*Ctrl.*) cages. Voles were weighed before and after the experiment. The mass of embryos of pregnant females was subtracted from the final body mass. *Numbers* on top of bars denote the number of voles

Table 2 ANCOVA tables for the effect of treatment (exposure to kestrels) and other independent variables on the final body mass of voles. The initial body mass was used as a covariate

Source	*df*	MS	*F*	*P*
Bank vole				
Treatment	1	3.25	1.0	0.33
Year	2	1.15	0.3	0.71
Age	1	0.32	0.1	0.76
Sex	1	37.54	11.2	0.002
Treatment × Year	2	2.66	0.8	0.46
Treatment × Age	1	0.35	0.1	0.75
Treatment × Sex	1	7.68	2.3	0.14
Year × Age	2	18.35	5.5	0.008
Year × Sex	2	8.74	2.6	0.09
Age × Sex	1	17.45	5.2	0.028
Treatment × Year × Age	2	5.50	1.6	0.21
Treatment × Year × Sex	2	3.37	1.0	0.38
Initial body mass	1	119.32	35.6	<0.001
Error	38	3.35		
Microtus voles				
Treatment	1	0.56	0.1	0.79
Species	1	27.26	3.7	0.07
Sex	1	19.33	2.6	0.13
Treatment × Species	1	10.52	1.4	0.25
Treatment × Sex	1	3.27	0.4	0.52
Species × Sex	1	34.27	4.6	0.047
Treatment × Species × Sex	1	1.71	0.2	0.64
Initial body mass	1	127.18	17.2	<0.001
Error	16	7.40		

bank and *Microtus* voles during the experiment (Table 2), but the interaction of sex with the treatment factor did not reach significance. The same was true for the interactions of treatment with other independent factors (Table 2).

Discussion

The results we obtained do not indicate changes in behaviour of voles under high avian predation risk, because breeding parameters and the growth of voles seemed to be similar between experimental and control animals. In all vole species studied, the same treatment-independent pattern was observed in pregnancy rates during the experiment; one-third of bank vole and half of *Microtus* vole females became pregnant irrespective of the presence or absence of the kestrel nest. Therefore we suggest, despite relatively small sample sizes of females, that our results do not imply any trend towards breeding suppression of voles. We used captive voles in small cages but otherwise the situation was fairly natural, because the behaviour of kestrels was not manipulated, and because voles often live in and around small barns at similar distances to breeding kestrels as the experimental voles in the study. Although some wild voles might have refused to breed in captivity, the pregnancy rates of females in the experiment are comparable to pregnancy rates of free-living *Microtus* vole females in our study area at mid-summer (Norrdahl and Korpimäki 1993). To our knowledge, this is the first experiment where the reproductive output and growth of captive voles have been examined under high predation risk by avian predators.

High predation risk may reduce access to high-quality food and thus decrease resources needed in reproduction (e.g. Hik 1995). In our study, we did not find any obvious between-treatment differences in growth rates of voles, which suggests that avian predation risk of experimental group did not diminish their food intake. However, studies in captivity with high-quality food may not sufficiently reveal changes in the foraging of small rodents. Two recent studies on desert rodents clearly show the effect of experimental scale on the foraging behaviour of mammalian prey. Using large 2-ha enclosures and trained barn owls (*Tyto alba*) as avian predators, Abramsky et al. (1997) showed that gerbils (*Gerbillus allenbyi*) did not decrease their total foraging effort but shifted to safer foraging habitat when the owl predation risk was high. However, in a smaller-scale aviary (18 × 23 × 5 m) experiment, gerbils (*G. allenbyi*) also reduced their total foraging when barn owls were present (Kotler 1997).

Changes in behaviour of voles under high mammalian (family: Mustelidae) predation risk have recently been reported in several studies (e.g. Jedrzejewska and Jedrzejewski 1990; Heikkilä et al. 1993; Koskela and Ylönen 1995). As small mustelids (stoat, *Mustela erminea*, and least weasel, *M. nivalis*) mark their territories by scent (King 1989), and voles can detect and separate the scent of terrestrial mammalian predators (Jedrzejewski et al. 1993), it could be easier for voles to assess the magnitude of predation risk by mammals than by birds of prey. In addition, the home range of small mustelids is small, although variable depending on food resources and breeding status (Erlinge 1974, 1977; King 1975), and therefore their scent may indicate a significant local predation threat to voles.

In several laboratory experiments, captive voles exposed to small mustelid predators (or their scent) also show depressed reproductive investment (e.g. Ylönen 1989; Heikkilä et al. 1993; Koskela and Ylönen 1995; reviewed in Ylönen 1994; Mappes et al. 1998). However, the extrapolation of these results to natural circumstances is limited by the small spatial scale and unnaturally close connection between predator and prey (Lima and Dill 1990; Lambin et al. 1995; Korpimäki and Krebs 1996; Mappes et al. 1998). Larger-scale field experiments in replicated unfenced study areas showed that experimental reduction of predation risk in the crash phase of population cycle increased the pregnancy rate of free-living bank vole and *Microtus* vole females (Korpimäki et al. 1994; Klemola et al. 1997; see Norrdahl and Korpimäki 1995b for observational data). The breeding suppression of voles under high predation risk is a possible explanation for these results, but the selective killing of pregnant females by small mustelids may be more probable mechanism leading to the same final outcome; increased proportion of breeding voles in areas with reduced densities of predators (Klemola et al. 1997; see also Norrdahl and Korpimäki 1998). The negative result of our experiment with kestrels is comparable to recent studies conducted with penned *Microtus* voles by Parsons and Bondrup-Nielsen (1996), Wolff and Davis-Born (1997) and Mappes et al. (1998). These studies did not demonstrate any obvious effect of manipulated small mustelid predation risk on reproductive investment and behaviour of voles in controlled field situations.

More studies on indirect effects by avian predators on the behaviour of their mammalian prey are required. This is because changes in behaviour of small rodent prey that may reduce mortality from one predator type may expose prey to a second predator type (i.e. "predator facilitation"; see Kotler et al. 1991, 1992; Korpimäki et al. 1996). For example, a vole which shifts from short-grown grassland to a habitat with high ground vegetation is well sheltered against avian predation but concurrently more vulnerable to small mustelid predation. Therefore, in future, antipredatory behaviours of voles should also be studied in experiments that include both avian and mammalian predators (Korpimäki et al. 1996).

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