Non-lethal effects of avian predators on root voles (*Microtus oeconomus*).

Kirsti Eikenes

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Department of Biology
Division of Zoology
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Forord

En stor milepæl er snart nådd. Det har vært en lang og slitsom prosess, men du verden hvor mye jeg har lært. Det er mange som fortjener en takk og uten all hjelp jeg har fått hadde ikke dette vært mulig! Først og fremst vil jeg takke veilederne mine, dere har vært helt unnværlige!! Rolf, takk for at jeg ble så godt mottatt på kontoret ditt den dagen jeg var på desperat leting etter hovedfagsoppgave, og ikke minst for at jeg fikk være med på prosjektet på Evenstad. Harry, for dine optimistiske og interessante diskusjoner på Evenstad under feltperioden og veldig god hjelp under kommentering av oppgaven. Gry, takk for uvurderlig god hjelp til oppgaven og oppmuntring når jeg så svart på alt, uten deg hadde dette ikke vært mulig! Selv om du hadde mye å gjøre tok du deg tid til meg når jeg trengte hjelp.

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Abstract

Anti-predation behaviour in many rodents has mainly been studied under laboratory conditions, and less in naturally conditions in the field. Here we studied the results of an experiment specifically designed for testing the effect of avian predators on root vole *Microtus oeconomus* sub-populations. We compare the frequency of risk-prone behaviour in six protected versus six unprotected sub-populations, and study possible costs connected to such risky behaviour. More specifically, we predicted that root vole are able to detect the current risk of predation by avian, and therefore we assume that the degree of risk prone behaviour in root voles will be higher in areas protected from avian predators compare with unprotected areas. Additionally, we also investigate the possibility that the preceding mortality rate of the sub-populations is the specific cue used for detecting the current predation level and risk of being killed by a predator. In accordance with our hypothesis, the results showed that adults root voles performed less out-of-patch excursions when inhabiting areas with high levels of predation. Juveniles, on the other hand, did not differ between high and low predation levels. The frequencies of adult out-of-patch excursions were also positively correlated with the preceding mortality rate of the sub-population, we therefore suggest that mortality rate may be the cue used by the individuals as a demographical indicator of the current risk of predation.

Introduction

Predators can affect prey populations in several ways. One is the obvious direct effect they exert by killing individuals and thus perform a numeric influence on prey population dynamics (Post et al. 2002; Sinclair and Pech 1996; Stenseth et al. 1997), but predators may also affect their prey indirectly by changing the prey's activity pattern and demography (Korpimaki et al. 2002; Lima and Dill 1990). When confronted with high risk of predation, prey species may benefit from minimizing their normal spacing behaviour, and in that way be more difficult to detect (Borowski 1998). The clear benefit of such anti-predator behaviour is the reduced probability of being killed. However, reduced spacing behaviour may also be costly for the animal due to lowered chances of acquiring food (Hovland et al. 1999; Lima and Dill 1990; Werner et al. 1983) and may result in secondary consequences such as reduced rates of growth and reproduction (Bolbroe et al. 2000; Boonstra et al. 1998a).

Predation is acknowledged as one of the strongest selective forces, which is clearly demonstrated by the look of anosmatic and cryptic animals as well as other morphological

traits such as protective armor and chemical defence (Sih 1987). Such adaptations reflect the outcome of the constant interaction between predators and prey over evolutionary time. However, viewed at a smaller time-scale, i.e. ecological time, prey populations may experience large variation in predation pressure which may vary greatly on a seasonal or yearly basis. Behavioural flexibility driven by predation risk, i.e. a trade-off between predation avoidance and energy acquisition, should therefore be expected to be found in species that experience large seasonal or yearly fluctuations in predation levels (Kotler et al. 1994; Norrdahl and Korpimaki 1998; Ylonen 1994).

The literature of non-lethal effects of predation on small mammals is based on both theoretical (Brown 1992; Gilliam and Fraser 1987) and empirical studies (Hughes et al. 1994; Kotler 1984; Kotler et al. 1992). The interest in this issue may be due to the fact that demographic processes result from individual behaviour and that individual anti-predator behaviour may have consequences registered at the population dynamics level (Lima 1998; Lima and Zollner 1996). In a study of cyclic populations of snowshoe hares *Lepus americanus* Hik (1995) concluded that non-lethal (or sub-lethal) effects caused by the presence of predators initiate a cascade of behavioural and physiological responses in the snowshoe hare populations that contribute in maintaining the low-phase of the cycle. If such time lag of recovery of the prey population is of a certain length it could, according to May (1974; 1981), actually play an important role in generating population cyclisity. High levels of predation risk has also been proposed to cause the prolonged low abundance phase of the population cycle of voles through restricted behavioural activities of the voles (see also Boonstra et al. 1998a; Boonstra et al. 1998b; Korpimaki et al. 1994; Ylonen 1994). Non-lethal effects of predation have also been suggested to play an important role in the demographic dynamics of the neotropical leaf eared mouse *Phyllotis darwini* (Lima et al. 2001).

Here we present the results of an experiment specifically designed for testing the effect of avian predation (e.g. common buzzard *Buteo buteo* and long-eared owl *Asio otus*) on root vole *Microtus oeconomus* sub-populations. We compare the frequency of risk-prone behaviour in six protected versus six unprotected sub-populations, and study possible costs connected to such risky behaviour. Specifically, we predict that root voles are able to detect the current predation risk. Consequently the degree of risk prone behaviour in root voles will be higher in areas protected against avian predators than in the unprotected areas. In addition, we also investigate the possibility that the mortality rate of sub-populations is the specific cue used for detecting the current predation level or risk of being killed by a predator.

Materials and methods

Experimental area and animal

The present study was performed at Evenstad Research Station, Østerdalen; eastern Norway, between the middle of May and late October 2001. The study area consisted of 3 ha (i.e. 30 000 m^2) total area, which was partitioned in six "vole-proof" plots, each of size 0.5 ha (see Fig. 1). Each plot or enclosure was restricted with galvanized steel sheet fences extending 0.6 m above and 0.4 m below ground. In each plot there were four habitat patches in a paired design that consisted of meadow vegetation (grass and clover) of the same type as natural root vole habitat in the areas surrounding the experimental plots. The patches has been burned yearly, tilled and fertilised to maintain a high quality vegetation for fulfilling the habitat requirement for the root vole (Ims et al. 1993; Tast 1966), and to smooth out any potential heterogeneity within and between the habitat patches. However, in the year of the present study we incorporated habitat quality as an experimental treatment factor and therefore treated only one patch in each pair with the usual preparation procedure. As later analysis showed that there was no effect of habitat quality on demography of root voles (G. Gundersen, unpublished data), we treated each pair of patches as a unit and omitted habitat quality from the analysis. Since there was very little immigration between the plots and paired patch this was not further analysed. The matrix surrounding the habitat patches, was frequently herbicided (Roundup) and mowed during the whole plant-growing season to keep this area free for any vegetation, and thus not habitable for voles. Between each of the six plots there was a 10 cm opening in the fence to let animals disperse from one plot to the other (Fig. 1). The total study area was surrounded by a wire mesh fence to prevent mammalian predators from entering the area.

The experimental treatment consisted of excluding avian predators. An anti-avian predator net were extended vertically (walls) and horizontally (roof) above two of the four patches in each enclosure (Fig.1). The net had a 10 x 10 cm mesh width and were raised by nine 3 - 4 meter long wooden pillars.
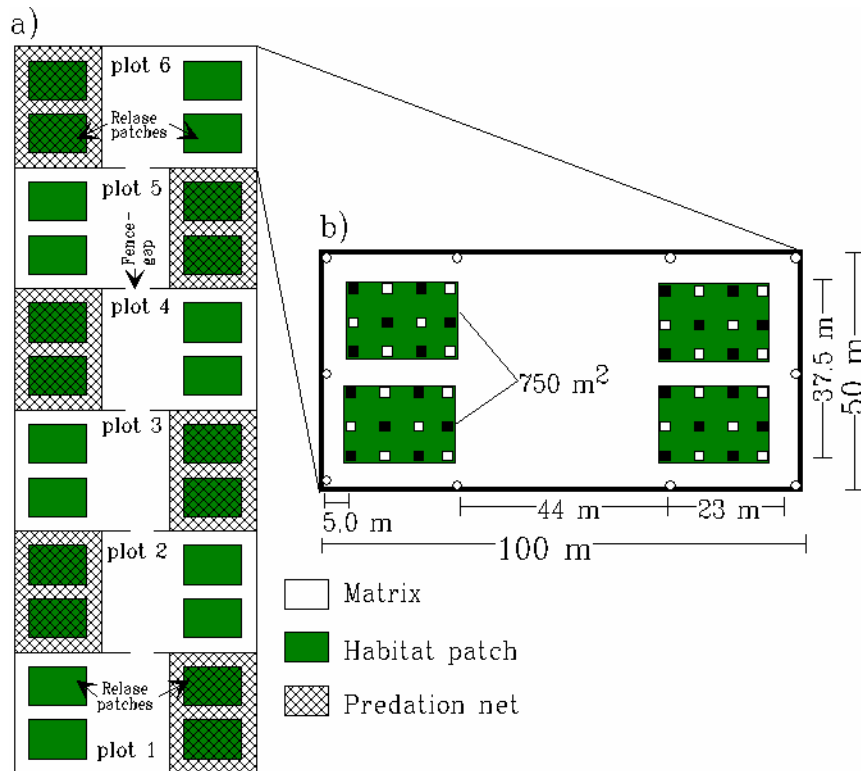
Figure 1. a) Design of the experimental area. The six plots contained four habitat patches each in a paired design. One pair of habitat patches in each plot was covered by a predator net (shaded area). The areas surrounding the habitat patches (unshaded areas) illustrate the non-habitat matrix. **b)** An enlarged view of the details of a plot. Location of trap stations indicated by small squares. Filled squares: only Ugglan traps present, open squares: trap stations with both Ugglan and pitfall traps present. Open circles: Dyed bait stations. Since the habitat quality treatment was given to the two outermost patches, the next outermost patches were used as release patches. See text for further description of the study design.

The root voles used in this experiment were laboratory raised animals originating from Valdres in southern Norway. They were kept in the laboratory at the Animal Division of the University of Oslo, where they were allowed to reproduce under controlled conditions. On May 16th, twelve mothers (first generation from the wild captured animals) with their newly weaned offspring (second generation) were released into the two outermost enclosures (plot 1 & 6), in the next outermost habitat patches, i.e. the *release patches* indicated in Figure 1. A total of 12 mothers, 27 daughters and 30 sons were released in the study area. The animals were distributed as evenly as possible among the four release patches without breaking up the matrilineal groups (mother with her litter). All animals were individually toe-clipped before they were released into the experimental field area. All the enclosures had been emptied for animals overwintering in the area. After a period of nine days for establishment, we made the 10 cm gaps between plots to permit colonisation of the whole experimental landscape.

Table 1. Date schedule of release and trapping sessions for year 2000 and 2001.

Trap session		Date
0	Release of laboratory animals	16 May
1	Trapping session	14 Jun
2	Trapping session	30 Jun
3	Trapping session *	12 Jul
4	Trapping session *	30 Jul
5	Trapping session *	17 Aug
6	Trapping session *	4 Sep
7	Trapping session *	21 Sep
8	Trapping session *	10 Oct
9	Trapping session *	28 Oct

* Trapping sessions when dyed bait was used (see section below).

Live-trapping

Regular live trapping started on June 14th (see Table 1 for a detailed schedule of date of release and trapping sessions). Live trapping sessions were conducted with approximately 15 days intervals (Table 1). Each trapping session lasted for 3 days and included six trap-checks (traps activated from 24:00 h to 12:00 h and checked at 06:00 h and 12:00 h). In total, eight trapping sessions were completed during the field season (5 months). We used Ugglan multiple capture live traps (Gundersen 2002) in each plot combined with pitfall traps. The traps were activated and baited with whole grained oats and a piece of fresh carrot. Twelve trap stations were located in a grid system with 5 m spacing within each habitat fragment (Fig. 1b). For all captures we registered trap positions, toe codes, sex, weight, and reproductive status. For females, sexual status was recorded as visible pregnancy, perforated vaginal opening and lactation. For males, sexual status was recorded as scrotal or abdominal testes. Young unmarked animals were toe-clipped (removal of different toe for individual marking) at the time of first capture.

Dyed bait

In addition to live trapping we used a method with dyed bait (Hovland and Andreassen 1995) to register risky movements outside the patches. Bait, consisting of 70 % water and 30 % oatmeal, were dyed and placed in petri dishes along the fences in the matrix area (Fig. 1). Fluorescent pigment (Radiant colour, Richmond, California) was used as marker in the bait. The pigment is visible in faeces examined in UV-light from a period of 2 - 3 hs after the bait

has been eaten, and is still evident 36 – 48 hs after the removal of bait. See Hovland and Andreassen (1995) for a more thorough description of the method.

The bait was put out in the field at 24:00 h, 48 hs before the first activation of traps each session. We then sampled faeces from Ugglan traps in individual plastic bags during regular trapping sessions. Sampling of faeces was performed only from captures of solitary individuals since it is impossible to identify from witch individual the faeces belong to in multiple captures. Before reactivating, the traps were cleaned to avoid colour contamination in future captures (Hovland et al. 1999). The faeces were later examined for contents of fluorescent pigments under an UV-lamp. In total, there were performed seven trapping sessions including dyed bait. All petri dishes were removed after the end of a trap session.

Analyses

Demographic background

Population development was analyzed as the time specific minimum number of voles known to be alive (MNA) in each paired patch. Previous study's (Aars and Ims 1999, 2000) from the same experimental area show that the there are nearly 100 % capture-recapture rate. Population development is presented as the average minimum number of individuals known to be alive in each paired patch with bars showing standard deviation.

Survival was analysed as the proportion of animals in each paired patch that was known to be alive from one trapping session to the next. Survival response variables (Table 2) were analysed by logistic regression according to the two predictors; experimental treatment (predation net) and season (Table 3).

Risky behaviour

Two types of potentially risky behaviours were recorded; 1) *Out-of-patch excursion rates* were defined as the proportion of individuals in each paired patch that had eaten dyed bait. 2) *Interpatch movement rates* were defined as the proportion of individuals that had moved between the paired patches within one trapping session. Both responses were analysed according to the experimental treatment and the co-variables season, sex and age, and all possible two way interactions (Table 2).

Table 2. Description of the response variables. All variables were analysed at the level of the paired patch.

Response variables	Description
MNA	The time specific minimum number of animals known to be alive.
Survival	Proportion of survived animals from trapping session t to t + 1.
Out-of-patch excursion	Proportion of animals captured with faeces containing dyed bait. [*]
Interpatch movement	Proportion of animals that were captured in both of the paired patches[+].
Mortality	Mortality from trapping session t to t + 1, 1 - survival.
Individual body growth	Individual growth of body mass between trapping sessions t to t + 1.

[*] Only individuals that were captured solitary were included in the analysis (see text).
[+] Only individuals that were trapped more than once during the trapping session were included in the analysis.

Consequences of risky behaviour

In order to reveal possible fitness consequences of the different movement behaviours (out-of-patch excursion and interpatch movement), we analysed mortality rates and body growth according to the individuals movement history (i.e. performed risky behaviour or not during the last trapping session, Table 3). The analyses were performed separately for the two behavioural responses; out-of-patch excursion and interpatch movement.

Table 3. Description of the predictor variables.

Predictor variables	Description
Experimental treatment	Anti-avian predator net constituted the experimental treatment. Treatment = covered patches, control = uncovered patches.
Age	The individuals' age. For females the adult stage was defined to start when she had been pregnant with her first litter. Males were defined as adults when they had been recorded with scrotal testes.
Sex	Female / male
Season	Defined through the nine trapping sessions.
MNA	The time specific minimum number of animals known to be alive.
Mortality rate	Proportion of dead individuals in each paired patch between trap session t - 1 and t.
Interpatch movement history	Whether or not the individual performed interpatch movement during the last trapping session.
Out-of-patch excursion history	Whether or not the individual performed out-of-patch excursion during the last trapping session (used in the analysis of the demographical consequences of risky behaviour).
Growth	Average individual body growth in grams during trapping session t.

Cues used for recognition of predation level

In search for potential demographic cues that animals could use to detect predation level, we analysed the association between mortality rate (i.e. the proportion of animals that died between trap session t -1 and t specific to each paired patch, Table 3) on the two movement responses; out-of-patch excursion and interpatch movement performed at time t.

Statistical analyses

All responses specific to trap session were analysed by repeated-measurement with the paired patch as a subject-level random factor. Binomial responses (i.e. survival, out-of-patch excursion rate and interpatch movement rate) were analysed by logistic regression, and the poisson distributed response (MNA) by log-linear model, all implemented by the macro GLIMMIX in SAS version 8.00 (Littell et al. 1996). The fixed factors; treatment (predator net / no predator net), season (i.e. trapping session), sex (female / male) and age (adult / juvenile) and all possible two- and three-way interactions were included in the full models (Table 4) and thereafter successively removed by a backward selection procedure to leave only significant (p < 0.05) parameters in the final model. We used also AIC (Akaike Information Criterion) were the best model have the smallest value. Number of animals (MNA) was also included as a co-variable in the analyses of risky behaviour (Table 4).

Table 4. Overview of the variables included in the full models.

| Section	Response	Predictors
Demographical background		
	MNA [*]	Treatment
		Season
	Survival [*]	Treatment
		Season
Risky behaviour		
	Out-of-patch excursion [*]	Treatment
		Season
		Sex
		Age
		MNA
	Interpatch movement [*]	Treatment
		Season
		Sex
		Age
		MNA
Consequences of risky behaviour		
	Mortality [+]	Treatment
		Out-of-patch excursion history
	Mortality [+]	Treatment
		Interpatch movement history
	Individual body growth	Sex
		Age
		Season
		Out-of-patch excursion history
		Individual body weight
	Individual body growth	Sex
		Age
		Season
		Interpatch movement history
		Individual body weight
Cues used for recognition of predation level		
	Out-of-patch excursion [*]	Preceding mortality rate
		Season
		Sex
		Age
	Interpatch movement [*]	Preceding mortality rate
		Season
		Sex
		Age

[*] All analyses of season-specific data were analysed by repeated measurements with the paired habitat patch as a subject level random factor.

[+] Simpler full models were chosen here as the data structure did not allow convergence of complex models.

Results

Demographic background

Overall survival was higher in the protected patches compared to the unprotected patches ($F_{1, 94} = 4.20$, p = 0.043; Fig. 2). However, due to high levels of immigration into the uncovered areas (Gundersen and Ims, in prep.) there was in general a higher number of voles in the unprotected than in the protected patches throughout the main part of the field season (on average 2.97, SE = 1.6 ($F_{1, 10} = 3.45$, p = 0.093) more individuals in uncovered compared to covered, Fig. 3).
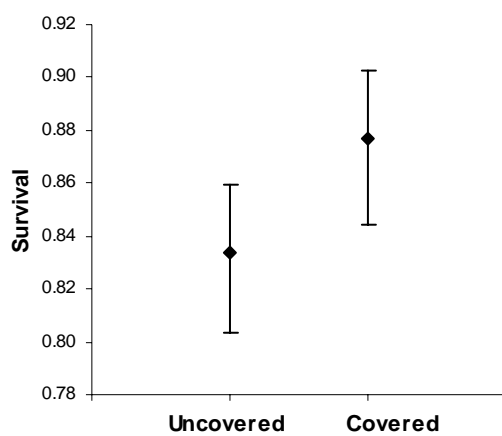
Figure 2. Survival probabilities of individuals inhabiting paired patches covered by a net and those that were not covered by a net (with 95% CI).
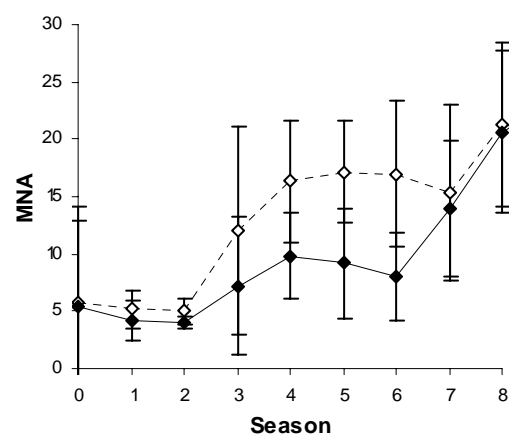
Figure 3. Minimum number of individuals known to be alive (MNA) in average for each paired patch throughout the season with SD. Continuous line: patches covered with a net, dotted line: Patches not covered with a net.

Risky behaviour

Out-of-patch excursions

Adults inhabiting patches protected by predator net performed more out-of-patch excursions than adults inhabiting unprotected patches, whereas juvenile out-of-patch excursion rates were fairly unaffected by the treatment (interaction effect between age and experimental treatment: $F_{1, 44} = 4.95$, p = 0.031; Fig. 4). For all categories of animals the probability to perform out-of-patch excursions decreased significantly throughout the season (logistic slope = -0.15, SE = 0.05, $F_{1, 214} = 7.82$, p = 0.006).
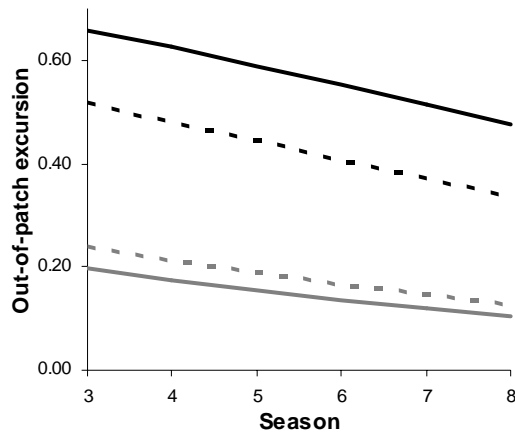
Figure 4. The probability to performing out-of-patch excursions among individuals inhabiting paired patches covered by a net (continuous line) and those uncovered by a net (dotted line). Black colour: adults, grey colour: juveniles.
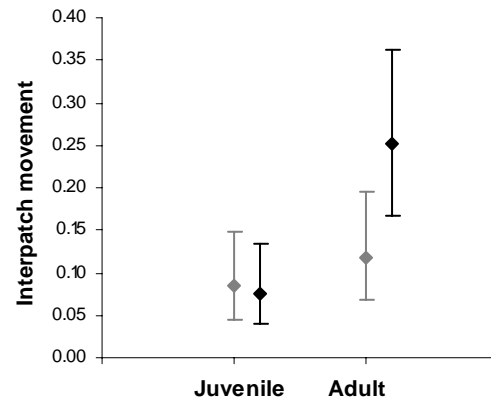
Figure 5. The probability to perform interpatch movements. Black colour: males, grey colour: females.

Interpatch movements

The probability to perform interpatch movements was not associated to treatment ($F_{1, 43} < 1.89$, $p > 0.1765$). There was, however, a tendency for an interaction between sex and age ($F_{1, 44} = 3.44$, $p = 0.070$), with adult males showing the highest frequency of interpatch movement (Fig. 5). Interpatch movements decreased throughout the season (logistic slope = -0.38, SE = 0.08; $F_{1, 44} = 21.42$, $p = 0.001$).

Consequences of risky behaviour

Mortality consequences of movement history

There was a tendency for animals that performed out-of-patch excursions in covered patches to have lower mortality than animals that performed out-of-patch excursions in uncovered patches ($F_{1, 994} = 2.90$, $p = 0.089$; Table 5). Similar results as for out-of-patch excursions was detected for interpatch movements in that there was a tendency for animals that performed interpatch movements in covered patches to have a lower mortality than those in uncovered patches ($F_{1, 994} = 2.50$, $p = 0.114$; Table 6).

Body growth consequences movement history

Growth of body mass was higher for individuals that had performed out-of-patch excursion than for those that did not perform out-of-patch excursions ($F_{1, 616} = 4.05$, $p = 0.045$). In

addition, growth of body mass was dependent on sex among juveniles (effect of the interaction age*sex: $F_{1, 616} = 7.38$, $p = 0.007$). Body growth were also associated to the age*season interaction ($F_{1, 617} = 6.26$, $p = 0.013$) where the negative seasonal association with body growth was stronger for juveniles than adults (Fig. 6 and Fig. 7). There was no association between body growth rate and performance of interpatch movements ($F_{1, 616} = 2.08$, $p = 0.149$).

Table 5. Predicted mortality rates for the four level combinations of treatment and out-of-patch excursion history with 95 % CI.
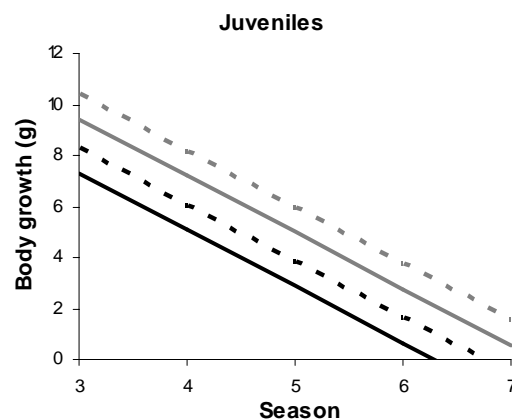
Treatment	Out-of-patch excursion history	
	Performed out-of-patch excursion	Not performed out-of-patch excursion
Covered	0.09, 95 % CI = [0.04, 0.16]	0.15, 95 % CI = [0.10, 0.21]
Uncovered	0.19, 95 % CI = [0.12, 0.28]	0.17, 95 % CI = [0.12, 0.24]

Table 6. Predicted mean values from the four level combinations of treatment and interpatch movement history with 95 % CI.

Treatment	Interpatch movements history	
	Performed interpatch movement	Not performed interpatch movement
Covered	0.07, 95 % CI = [0.02, 0.17]	0.14, 95 % CI = [0.10, 0.20]
Uncovered	0.20, 95 % CI = [0.11, 0.35]	0.17, 95 % CI = [0.13, 0.23]
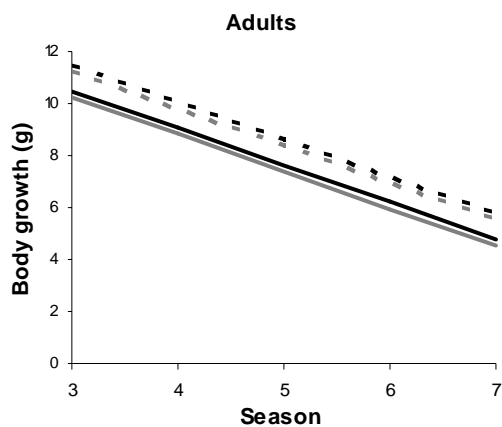
Figure 6. Body growth consequences of out-of-patch excursion history for adults. Dotted lines: Animals that performed out-of-patch excursions, continuous lines: animals that did not perform out-of-patch excursions. Black colour: males, grey colour: females.

Figure 7. Body growth consequences of out-of-patch excursion history for juveniles. Dotted lines: Animals that performed out-of-patch excursions, continues lines: animals that did not perform out-of-patch excursions. Black colour: males, grey colour: females.

Cues used for recognition of predation level

Out-of-patch excursion

The probability to perform out-of-patch excursions was associated to the interaction between mortality rate and age ($F_{1, 212} = 6.41$, p = 0.012). Out-of-patch excursions decreased with increasing mortality rates in adults, while this correlation tended to be positive for juveniles, (Fig. 8).

Interpatch movement

The probability of performing interpatch movements was significantly correlated to mortality rates ($F_{1, 200} = 6.07$, p = 0.015; logistic slope = 2.07, SE = 0.84). Interpatch movement did also depend on age ($F_{1, 46} = 8.02$, p = 0.007), where adults showed a higher movement probability than juveniles (Fig. 9). There was also significant effect of season (season: $F_{1, 200} = 20.30$, p = 0.001), where the probability for interpatch movements for both adults and juveniles decreased throughout the season (logistic slope = -0.35 SE = 0.08).
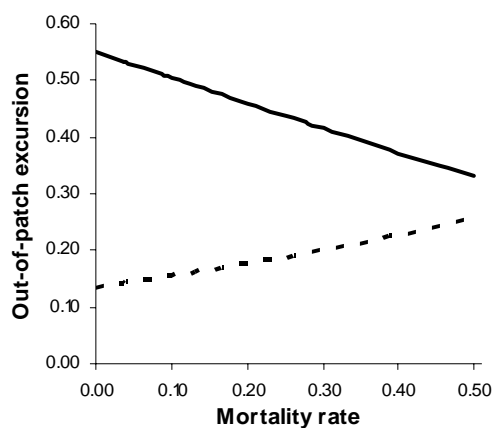
Figure 8. The probability of performing out-of-patch excursion change with mortality rate and depends on age. Dotted line: adults, continuous line: juveniles
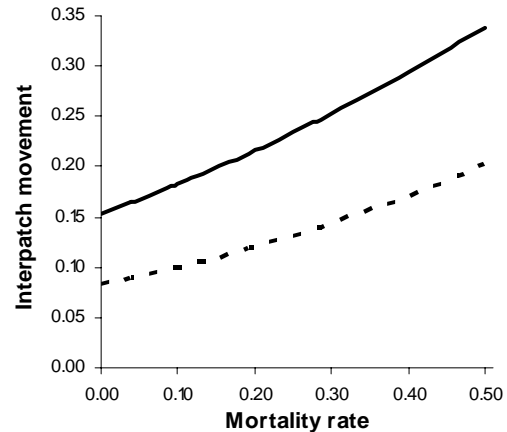
Figure 9. Probability for interpatch movement (transfer between patches) related to proportion dead. Dotted line: adults, continuous line: juveniles.

Discussion

The experimental treatment in this study, the anti-avian predation net, caused significant differences in mortality, i.e. mortality was higher in control than treatment sub-populations. The experimental treatment factor could therefore be used as an indicator of high and low levels of predation risk, and hence be used to test the hypothesis that the degree of risky behaviour among root voles is dependent on the current level of predation. Our primary prediction; that root voles are able to detect the current risk of predation and consequently adjust their degree of risk prone behaviour according to the levels of predation, were partly supported bye the fact in that adult root voles performed less out-of-patch excursions when inhabiting unprotected areas. Out-of-patch excursions of juveniles, on the other hand, did not differ between high and low predation level. The age specific difference in this response is, however, not very surprising. Juvenile root voles (and small mammals in general) undergoes a stage of dispersal where they leave the area where they are born and thereafter follows a period of search for a new place to settle down (Gundersen and Andreassen 1998; Johnson and Gaines 1990; Stenseth and Lidicker 1992). For juveniles the ultimate reason behind out-of-patch stay may therefore be far different from the excursions established animals take in open areas as part of their daily behaviour, e.g. in search for food. The other risky behaviour response; interpatch movement, did not vary according to predation level. One possible explanation for this may be that the root voles do not consider the interpatch distance of 5 m as a risky distance to traverse. Adult males showed a higher frequency of interpatch movement than adult females and juveniles, not surprisingly as male root vole territories often may exceed 375 m^2 (the size of one patch) and that males often include several females within their territories (Eikeset et al., in prep.; Gliwicz 1997; Ims 1988; Lambin et al. 1992; Tast 1966).

In the present study there was a tendency for higher mortality among for those individuals belonging to uncovered patches and in addition had performed risky out-of-patch excursions. The same trend was apparent regarding the other measurement of risky behaviour; the interpatch movement. Such behaviour has previously been found to increase the risk of mortality in this experimental system (Andreassen and Ims 2001). Body growth was also generally higher for individuals that had performed out-of-patch excursions than those that did not perform this risky behaviour. In the present study we were thus able to test the assumption that our selected measurements of risky behaviour (i.e. out-of-patch excursions

and interpatch movement) were risky in terms of higher probability of predation, and that there are benefits associated to this behaviour, namely increased energy acquisition. Hence, showing a trade off between costs and benefits connected to different behavioural choices is the basis of the theory of *anti-predator decision-making* (Lima 1998).

Anti-predation behaviour in many rodents has mainly been studied under laboratory conditions, but some are also performed under more natural conditions in the field. Many laboratory studies have been able to show anti-predator responses in rodents when exposed to different cues of predation like scent from mammal predators (e.g. Jedrzejewski et al. 1993; Koivisto and Pusenius 2003; Ylonen and Ronkainen 1994) or sounds from avian predators (Eilam et al. 1999; Hendrie et al. 1998). However, replications of these results in field experiments have rarely been successful (Jonsson et al. 2000; Powell and Banks 2004; Sundell et al. 2004). Common for these studies is that the study animal most often is treated with *indirect* cues of high predation levels (e.g. presence of stout scent in some areas and not in others). Presence of the actual predator (encaged) has also constituted the treatment in one study without any success (Sundell et al. 2004). In these studies it is not obvious whether or not the prey actually consider the predator as a real threat, because no attacks occur. In the present study, however, we demonstrate that risky behaviour of adult root voles is performed more frequently in protected- high mortality sub-populations than unprotected- low mortality sub-populations. Another large scale field study that has successfully demonstrated differences in the level of performed risky behaviour (i.e. mobility) is the study of Norrdahl and Korpimäki (1998). They manipulated predator densities in large, unfenced areas and found that experimentally reduced predation risk increases the mobility of radio-collared voles. Survival rates of the vole populations were not estimated for these vole populations. However, there are reasons to believe that intense predator exclusion (both mammalian and avian predators) also will affect the mortality rates in the treatment vs. control areas. From this we suggest that voles, in order to attain information about their current risk of being predated, they use the most direct cues of predation risk, namely the current mortality level of conspecifics in their immediate surroundings. Our suggestion is thus related to the theory of *public information*, where individuals are gathering information through observation of conspecifics to attain honest and direct measures of e.g. fitness of the individuals in the area and thereafter use this information to select habitat for settlement (Danchin et al. 2001). Further studies should try to elucidate how animals detect demographical changes in their environment and how this information is used in behavioural decision making.

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