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Body size-dependent refuges in voles: an alternative explanation of the Chitty effect

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In cyclic vole populations the body size of voles tends to vary with population density, voles being smaller in the decline and low density phases than in the peak phase of the cycle. We have studied this 'Chitty effect' using field measurements of vole (*Microtus agrestis*, *M. rossiaemeridionalis*) body size and predator densities, and laboratory experiments on the minimum passable hole size for voles and their major predator, weasels (*Mustela nivalis nivalis*). We found that many voles can pass through smaller holes than the smallest weasels, which implies that these small voles can have a refuge from weasel predation. Consequently, predation pressure is expected to be greater on larger voles. In the field we found a negative association between the mean body size of voles and weasel abundance. Our laboratory and field results suggest that size selective predation might be an important cause of the observed smaller size of voles in the decline phase of cycles.

Introduction

In northern Fennoscandia most vole species exhibit synchronous fluctuations in abundance, with successive peaks at 3–5 year intervals (e.g. Hansson & Henttonen 1985, 1988). In synchrony with fluctuations in numbers, the mean body size of voles varies in a systematic manner during the cycle: voles tend to be relatively large in the peak phase and small in the decline and low phases. This phenomenon was first described by Chitty (1952). Many hypotheses have been developed to explain the 'Chitty effect' (*sensu* Boonstra & Krebs 1979). According to Chitty (1967), larger body size in peak populations may be associated with genetically-based differences in the behaviour and reproductive capacity of voles, acting via spacing behaviour, and these differences are the main cause of population cycles. Other studies have explained the large body size of voles in the peak phase by favourable environmental conditions and better survival (Lidicker & Ostfeld 1991), allocation of energy to somatic growth instead of reproduction (Oli 1999), or by selective advantage of larger voles with large intestines and better digestive efficiency during the high density phase, when much of the food available is of low quality (Hansson & Jaarola 1989). These latter studies thus suggest that the Chitty effect is only an epiphenomenon of the vole density regulation.

During the last few decades, there have been many studies and much discussion about the role of specialist predators in the dynamics of cyclic vole populations (e.g. Korpimäki & Krebs 1996, Hanski *et al*. 2001). The importance of small mustelids and particularly the least weasel (*Mustela nivalis nivalis*) in shaping the dynamics of northern vole populations has been the focus of many studies (e.g. Henttonen 1987, Henttonen *et al*. 1987, Korpimäki *et al*. 1991, Hanski *et al*. 1993, Korpimäki & Norrdahl 1998). The least weasel is a highly specialized predator, feeding on small rodents. In the cyclic vole populations in western Finland the proportion of voles in the least weasel diet does not drop below 45%, and is usually well above 80% (Korpimäki *et al*. 1991). It has been suggested that the small size and elongated body of the weasel allows it to hunt voles in their burrows and in the subnivean space, so that there are no refuges for voles (e.g. Simms 1979). Simms (1979) conducted experiments with North American stoats (*Mustela erminea*) to determine the minimum passable tunnel size, and concluded that there is no refuge for voles against female stoat predation.

The presence of a size-dependent refuge for prey in a predator–prey system with population cycles would have clear implications for both the body size variation in prey, and the long-term population dynamic properties of the system; a predator–prey interaction with a refuge for prey is more stable and likely to persist than a corresponding interaction without a refuge (e.g. Crawley 1992). Here we propose an alternative hypothesis about size-dependent refuges in voles to explain the Chitty effect. The hypothesis we present here results from a laboratory experiment, in which we studied the size of holes that voles and least weasels are able to pass through. Following the laboratory experiment, we re-analyzed long-term field data to see whether there exists a relationship between the mean size of voles and predation pressure. In their study on the Chitty effect, Boonstra and Krebs (1979) put forward the question: What is the advantage of being large? We turn the question the other way round and ask: What is the advantage of being small?

Material and methods

Laboratory experiment

Experiments on the minimum passable hole size were conducted in the Lammi Biological Station in southern Finland. A weighed and sexed vole or least weasel was placed in a cage, which had been divided into two sections by a plywood wall (0.5 cm thick). Our assumption was that the most important measurement of tunnels and cavities used by voles and weasels in nature is the narrowest diameter of the tunnel complex. These ‘bottlenecks’ are usually confined by tree roots and stones (personal observations), and therefore, not easily enlarged by predators. In wintertime — with hard snow and frozen ground — narrow parts of tunnels are especially hard to widen, particularly for a small predator like the weasel.

The size of the cage for voles was 60 × 35 × 20 cm and for weasels 120 × 60 × 60 cm. The plywood wall had a round hole 1 cm above the bottom of the cage. In each trial, the diameter of the hole was reduced in steps of 1 mm to find the smallest hole size that the animal could pass through, starting with a hole size clearly passable for the particular animal. Following at least three unsuccessful attempts to go through the hole, or if the individual became stuck in the hole, the subject was deemed to be too large for that particular hole size. Sibling voles (*Microtus rossiaemeridionalis*), field voles (*M. agrestis*) and least weasels originating from laboratory colonies were used in the experiments. Altogether 87 sibling voles, 50 field voles and 30 weasels were tested. Their weights ranged from 9 to 45 g, 12 to 45 g, and 28 to 105 g for sibling voles, field voles and weasels, respectively. In

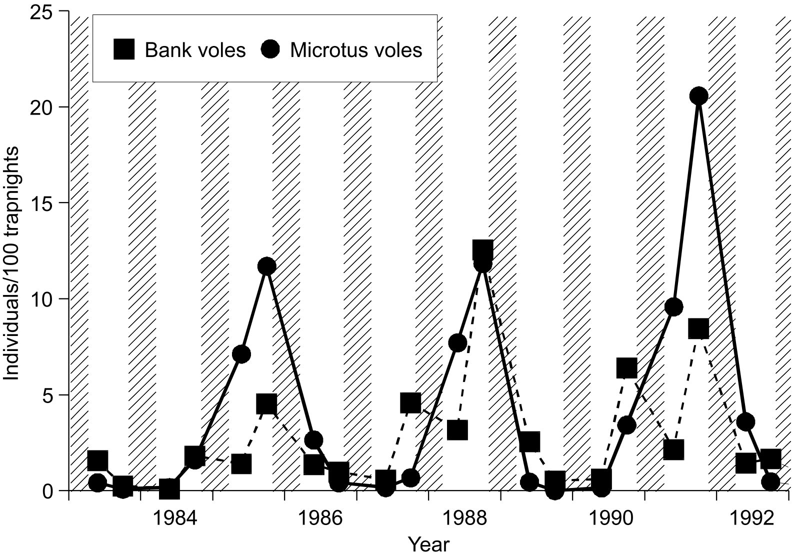

Fig. 1. The population fluctuations of *Microtus* voles and bank voles in Lapua and Kauhava in western Finland. Hatched bars denote snowy periods. Data are obtained with regular snap-trappings performed every spring and autumn in agricultural fields and forests. For details, *see* Norrdahl and Korpimäki (1995a).

general, each individual was tested only once, but a small fraction of voles (< 10 sibling voles) may have been used twice because voles in the first experiments were not marked successfully. Visibly pregnant animals were not used.

The minimum passable hole size between the species was tested by ANCOVA (GLM procedure of SYSTAT) using weight as the covariate.

Field observations

The field data for voles were collected in the Alajoki agricultural area, Lapua and Kauhava, in western Finland (62°N, 23°E), using Finnish metal snap-traps (for a detailed description of the trapping procedure and trapping area *see* Norrdahl & Korpimäki 1995a). Data were collected in each autumn from 1984 to 1992, during which period three complete cycles of voles were observed. 1984, 1987 and 1990 were increase years, 1985, 1988 and 1991 were peak years, and 1986, 1989 and 1992 were years of declining vole density (Fig. 1). Abundance indices of the least weasel were obtained by snow-tracking in the autumn and the spring following a snowfall. As an index of predator abundance (indicating predation pressure) we used the number of weasel individuals per km of track line (for a more detailed description of the snow-tracking method *see* Korpimäki *et al.* 1991).

Linear regressions between predator abundance, vole density and mean weight of voles were conducted using the REG procedure of the SAS statistical package. The effect of cycle phase on the mean body size of voles during September–October was tested by ANOVA (MIXED procedure of SAS) and differences between the phases were tested using Tukey's (adjusted) *a posteriori* test.

Results

Laboratory experiments

The smallest voles used in the experiments weighed 9 g, which is close to the weight of young voles leaving their nest. Even these smallest voles were not able to pass a hole of 12 mm in diameter, whereas most of the largest voles, above 40 g, were able to go through a hole of 20 mm. No significant difference in passable hole-size was detected between the vole species (ANCOVA using weight as covariate for species; $F_{1,133} = 0.55$, $p = 0.46$; species by weight interaction; $F_{1,133} = 1.1$, $p = 0.30$).

The smallest weasel weighed 28 g and was capable of going through a hole 16 mm in diameter, while the largest weasel (105 g) was not able to go through holes smaller than 23 mm. Voles smaller than approximately 20 g were able

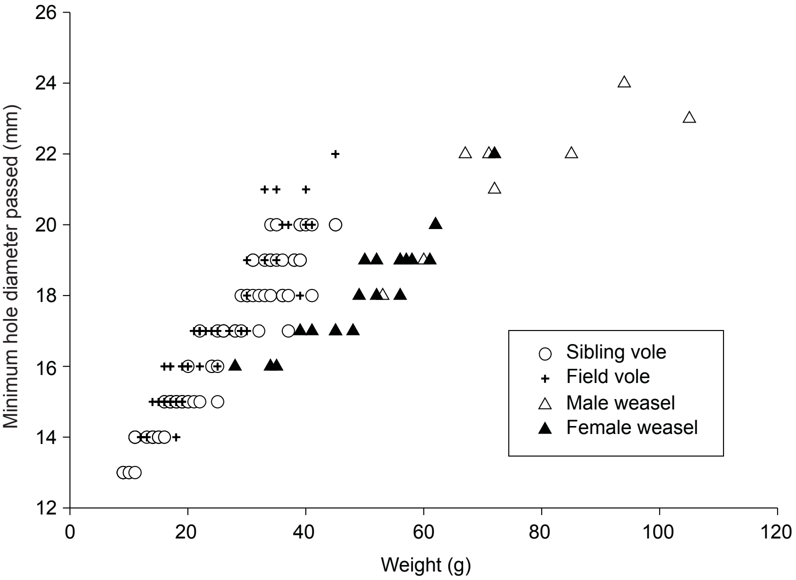

Fig. 2. Minimum passable hole diameter of different sized voles and weasels. Sample sizes are 30, 87 and 50 for the least weasel, the sibling vole and the field vole, respectively. The regression coefficients (± SE) are 0.21 (0.01), 0.22 (0.01), and 0.12 (0.01) for the sibling vole, field vole and least weasel, respectively.

to enter smaller holes than the smallest weasel (Fig. 2). The interaction between species and weight was significant when all species were compared (ANCOVA $F_{2,161} = 45.54$, $p < 0.001$). This was caused by a steeper regression line in voles than in weasels (Fig. 2)

Field observations

Voles that were trapped in the decline phase were significantly smaller than voles trapped in the increase and peak phases, while the interaction between phase and species was not significant (ANOVA; phase: $F_{2,18} = 25.97$, $p = 0.0001$; species: $F_{2,18} = 28.74$, $p = 0.0001$; phase by species: $F_{4,18} = 2.26$, $p = 0.103$; Tukey's *a posteriori* test: increase vs. peak: $p = 0.68$; increase vs. decline: $p < 0.0001$, peak vs. decline: $p = 0.0001$: Fig. 3).

The relationship between the mean body size of voles in the autumn and the current abundance of the least weasel (as well as the corresponding abundance in the preceding spring) was negative. When the weasel abundance was high, the mean body mass of field and sibling voles was small, close to the mean body mass of bank voles (*Clethrionomys glareolus*; Fig. 4).

Table 1. The relationship between the autumn (current) and spring (past) abundance of *Microtus* and *Clethrionomys* and least weasels and the yearly mean body mass of field, sibling and bank voles in autumn (September–October). Data are from the time period 1984–1992. df = 6 in all cases.

	Field vole		Sibling vole		Bank vole	
	r^2	*p*	r^2	*p*	r^2	*p*
Weasel, current	0.69	0.01	0.55	0.04	0.73	0.007
Weasel, past	0.89	0.0005	0.66	0.01	0.49	0.05
Microtus, current	0.11	0.4	0.19	0.3	0.02	0.7
Microtus, past	0.00	0.9	0.04	0.6	0.00	0.9
Clethrionomys, current	0.15	0.3	0.13	0.4	0.04	0.6
Clethrionomys, past	0.18	0.3	0.14	0.4	0.29	0.17

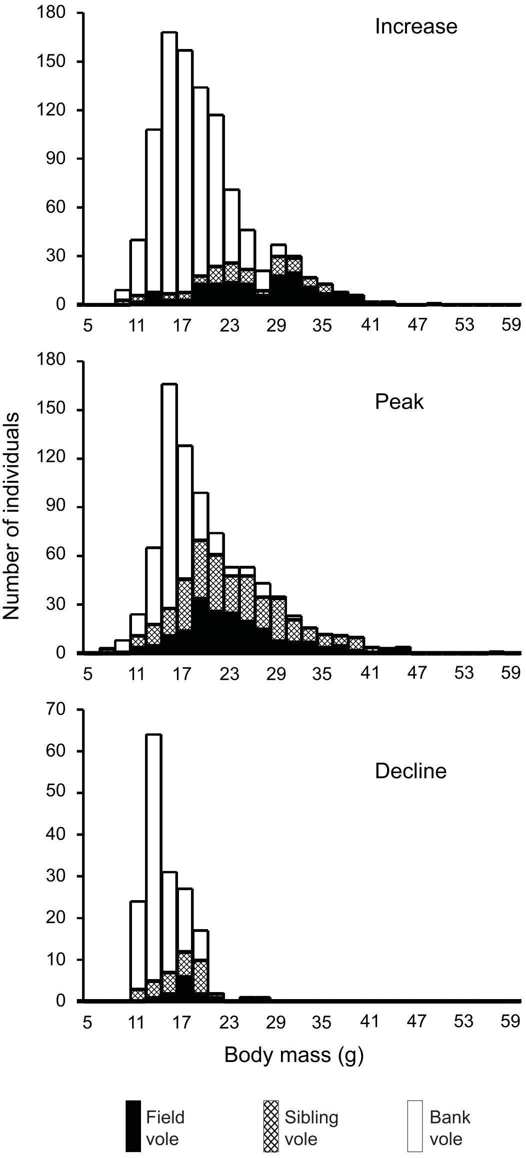

Fig. 3. Autumn weights (September–October) of three species of voles in different phases of the vole cycle. The mean (± SE, sample size) weights (g) of voles are: field vole, 27.0 (0.6, 147), 23.8 (0.5, 193), 17.3 (0.6, 12); sibling vole, 24.9 (0.7, 92), 23.6 (0.4, 292), 17.2 (0.7, 29); bank vole, 17.6 (0.7, 748), 16.3 (0.2, 350), and 14.1 (0.2, 126) for increase, peak and decline phases, respectively.

The least weasel abundance (spring or autumn) explained the mean weight in all three species of voles better than the preceding or current density of voles (Table 1).

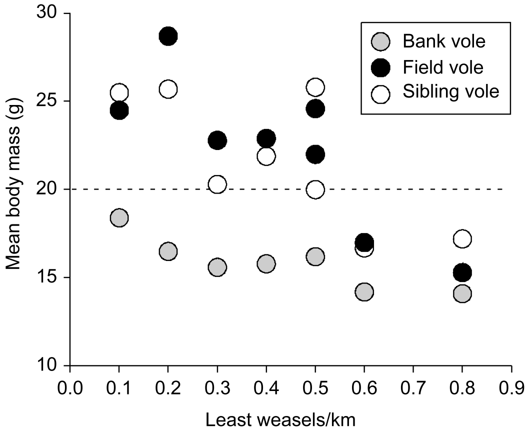

Fig. 4. The autumn weights of voles in relation to current least weasel abundance (least weasels/km of tracking route). The dashed line indicates the critical 20 g body mass of voles, which are able to go through smaller holes than the smallest weasels.

Discussion

Our experimental and observational results suggest that weasel predation impacts the mean body size of voles. The smallest voles, weighing less than or close to 20 g, may use holes that are not passable to weasels as refuge sites. Therefore, we hypothesize that the smaller size of voles in declining vole populations may be, at least partly, caused by selective predation on heavier individuals. Alternative explanations of how predators may affect the mean body size of prey are also possible. For example, reduced activity in prey during high predation risk might lead to reduced foraging and consequently smaller size (e.g. Oksanen & Lundberg 1995). Taken together, our present findings and the previous papers on the role of predation in cyclic small mammal–predator systems (e.g. MacLean *et al.* 1974, Andersson & Erlinge 1977, Korpimäki *et al.* 1991, Norrdahl & Korpimäki 1995b, Korpimäki & Norrdahl 1998, Klemola *et al.* 2000) suggest an important role of predators in the Chitty effect.

Although the proposed causality in our field results of the relationship between mean body mass of voles and index of weasel abundance cannot be directly verified, our interpretation is further supported by other findings. For example, Norrdahl and Korpimäki (1995b) have shown that predation by small mustelids was the major mortality factor of voles in declining populations in western Finland. In their study area, vole populations fluctuate up to 100-fold, hence only 1 vole of 100 may survive through the crash phase (Korpimäki *et al.* 1994), implying the potential for strong selective predation on voles during that phase. In our data the pronounced loss of larger individuals during the decline phase was significant. Furthermore, *Microtus* voles have also been reported to increase burrowing when there are predators around compared to a predator-free situation (Harper & Batzli 1996)

Selection may thus favour small body size during the decline phase, because of the presumed size-selective predation. Conversely, during the other phases of the cycle, selection may favour larger size, which enhances reproduction. In general, larger and heavier individuals tend to compete better for mates, territories and other resources, and therefore their reproductive output may be higher than that of smaller individuals (e.g. Alcock 1989, Gaillard *et al.* 2000). These fluctuating selection pressures probably maintain the mean body size of voles in cyclic populations within the current range. Assuming that periodically heavy size-selective predation is the key factor preventing directional selection towards a larger mean body size in voles, our hypothesis predicts that a reduction in the abundance of predators, or the absence of common and effective mammalian predators, would lead to a population with an increased mean body size (Martinsson *et al.* 1993, Yoccoz & Mesnager 1998, Wilson *et al.* 1999). It should be noted, however, that the hypothesis we propose does not necessarily involve a genetic component in size variation. Indeed, it is known that heritability of size in voles is low (Boonstra & Boag 1987). Reduced foraging activity (and hence slower weight gain) during periods when predation risk is high outside refuges, combined with selective predation of older (larger) individuals, might lead to a population characterized by lean individuals even without genetical changes in the population.

Bank voles are generally smaller than *Microtus* species. Their mean weight is constantly below the critical 20 g, which might lead to the false conclusion that the size of bank voles should not vary during the cycle if size-selective predation with a critical threshold at the weight of 20 g play a role. However, according to our data the mean body mass of bank voles varied, even though the weight variation during the vole cycle was not as pronounced as in *Microtus* (Fig. 4). This can be explained by the fact that a considerable number of bank voles during increase and peak phases are over 20 g (Fig. 3), and are therefore more exposed to weasel predation. Actually, the minor variation in size of bank voles compared to *Microtus* voles is just what the hypothesis predicts. Weasels tend to search for high density vole patches, which are especially important for breeding female weasels (Erlinge 1974). Because of differences in the social systems of *Clethrionomys* and *Microtus* species, *Microtus* voles reach higher densities than *Clethrionomys* voles (Viitala 1977, Viitala & Hoffmeyer 1985). This should lead to a heavier predation pressure on *Microtus* voles, while *Clethrionomys* species can be considered as a secondary prey (*see* also Korpimäki *et al.* 1991, Oksanen *et al.* 2000). Vole species might have different escaping tactics when chased by mammalian predator (Erlinge 1975, Jędrzejewska & Jędrzejewski 1990). On the other hand, if voles are already in their nests or in another refuge site when detected by the predator, and if this refuge site has an inaccessible small ‘entrance’ for the predator, the different escaping tactics of vole species — climbing up trees or running down to burrows — may not play an important role between vole species.

Although we have focused on a northern study system in which the least weasel is the main predator, size selective predation may also explain weight variation of voles in more southern areas where the least weasels are not among the main predators of voles. Voles are stable food for many different predators of different size, but smaller voles always have more abundant refuge sites than larger ones, because they can also use refuge sites available for larger animals, but not *vice versa*. This might increase the chances of small sized voles to escape from other larger mammalian predators too. This leads to a general conclusion that the size of the predator is not the most critical element of our hypothesis, but the relationship between the size variation of prey and the size variation of available refuge sites play a much more important role. Therefore the critical weight of 20 g holds only in systems where the least weasel is the most important predator of voles.

We have used body mass as an index of body size in our analysis, although the size (width) of the skull probably limit the ability to pass through small holes in many, if not most, voles, and thus the width of the skull would probably be a better measure of the ability to use body size-dependent refuges. However, it is a reasonable assumption that individuals within the same population at the same time have an approximately similar relationship between body mass and skull size. It is known that the body mass of voles decreases for winter (e.g. Yaskin 1984), and that the weight change is proportionally larger in bank voles than in field voles (Hansson 1990). Despite the decrease in body mass (and brain mass), the structural size, for example the size of the skull, is much more stable (Hyvärinen 1984), and therefore the ability of voles to use tunnels and burrows probably does not change much between seasons.

Another factor that might have caused a small quantitative bias in our results is the use of the snow-tracking method in estimating the weasel abundance. Korpimäki and co-workers (1991) have shown, in the same study area, that the number of weasels lags behind the number of voles in cyclic vole populations, and that the ratio of voles to small mustelids, including least weasels, is smallest in good vole years and largest in poor years. In our opinion, these observations justify the use of weasel numbers as a crude estimate of predation pressure against an individual vole.

A few hypotheses on how weasel activity should change at different prey densities have been suggested. Increased home range size and length of daily movements were reported at low densities (Jędrzejewski *et al.* 1995, Jędrzejewski and Jędrzejewska 1996, Klemola *et al.* 1999), but no relationship with the duration of daily activity was found (Jędrzejewski *et al.* 2000). If the home range size and length of daily movements of weasels increase considerably at the low prey densities, it may have reduced phase-related differences in abundance estimates. However, this source of uncertainty should not change the qualitative difference in predation pressure between the phases of the vole cycle, especially as we counted the number of individual weasels crossing the snow-tracking route (by following weasels tracks to ensure that the same individuals were not counted twice), not just the number of weasel tracks in the census route.

Simms (1979) studied the interactions between the North American stoat (stoats are called ermine in North America) and its main prey species, the meadow vole (*Microtus pennsylvanicus*), to find out whether there were refuges for voles. He experimentally tested the minimum tunnel diameter for stoats and voles and measured the underground and subnivean tunnels of voles. He argued that there were no refuges for meadow voles against female stoat predation, but he used only a limited number of ‘adult’-sized voles and stoats in his experiments.

To critically test our hypothesis, we need direct data on size-selective predation of the least weasel, similar to that now available for avian predators (e.g. Koivunen *et al.* 1996a, 1996b, 1998). The most difficult data to obtain is the size distribution, and especially the critical ‘bottlenecks’ of vole tunnels and other natural holes and cavities not made by voles in the field. These refuge sites are probably scarce in nature, as otherwise more voles would persist through the decline and low phases of the cycle.

If the hypothesis of body-size dependent refuges holds, it has interesting consequences for the stability of predator–prey dynamics; the presence of a refuge for prey increases the stability of predator–prey dynamics in cases where a fixed number of prey have a refuge, although this effect may not be strong enough to would stabilize otherwise oscillating dynamics (e.g. Crawley 1992). In cyclic vole populations, prey refuges should reduce the probability of a local extinction during the decline and low phases of the cycle when predation pressure is heaviest, and hence should make the long-term persistence and regularity of high amplitude vole cycles more likely.

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