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Synchronous switch in diet and hunting habitat as a response to disappearance of snow cover in Tengmalm's Owl *Aegolius funereus*

Bjørn V. Jacobsen & Geir A. Sonerud

Jacobsen, B. V., Department of Biology, Division of Zoology, University of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo, Norway — Present address: Martin Linges vei 3, N-0692 Oslo, Norway
Sonerud, G. A., Department of Biology, Division of Zoology, University of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo, Norway — Present address: Department of Biology and Nature Conservation, Agricultural University of Norway, P.O. Box 14, N-1432 Ås, Norway

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To test the hypothesis that the snow-dependent diet switch in Tengmalm's Owl *Aegolius funereus* is caused by a simultaneous habitat shift, we studied seasonal changes in prey availability and the selection of major prey and habitat types by two radio-equipped nesting males. When the ground was completely snow-covered, bank voles *Clethrionomys glareolus* were the commonest prey, and the owls hunted more in forest than could be expected from random use. When snow-free ground appeared, the owls switched their prey and habitat; field voles *Microtus agrestis* and root voles *M. oeconomus* became the commonest prey, and clear-cuts and forest were used in proportion to availability. Snap-trapping showed that bank voles were commoner in forest than in clear-cuts, while field and root voles occurred almost only in clear-cuts. Snow-tracking showed that long small mammal trails (>1 m) were commonest in forest, short trails (<1 m) were equally common in the two habitat types, and ventilation holes were commonest in clear-cuts. Thus, prey animals occurring above the snow were probably more available to the owls in forest than in clear-cuts. When the snow melted, prey availability therefore increased in clear-cuts relative to that in forest. Thus, the owls seemed to select their microtine prey indirectly by selecting the habitat according to gain. Although the ratio of field and root voles to bank voles in the prey delivered to the nests increased as the ratio of clear-cut to forest increased among the habitats used by the hunting owls, field and root voles were consistently delivered more than could be expected from the owls' habitat use. The most likely reason is that these voles move slower than bank voles and are more easily taken by the owls once encountered.

1. Introduction

The basic mechanisms of prey selection by rodentivorous predators in the boreal forest in general, and the mechanisms of snow-induced differential predation on sympatric microtines by owls in particular, are still inadequately known. Do owls select directly between microtine prey species on the basis of species-specific encounter rates and profitabilities, or do they select indirectly by choosing the habitat patches with the highest gain, and foraging unselectively within these patches?

Both the diurnal Hawk Owl *Surnia ulula* and the nocturnal Tengmalm's Owl *Aegolius funereus* have recently been found to switch from a diet consisting mainly of bank voles *Clethrionomys glareolus* in winter to one of field voles *Microtus agrestis* and root voles *M. oeconomus* as the snow cover disappears during spring (Sonerud 1986, Hörnfeldt et al. 1990, Nybo & Sonerud 1990). This indicates that bank voles differ from field and root voles in the extent to which they are active on top of the snow and thus exposed to avian specialist predators (Sonerud 1986, Hörnfeldt et al. 1990, Nybo & Sonerud 1990).

In boreal forests in Fennoscandia, field and root voles are confined to clear-cuts. Bank voles occur in a wide range of habitats, but reach their highest densities in old forest, partly because of exclusion from clear-cuts by the larger and dominant field and root voles (e.g. Henttonen et al. 1977, Hansson 1978, 1983, Sonerud 1986, Nybo & Sonerud 1990). As trails of small mammals on top of the snow are found more frequently in old forest than in clear-cuts (Hansson 1982, Sonerud 1986), and as bank voles do not move to a different habitat during winter (Karlsson 1986), bank voles probably spend more time on top of the snow than do field and root voles. Unlike field and root voles, bank voles may also forage in trees (Olszewski 1968, Holisova 1969, Hansson & Zejda 1977, Pulliainen & Keränen 1979, Montgomery 1980, Viro & Sulkava 1985).

Since field and root voles are found mainly in a different habitat from bank voles, it has been hypothesized that the owls' snow-dependent diet switch in spring is caused by a simultaneous habitat shift, and that the owls hunt more in clear-cuts and less in old forest stands as the snow melts (Sonerud 1986, Nybo & Sonerud 1990). Indeed, Sonerud (1986) made observations which suggested that Hawk Owls and Tengmalm's Owls hunted more in a clear-cut as the ground became snow-free and the ratio of field and root voles to bank voles in the diet increased. However, since his study was based on observations of the owls as they hunted in a single clear-cut, nothing is known about their use of other habitats. We therefore began a study with the aim of monitoring prey selection and habitat selection in Tengmalm's Owls simultaneously during the transition from snow-covered to snow-free ground in spring. To our knowledge, no such comparative study of prey and habitat selection in owls has previously been conducted.

Tengmalm's Owl is nocturnal and locates its prey mainly by auditory clues (Norberg 1970, 1987). It searches for prey by pause-travelling (*sensu* Andersson 1981), perching near ground level (Norberg 1970, Bye et al. 1992). In Fennoscandia, Tengmalm's Owl preys mainly on shrews (Soricidae) and microtine rodents (Microtidae) during the nesting season (e.g. Mikkola 1983). The male (average body mass about 110 g (Korpimäki 1990)) provides all the food for his mate and offspring from before egg laying until the nestlings are thermally independent of the female, about three weeks after hatching, and most of the food thereafter (e.g. Korpimäki 1981).

Here we test whether the snow-dependent diet switch is caused by a simultaneous habitat shift, as hypothesized by Sonerud (1986). We present data on the selection of the main prey species (bank voles vs. field and root voles) and main hunting habitats (forest vs. clear-cuts) by two radio-equipped Tengmalm's Owl males on snow-covered and snow-free ground. If the hypothesis of Sonerud (1986) is correct, the proportion of field and root voles in the diet should increase as the proportion of hunting devoted to clear-cuts increases. To ensure that all assumptions of this hypothesis are met, we also present data on the availability of the two prey types in the two habitat types. Finally, we use these data and data from related studies to predict the annual pattern of habitat utilization by Tengmalm's Owl, and relate this to the owl's role as a predator on microtines in the boreal forest throughout the year.

2. Methods

2.1. Study area

The study was conducted during October 1984 – June 1985 within an area of 10 km^2 at an altitude of 500–620 m in the northern boreal zone (*sensu*

Abrahamsen et al. 1977) at 60°56′N, 11°08′E, in Hedmark county, SE Norway. The study area had been modified by modern forestry for two decades prior to our study, and was a mosaic of approximately equal proportions of clear-cuts and old forest stands dominated by Norway spruce *Picea abies*. A more detailed description of the study area is given by Sonerud (1986).

2.2. Prey selection

We studied two neighbouring Tengmalm's Owl males. Their nests were 1600 m apart, and their home ranges just touched each other. Male 1 nested in the attic of a cottage (our "field station") located in forest, while male 2 nested in a box located in a clear-cut (described by Sonerud 1986). Laying (7 eggs in both nests) began on 23 March and 9 April, respectively, when the ground was completely snow-covered, and the young (5 in both nests) fledged in late May and mid-June, respectively, when the ground was completely snow-free. Before the nestlings started to produce pellets about two weeks after hatching, prey items stored around the incubating or brooding female were identified and marked at each nest check. Thus, new items could be distinguished from previously recorded ones. Pellets from the nestlings in nest 1 were collected at regular intervals to separate prey caught on snow-covered, partly snow-covered and snow-free ground. At nest 2, pellets dropped by the nestlings while the ground was partly snow-covered were separated from those dropped later by covering them with paper and sawdust as the last patches of snow disappeared. Both piles of pellets were collected after the young had fledged.

The pellets were analysed as described by Sonerud (1986). During pellet formation loss of cranial parts may be higher for bank voles than *Microtus* voles (Southern 1969, Nilsson 1981). This may affect the results if the species composition of stored prey is compared with that of pellets (for a discussion see Sonerud (1986)), as in the comparison between snow-covered and partly snow-covered ground for nest 2. Our other results on changes in diet from snow-covered to snow-free ground are not affected.

2.3. Prey availability

The availability of small mammals in clear-cuts and forest was estimated by snap-trapping on 12–16 October 1984, as late as possible before the ground became snow-covered, and on 2–6 June 1985, as soon as the ground was completely snow-free. Each time, four trap lines with a total of approximately 230 traps were set in the 20 ha clear-cut where male 2 nested, and three lines with a total of approximately 80 traps were set in the surrounding forest (see Sonerud 1986, 1988). All traps were within the home range of male 2, and thus entirely outside the home range of male 1. The traps were checked on four consecutive days (see Sonerud 1986, 1988). During our study the microtine population declined from a peak in autumn 1984, but did not reach the trough of the cycle until spring 1986 (see Sonerud 1988).

During January–March, supranivean tracks of small mammals were censused along transects in the 20 ha clear-cut and the surrounding forest within the home range of male 2. The number of ventilation holes within a 4 m wide transect strip, and the number of trails within the strip or crossing it, were counted (see Sonerud 1986). Trails were assigned to one of three groups depending on their length; <1m, 1–10 m, and >10 m. For each track type an index (I) was calculated as $I = N \times (L \times D)^{-1}$, where N is the number of tracks, L is the length of the transect (km), and D is the number of nights since the last snowfall. Supranivean activity could only be censused under excellent tracking conditions, i.e. on soft snow not disturbed by wind, which rarely occurred.

2.4. Habitat selection

The owls were caught at the nest site and equipped with radio-transmitters (Televilt, Sweden for male 1 and Biotrack, England for male 2). The transmitter was attached as a back-pack with a harness made of tubular teflon tape (Bally Ribbon Mills, PA, USA). The whole package of transmitter and harness weighed 5–9 grams. Male 1 was tracked for a total of 54 hours on 10 nights between 12 April and 4 June, and male 2 for a total of 59 hours on 13 nights between 9 May and 5

June. Tracking was done with a portable receiver (Televilt) and a hand-held 4-element yagi-antenna, as we walked as close as possible to the owl trying to keep continuous contact with it. Tengmalm's Owls do not seem to be disturbed by an observer's activity while they are hunting (Norberg 1970, Bye et al. 1992).

During tracking the habitat in which the owl was hunting was recorded at 15-minute intervals, and determined either by direct observation or by cross-triangulation. Usually, the owls moved several times during each interval and thus had several opportunities to move to another habitat patch. Of the recorded perches of eight Tengmalm's Owls radio-tracked during the nesting season in 1987–88, 87% had been abandoned after 5 minutes (F. N. Bye and G. A. Sonerud, unpubl.). A 15-min interval is thus long enough to ensure that most observations are independent of one another. However, this requires that the inter-perch flight distances were not too short compared to the size of the habitat patches. If an owl remained on the same perch between two consecutive records of its position, only the first record was used. Some of the locations could not be determined exactly and were excluded from the subsequent analysis. On average 9.4 locations per night were used for male 1 and 12.0 for male 2, equivalent to 1.7 and 2.6 per hour, respectively. Thus, on average the positions of male 1 and 2 used in the analysis were recorded at intervals of 34 and 23 min, respectively. This makes it even more likely that most observations were independent of one another.

To reveal any habitat preferences during the owls' nocturnal activity, habitat use was compared with availability. Almost all of our study area consisted of clear-cuts or old forest stands ready for harvesting. For the purpose of this study, the habitat patches were therefore assigned to one of two groups: clear-cut (tree height <5 m) or forest (tree height >5 m). The availability of each of these two habitat groups was estimated from aerial photos (scale 1:15000) by dividing each convex polygon home range (see Jacobsen & Sonerud 1987) into grid cells of 100 m × 100 m, and then determining the habitat type for each grid line intersection inside the home range.

2.5. Statistical testing

The statistical tests follow Siegel & Castellan (1988), and are all two-tailed. Differences in the composition of the prey by species between periods were tested for significance by the χ^2-test, although some successive captures may have been dependent, since the owls' search was influenced by where the last prey animal was captured (Jacobsen 1989; cf. Sonerud 1985). Differences in the ratio between the number of ventilation holes and the number of trails between the clear-cut and the surrounding forest stands were tested by the χ^2-test if $n > 40$, and by Fisher's exact probability test if $n \leq 40$, assuming that the recorded small mammal tracks were independent. The same procedure was followed for other tests of differences between the frequencies of two samples.

3. Results

3.1. Prey selection

Bank voles and field and root voles made up 96% of the prey items recorded for male 1 and 85% for male 2. When the ground was completely snow-covered, bank voles were the prey type most frequently delivered to the nest by both males (Fig. 1). When patches of snow-free ground appeared, the ratio of field and root voles to bank voles in the prey delivered increased, and both owls delivered a majority of field and root voles (Fig. 1). The ratio of field and root voles to bank voles was significantly higher when the ground was partly or completely snow-free than when it was completely snow-covered (62% vs. 28%, $\chi^2 = 10.31$, $P = 0.0013$ for male 1, and 72% vs. 47%, $\chi^2 = 9.90$, $P = 0.0030$ for male 2).

For nest 1, the ratio of field and root voles to bank voles increased from the period with partly snow-free ground to that with completely snow-free ground (Fig. 1; $\chi^2 = 5.55$, $P = 0.019$). In contrast, for nest 2 the corresponding ratio decreased as the snow cover disappeared completely (Fig. 1; $\chi^2 = 9.97$, $P = 0.0016$).

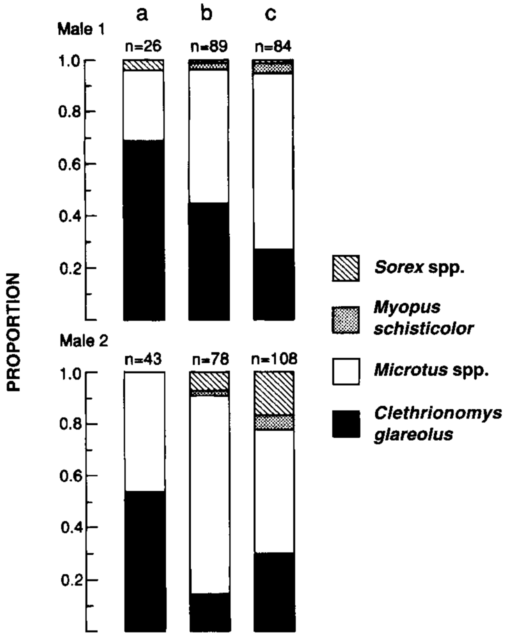

Fig. 1. Proportions of small mammal species in prey delivered to the nests of two radio-equipped Tengmalm's Owl males when the ground was completely snow-covered (a), partly snow-covered (b), and completely snow-free (c). Number of prey items recorded given above each bar.

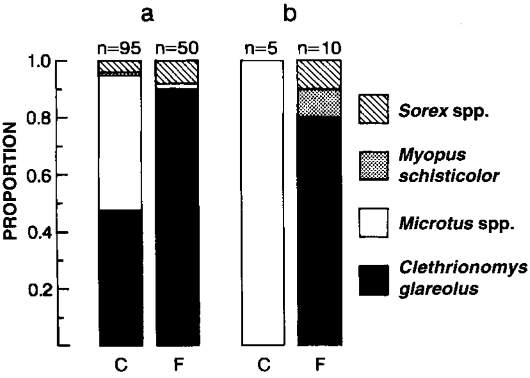

Fig. 2. Proportions of small mammal species snap-trapped in the clear-cut (C) and the surrounding forest (F) within the home range of male 2, 12–16 October 1984 (a) and 2–6 June 1985 (b). Number of individuals trapped given above each bar.

3.2. Prey availability

The distribution of the microtine species trapped differed between the clear-cut and the surrounding forest stands (Fig. 2). In early June, field and root voles were caught exclusively in the clear-cut and bank voles exclusively in the forest (P = 0.0008, Fisher's exact probability test). In October the previous autumn, field and root voles were caught almost exclusively in the clear-cut, while bank voles were caught both in the forest and in the clear-cut (χ^2 = 31.11, P = 0.0001). However, the density of bank voles was almost three times as high in the mature forest as in the clear-cut (15.3 vs. 5.8 animals caught per 100 trap nights).

Of the specimens trapped in spring, field and root voles were significantly heavier than bank voles (median 29 g vs. 23.5 g, U = 5.5, n_1 = 5, n_2 = 8, P = 0.032, Mann-Whitney U-test).

There were significant differences in all censuses between the clear-cut and the surrounding forest in the relative number of ventilation holes and trails made by small mammals. There were relatively more ventilation holes and fewer trails in the clear-cut than in the forest (Table 1). In addition, ventilation holes were on average almost six times as frequent in the clear-cut as in the forest, which is a significant difference (Table 1; T_s = 0, n = 6, P = 0.028, Wilcoxon's signed ranks test). In contrast, the overall frequency of trails did not differ significantly between the clear-cut and the forest (Table 1; T_s = 3, n = 6, P = 0.11). When the trails were split according to length, there was no significant difference between clear-cut and forest for trails measuring <1 m or 1–10 m (Table 1; T_s = 4, n = 5, P = 0.34, and T_s = 4, n = 6, P = 0.17, respectively), whereas trails longer than 10 m were more than twice as frequent in the old forest as in the clear-cut, a significant difference (Table 1; T_s = 0, n = 5, P = 0.043). If all trails longer than 1 m were pooled, they were also more than twice as frequent in the forest as in the clear-cut, also a significant difference (T_s = 1, n = 6, P = 0.046). Thus, small mammals in the forest seemed to be more exposed to avian predators on top of the snow than those in the clear-cut.

If we compare the distribution of ventilation holes and trails (Table 1) with that of trapped specimens (Fig. 2), it is reasonable to conclude that most trails longer than 1 m were made by bank voles, while most ventilation holes were made by field and root voles. Thus, bank voles seemed to be more exposed to avian predators than field and root voles when the ground was snow-covered.

3.3. Habitat selection

As long as the ground was completely snow-covered, both males used forest significantly more and clear-cuts significantly less when hunting than could be expected from a random choice (Fig. 3). After the ground became snow-free, both owls used forest and clear-cuts in proportion to availability (Fig. 3). This habitat switch was significant for both owls ($\chi^2 = 22.83$ and $\chi^2 = 18.75$, $P = 0.0001$).

When the ground vegetation leafed out, male 2 switched to using forest more than clear-cuts again; forest was used significantly more after 3 June than in the snow-free period before 3 June ($\chi^2 = 5.20$, $P = 0.023$). The data on male 1 during this period were too sparse for a corresponding comparison.

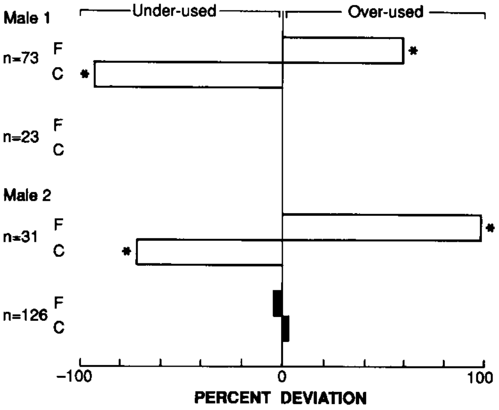

Fig. 3. Deviations from expected use of clear-cuts (C) and forest (F) by two radio-equipped Tengmalm's Owl males during their nocturnal hunting, when the ground was completely snow-covered (open bars) and partly or completely snow-free (filled bars). Expected use, based on the proportions of the two habitat types in the home range of the owl, is represented by the vertical line through zero. Observed use is based on the numbers of records of the owls in the two habitat types. Deviations are given as percentage of expected use and tested by the χ^2-test (* denotes $P < 0.001$). Numbers of records are given to the left.

Table 1. Indices of supranivean activity of small mammals during January–March 1985 within the home range of Tengmalm's Owl male 2. Numbers of tracks are given in brackets. Differences between the clear-cut and the surrounding forest in numbers of ventilation holes and trails were tested by the χ^2-test if $n > 40$ and by Fisher's exact probability test if $n \leq 40$ (* denotes $P < 0.05$, and *** denotes $P < 0.001$).

	Ventilation holes		Trails (m)								
	Forest	Clear-cut	Forest				Clear-cut				
Date			< 1	1–10	> 10	Total	< 1	1–10	> 10	Total	Diff.
17 Jan	4.3 (13)	11.5 (38)	1.7	5.3	3.7	10.7 (32)	7.0	1.5	2.7	11.2 (37)	*
6 Feb	2.0 (2)	11.4 (25)	0.0	2.0	7.0	9.0 (22)	0.0	0.0	2.7	2.7 (6)	***
18 Feb	1.5 (3)	6.8 (15)	0.5	0.5	1.5	2.5 (5)	0.9	0.0	0.0	0.9 (2)	*
21 Feb	0.0 (0)	16.4 (18)	3.0	4.0	0.0	7.0 (7)	0.0	0.0	0.0	0.0 (0)	***
22 Feb	1.5 (6)	9.5 (21)	0.3	1.5	3.0	4.8 (19)	0.9	0.0	2.3	3.2 (7)	***
8 Mar	1.5 (6)	7.3 (16)	0.3	0.3	3.8	4.3 (17)	0.9	2.7	1.4	5.0 (10)	*
Average	1.8	10.5	1.0	2.3	3.2	6.4	1.6	0.7	1.5	3.8	
SD	1.4	3.5	1.2	2.0	2.4	3.1	2.7	1.1	1.3	4.0	
Median	1.5	10.5	0.4	1.8	3.4	5.9	0.9	0.0	1.9	3.0	

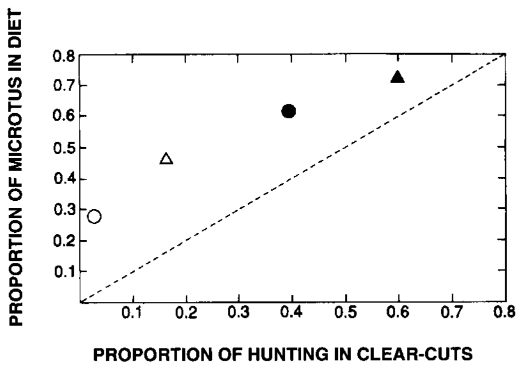

Fig. 4. Relationship between proportion of field and root voles among voles (bank voles and field and root voles pooled) delivered to nests by two radio-equipped Tengmalm's Owl males, and the proportion of records in clear-cuts among all habitat records of the hunting owls. Circles denote male 1 and triangles male 2, while open symbols denote completely snow-covered ground and filled symbols snow-free ground.

3.4. Relationship between prey selection and habitat selection

The ratio of field and root voles to bank voles in the prey delivered to the nest increased as the ratio of clear-cuts to forest among the habitats used by the hunting owls increased (Fig. 4). However, field and root voles were delivered to a greater extent than could be expected from the owls' use of clear-cuts for hunting (Fig. 4).

4. Discussion

4.1. Indirect selection of microtine prey through habitat selection

The three assumptions of the hypothesis of snow-induced habitat shift were met: 1) a diet switch from bank voles to field and root voles, 2) higher availability of microtine prey on top of the snow in forest than in clear-cuts, and 3) habitat segregation between bank voles (forest) and field and root voles (clear-cuts). As predicted, the owls switched the hunting habitat from forest to clear-cuts as the snow disappeared. While the ground was snow-covered, bank voles predominated in the diet of the Tengmalm's Owls, the prey was most readily available in the forest, and the owls used forest for hunting more than could be expected from a random choice. When snow-free ground appeared, the owls increased the ratio of field and root voles to bank voles in their diet, and increased the extent to which they hunted in clear-cuts, so that field and root voles became dominant in the diet, and clear-cuts and forest were used in proportion to availability.

A similar switch in diet from snow-covered to snow-free ground has been reported for Tengmalm's Owls and Hawk Owls in a forest landscape (Bohlin 1985, Sonerud 1986, Hörnfeldt et al. 1990, Nybo & Sonerud 1990), and for Tengmalm's Owls in an agricultural landscape (Korpimäki 1986), but without direct information on where the owls were hunting. Sonerud (1986) found similar distribution patterns to those described here between clear-cut and forest, for ventilation holes and trails, and for bank voles and field and root voles. He hypothesized that the diet shift was caused by an increasing availability of prey in clear-cuts relative to forest as the snow disappeared, and thus by a shift in hunting habitat from forest to clear-cuts. The results of our study support the hypothesis of Sonerud (1986).

If the forager knows the rates of gain, and if these are constant, it should choose the habitat where it has the highest average rate of energy intake (Stephens & Krebs 1986). In winter, the highest supranivean prey availability for Tengmalm's Owls is in forest, where the bank vole is the commonest microtine. In spring, the snow melts first in clear-cuts (Sonerud 1986, cf. Korpimäki 1986), where field and root roles are the commonest microtines (e.g. Hansson 1978, Sonerud 1986, Nybo & Sonerud 1990, this study). The snow-melt combined with the poor cover offered by the previous year's vegetation results in a large absolute and relative increase in the availability of field and root voles, the heaviest and probably the most profitable prey (Sonerud 1986, cf. Korpimäki 1986). We would therefore expect Tengmalm's Owls to hunt more in clear-cuts during and shortly after the snow-melt. Thus, Tengmalm's Owls seem to select indirectly between the major microtine prey species by selecting the habitat with the highest rate of gain.

When the ground became completely snow-free, the ratio of field and root voles to bank voles further increased in the pellets from nest 1, but decreased in those from nest 2. This difference may be attributed to the fact that the young of nest 1 fledged in late May and those of nest 2 in mid-June. During early June, the ground vegetation leafed out, first in the clear-cut, and the availability of field and root voles therefore decreased more than that of bank voles during this period. Radio-tracking showed that male 2 began to use the forest more again after 3 June. This would increase the proportion of bank voles in the diet. Three Tengmalm's Owl males radio-tracked from late June to mid-July hunted more in forest and less in clear-cuts than could be expected from a random choice (Sonerud et al. 1986, Jacobsen 1989, G. A. Sonerud unpubl.).

Thus, the habitat selection pattern of the hunting owls can be explained as a response to the seasonal changes in prey availability (Sonerud 1986, cf. Korpimäki 1986). When the ground is snow-covered, prey is most readily available in forest. During the snow-melt, prey availability in clear-cuts increases relative to that in forest. As the ground vegetation becomes denser, prey availability is reduced relatively more in clear-cuts than in forest, and forest again becomes the most profitable hunting habitat (Sonerud et al. 1986).

4.2. Why were field and root voles taken more often than could be expected from the owls' habitat use?

There was a close association between the ratio of field and root voles to bank voles in the prey delivered to the nest and the ratio of clear-cut to forest among the habitats used by the hunting owls. The diet recorded reflected where the owls had hunted. However, the proportion of field and root voles delivered was higher than could be expected from the owls' use of clear-cuts. This may be caused by several factors. Firstly, the probability of capture may be higher when a Tengmalm's Owl encounters a field or root vole than when it encounters a bank vole. Nishimura & Abe (1988) showed experimentally that Ural Owls *Strix uralensis* captured *Microtus montebelli* more often than *Apodemus speciosus* and *A. argenteus*, even though the owls attacked all three prey species at random. Nishimura & Abe (1988) explained this as a result of the poorer escape ability in *Microtus* than *Apodemus*. Thus, our result may be taken as support for the hypothesis of Hansson (1987) that field voles move more slowly and are taken more easily by predators than are the more agile bank voles.

Secondly, the field and root voles were heavier than bank voles (cf. Sonerud 1986), and therefore more likely to be carried to the nest than bank voles once captured (e.g. Stephens & Krebs 1986). Selective transportation of large prey and consumption of small prey have been documented for several birds of prey (Sonerud 1992 and references therein). The bias introduced by this load-size effect may result in overestimation of the proportion of field and root voles in the prey captured, and underestimation of the proportion of bank voles (cf. Bull et al. 1989; Sonerud 1989). Assume that the foraging Tengmalm's Owl males consumed only bank voles, and carried all captured field and root voles to the nest. Assume also that the males consumed half of the captured biomass before hatching and a fifth after hatching, and that the ratio of body mass between bank voles and field and root voles was the same for voles captured by the owls and voles trapped in spring (median 29 g vs. 23.5 g). Then, if the owls captured voles according to habitat use (Fig. 4), the proportion of field and root voles among voles carried to the nest when the ground was snow-covered and snow-free should amount to respectively 5% and 50% for male 1, and 33% and 77% for male two, while the recorded corresponding values were 28% and 62%, and 47% and 72% (Fig. 4). Thus, these calculations suggest that the load-size effect can explain only part of the discrepancy between the observed and expected proportions of field and root voles in the prey delivered to the nest, except for male 2 on snow-free ground.

Thirdly, the encounter rate (with field and root voles) in clear-cuts may have been higher than that (with bank voles) in forest. When the ground was snow-covered voles may have been relatively more available in clear-cuts than estimated above, for instance if the prey was less than 3.3 times as available from trails as from ventilation holes. When the ground was snow-free, the trapping index was four times as high (for bank voles) in forest (2.6) as (for field and root voles) in clear-cuts (0.6). However, since the trappability of bank voles is higher than that of field and root voles (Hansson 1975), the density of voles may still have been higher in clear-cuts. Fourthly, field and root voles may have occurred more widely in forest than our trapping results indicate, for instance in small scattered patches of meadow-like vegetation overlooked by us in the forest when we classified the owls' habitat use and their habitat options. Fifthly, loss of cranial parts in pellets from the nestlings may have been higher for bank voles than field and root voles (cf. Southern 1969, Nilsson 1981). If the latter was the case, we should expect the proportion of field and root voles in the diet to exceed the level set by the relative use of clear-cuts to the greatest extent after the snow-melt. However, we observed the opposite pattern.

In our opinion, the higher proportion of field and root voles in the diet than could be expected from the owls' habitat use is most likely caused by poor ability of these voles to escape attack by Tengmalm's Owl.

4.3. Conclusion

Based on a ranking of Fennoscandian microtines from folivory and clumsiness to granivory and agility, Hansson (1987) hypothesized the exposure to predators to be higher for field voles than for bank voles. Our finding of a higher proportion of field and root voles in the diet than could be expected from the owls' habitat use supports the hypothesis of Hansson (1987) in the sense that when encountered by a predator, a field vole is more likely to be captured than a bank vole. However, the present study, together with those of Sonerud (1986), Hörnfeldt et al. (1990) and Nybo & Sonerud (1990), shows that field and root voles are more protected from avian predators when the ground is snow-covered than are bank voles.

The results of the present study and related ones using radio telemetry (Sonerud et al. 1986; Jacobsen 1989, Bye 1990, G. A. Sonerud, unpublished) suggest that Tengmalm's Owls use forest for hunting more than could be expected from a random choice during most of the year, except for a brief period, from the appearance of the earliest patches of snow-free ground until the ground vegetation leafs out a few weeks later, during which clear-cuts are also exploited. This supports the hypothesis of Hörnfeldt (1991) that in areas with continuous boreal forest Tengmalm's Owl is a major predator on bank voles during winter, and causes a larger part of the winter mortality in bank voles than in field voles.

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Yhteenveto: **Lumen sulaessa helmipöllöt vaihtavat samanaikaisesti ravintoa ja saalistusympäristöä**

Helmipöllöjen on todettu syövän talvisin pääasiassa metsämyyriä. Lumipeitteen sulettua ne alkavat saalistaa pelto- ja lapinmyyriä. Kirjoittajat testasivat kahta radiolähettimellä varustettua helmipöllökoirasta seuraten hypoteesia, jonka mukaan havaitun muutoksen ravinnossa aiheuttaakin itse asiassa saalistusympäristön vaihto.

Talvella koiraat saalistivat metsämyyriä. Metsät olivat saalistusmaina useammin kuin jos helmipöllökoiraat olisivat valinneet saalistuspaikkansa satunnaisesti. Keväällä koiraat alkoivat saalistaa pelto- ja lapinmyyriä. Metsä ja hakkuuaukeat esiintyivät saalistuspaikkoina siinä suhteessa kuin niitä oli tarjolla ympäristössä. Tutkijat arvelivat lumijälkien perusteella, että metsässä oli lumen päällä liikkuvaa saalista enemmän tarjolla kuin hakkuilla. Lumen sulamisen yhteydessä hakkuilta saatavan saaliin pyydettävyys parani. Pesälle pelto- ja lapinmyyriä tuotiin jatkuvasti enemmän kuin oli odotettavissa helmipöllökoiraiden ympäristön käytön perusteella. Syynä tähän tutkijat arvelivat olevan metsämyyrien vikkelyyden ja siksi hankalan pyydettävyyden.

References

Abrahamsen, J., Dahl, E., Jacobsen, N. K., Kalliola, R., Påhlsson, L. & Wilborg, L. 1977: Naturgeografisk regionindelning av Norden. (In Danish, Norwegian and Swedish with summaries in English and Finnish) — Nordiske Utredninger B No. 34.

Andersson, M. 1981: On optimal predator search. — Theor. Pop. Biol. 9:58–86.

Bohlin, J. 1985: Hökugglans Surnia ulula bytesval i Norra Värmland under häckningssesongen 1984. (In Swedish) — Värmlandsornitologen 13:3–6.

Bull, E. L., Henjum, M. G. and Rohweder, R. S. 1989: Diet and optimal foraging of Great Gray Owls. — J. Wildl. Manage. 53:47–50.

Bye, F. N. 1990: Home range, habitat selection and search tactics of Tengmalm's Owls Aegolius funereus in relation to sexual size dimorphism. — Cand. scient. thesis, Univ. of Oslo.

Bye, F. N., Jacobsen, B. V. & Sonerud, G. A. 1992: Auditory prey location in a pause-travel predator: search height, search time and attack range of Tengmalm's Owls Aegolius funereus. — Behav. Ecol. 3:266–276.

Hansson, L. 1975: Comparison between small mammal sampling with small and large removal quadrats. — Oikos 26:398–404.

— 1978: Small mammal abundance in relation to environmental variables in three Swedish forest phases. — Stud. Forest Suecia No. 147.

— 1982: Use of forest edges by Swedish mammals. (In Swedish with summary in English) — Fauna Flora 77:301-308.

— 1983: Competition between rodents in successional stages of taiga forests: Microtus agrestis vs. Clethrionomys glareolus. — Oikos 40:258–266.

— 1987: An interpretation of rodent dynamics as due to trophic interactions. — Oikos 50:308–318.

Hansson, L. & Zejda, J. 1977: Plant damage by bank voles (Clethrionomys glareolus Schreber) and related species in Europe. — EPPO Bull. 7:397–410.

Henttonen, H., Kaikusalo, A., Tast, J. & Viitala, J. 1977: Interspecific competition between small rodents in subarctic and boreal ecosystems. — Oikos 29:582–588.

Holisova, V. 1969: Vertical movements of small mammals in a forest. — Zool. Listy 18:121–141.

Hörnfeldt, B. 1991: Cycles of voles, predators, and alternative prey in boreal Sweden. — Dr. dissertation, Univ. of Umeå.

Hörnfeldt, B., Carlsson, B.-G., Löfgren, O. & Eklund, U. 1990: Effects of cyclic food supply on breeding performance in Tengmalm's Owl (Aegolius funereus). — Can. J. Zool. 68:522–530.

Jacobsen, B. V. 1989: Home range and selection of habitat and prey by nesting Tengmalm's Owl (Aegolius funereus) males, in relation to vole abundance. — Cand. scient. thesis, Univ. of Oslo.

Jacobsen, B. V. & Sonerud, G. A. 1987: Home range of Tengmalm's Owl: a comparison between nocturnal hunting and diurnal roosting. — In: Nero, R. W., Clark, R. J., Knapton, R. J. & Hamre, R. H. (eds.), Biology and conservation of northern forest owls: symposium proceedings: 152–156. USDA For. Serv. Gen. Tech. Rep. RM-142, USDA, Fort Collins, CO.

Karlsson, A. F. 1986: Effects of conspecifics on winter movements and dispersion in an overwintering bank vole (Clethrionomys glareolus) population. — Can. J. Zool. 64:593–598.

Korpimäki, E. 1981: On the ecology and biology of Tengmalm's Owl (Aegolius funereus) in Southern Ostrobothnia and Suomenselkä, western Finland. — Acta Univ. Ouluensis Ser. A Sci. Rerum Nat. No. 118 Biol. No. 13:1–84.

— 1986: Seasonal changes in the food of the Tengmalm's Owl Aegolius funereus in western Finland. — Ann. Zool. Fennici 23:339–344.

— 1990: Body mass of breeding Tengmalm's Owls Aegolius funereus: seasonal, between-year, site and age-related variation. — Ornis Scand. 21:169–178.

Mikkola, H. 1983: Owls of Europe. — Poyser, Calton. 397 pp.

Montgomery, W. I. 1980: The use of arboreal runways by the wooodland rodents Apodemus sylvaticus (L.), A. flavicollis (Melchior) and Clethrionomys glareolus (Schreber). — Mamm. Rev. 10:189–195.

Nilsson, I. N. 1981: Seasonal changes in the food of the Long-eared Owl in southern Sweden. — Ornis Scand. 12:216–223.

Nishimura, K. & Abe, M. T. 1988: Prey susceptibilities, prey utilization and variable attack efficiencies of Ural Owls. — Oecologia 77:414–422.

Norberg, R. Å. 1970: Hunting technique of Tengmalm's Owl Aegolius funereus. — Ornis Scand. 1:51–64.

— 1987: Evolution, structure, and ecology of northern forest owls. — In: Nero, R. W., Clark, R. J., Knapton, R. J. & Hamre, R. H. (eds.), Biology and conservation of northern forest owls: symposium proceedings: 9–43. USDA For. Serv. Gen. Tech. Rep. RM-142, USDA, Fort Collins, CO.

Nybo, J. O. & Sonerud, G. A. 1990: Seasonal changes in diet of Hawk Owls Surnia ulula: importance of snow cover. — Ornis Fennica 67:45–51.

Olszewski, J. L. 1968: Role of uprooted trees in the movements of rodents in forests. — Oikos 19:99–104.

Pulliainen, E. & Keränen, J. 1979: Composition and functions of beard lichen stores accumulated by bank voles, Clethrionomys glareolus Schreb.. — Aquilo Ser. Zool. 19:73–76.

Siegel, S. & Castellan, N. J. Jr. 1988: Nonparametric statistics for the behavioral sciences. 2nd ed. — McGraw-Hill, Singapore. 399 pp.

Sonerud, G. A. 1985: Brood movements in grouse and waders as defence against win-stay search in their predators. — Oikos 44:287–300.

— 1986: Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. — Holarct. Ecol. 9:33–47.

— 1988: What causes extended lows in microtine cycles? Analysis of fluctuations in sympatric shrew and microtine populations in Fennoscandia. — Oecologia 76:37–42.

— 1989: Allocation of prey between self-consumption and transport in two different-sized central place foragers. — Ornis Scand. 20:69–71.

— 1992: Functional responses of birds of prey: biases due to the load-size effect in central place foragers. — Oikos 63:223–232.

Sonerud, G. A., Solheim, R. & Jacobsen, B. V. 1986: Home range use and habitat selection during hunting in a male Tengmalm's Owl Aegolius funereus. — Fauna Norv. Ser. C, Cinclus 9:100–106.

Southern, H. N. 1969: Prey taken by Tawny Owls during the breeding season. — Ibis 111:293–299.

Stephens, D. W. & Krebs, J. R. 1986: Foraging theory. — Princeton Univ. Press, Princeton. 247 pp.

Viro, P. & Sulkava, S. 1985: Food of the bank vole in northern Finnish spruce forests. — Acta Theriol. 30:259–266.

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