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Seasonal changes in diet of Hawk Owls *Surnia ulula*: importance of snow cover

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The diet of three pairs of the Hawk Owl *Surnia ulula* nesting in the boreal zone of SE Norway was followed by analysing pellets collected at average intervals of six days during the breeding season, and compared with the occurrence of vole prey in the two main coniferous forest habitats of the species. When the ground was completely snow-covered, the smaller Bank Voles *Clethrionomys glareolus*, found in only mature forest, predominated in the diet, but when the ground was partly or completely snow-free, the larger Field Voles *Microtus agrestis* and Root Voles *M. oeconomus*, found only in clear-cuts, were the dominant prey. This change occurred rapidly, and coincided with the first appearance of snow-free ground. The data were consistent with the predictions of changes in diet based on optimal foraging theory when prey density was replaced by prey availability, as influenced by snow cover. Snow may influence the population dynamics of Bank Voles and Field/Root Voles differently by causing different degrees of exposure to specialist avian predators.

1. Introduction

Prey availability as experienced by avian predators has proved difficult to measure (Zach & Smith 1981). For birds that prey on microtine rodents, seasonal variation in prey availability is not reflected by seasonal variation in prey density, and cannot be reliably measured by trapping of microtines (Masman et al. 1988, Sonerud 1989). The availability of microtines may be influenced by the vegetation cover to such an extent that the selection of foraging habitat by their avian predators may differ greatly from what is predicted from prey density alone (e.g. Nilsson 1981, Sonerud 1986, Sonerud et al. 1986 and references therein). Seasonal or spatial variation in the vegetation cover may thus result in a diet different from that predicted from prey density alone. If growing field vegetation decreases prey availability, for instance, the range of the diet may expand even if the density of the most profitable prey type increases (Nilsson 1981, Korpimäki 1986a).

At northern latitudes microtine runways are almost completely snow-covered during a substantial part of the year. This lowers microtine exposure to avian predators to such an extent that individuals of only a few species of owls are able to reside in snow-covered areas (Sonerud 1986). Among these are Hawk Owls *Surnia ulula*, which range around the northern hemisphere in open boreal forests (Norberg 1987), and lead an essentially nomadic life, breeding in areas with temporarily high microtine abundance (Hagen 1956, Mikkola 1972, Byrkjedal & Langhelle 1986).

Hawk Owls prey primarily on microtines of the genera *Clethrionomys* and *Microtus* (e.g. Mikkola 1983), which they localize mainly by vision (Nybo 1986, Sonerud 1986, Norberg 1987). Both Bohlin (1985) and Sonerud (1986) found that the diet of Hawk Owls changed during the breeding season, consisting predominantly of Bank Voles *Clethrionomys glareolus* early in the season and *Microtus* voles later on. Bohlin (1985) explained this change as the effect of an assumed increase in the overall density of microtines during the breeding season, leading to a narrower diet consisting chiefly of the heavier, and presumably more profitable, *Microtus* prey. The density of the microtine prey may be insufficient, however, as a basis of theoretical predictions of the habitat and diet of Hawk Owls, because the snow cover can influence the availability of microtine prey species differently in different habitats. Sonerud (1986) therefore explained the diet change as mainly the effect of different prey availability in clear-cuts and older forest stands on snow-covered and snow-free ground; when the snow cover disappears, *Microtus* voles in clear-cuts can be assumed to become more available, both absolutely and relatively, than Bank Voles in older forest. However, neither Bohlin (1985) nor Sonerud (1986) recorded the diet with sufficient frequency. Furthermore, by pooling data from several pairs, Bohlin (1985) masked any abrupt change in diet (cf. Krebs et al. 1983).

The aim of the present study was therefore to reveal whether the seasonal change in the Hawk Owl diet during breeding can be attributed to changes in prey density, as suggested by Bohlin (1985), or to changes in prey availability due to the snow cover, as suggested by Sonerud (1986). Since individuals of *Microtus* are heavier on average than Bank Voles (e.g. Sonerud 1986), but probably do not take longer for Hawk Owls to handle, they should be the preferred prey (Bohlin 1985, Sonerud 1986); predators should prefer the prey with the highest average food gain per average handling time (Pyke 1984). Microtine density in boreal forests, as measured by trapping, decreases during winter and spring (e.g. Henttonen 1985, Korpimäki 1987, Sonerud 1988). Most Hawk Owl clutches hatch before the snow has disappeared (Sonerud unpubl.), and thus fledge before prey density starts to increase as weaned juveniles enter the microtine populations. Hence, if the diet is determined by prey density only, Hawk Owls can be expected to decrease the proportion of *Microtus* in their diet during the breeding period (cf. Pyke 1984). On the other hand, as individuals of *Microtus* move less on top of the snow cover and are thus less exposed to Hawk Owls during winter than are Bank Voles (Sonerud 1986), both the absolute and relative availabilities of *Microtus* prey increase when the snow cover disappears. Hence, if diet is determined by prey availability, Hawk Owls can be expected to increase the proportion of *Microtus* in their diet during the breeding period (cf. Pyke 1984).

2. Study area and methods

The study was conducted in two separate areas in SE Norway during March–June 1984. Study area 1 (Hawk Owl pairs 1A and 1B) is situated at 60°11′N, 12°20′E in the middle boreal zone, and area 2 (pair 2A) at 60°56′N, 11°08′E in the northern boreal zone (sensu Abrahamsen et al. 1977). Both areas consist of a mixture of clear-cuts and coniferous forest stands of different ages. Area 1 is described in more detail by Wegge (1984), and area 2 by Sonerud (1986).

Pair 1A nested in a hollow snag situated in a 5-ha clear-cut, and 1B in a Black Woodpecker *Dryocopus martius* hole in an aspen *Populus tremula* situated in a 6-ha clear-cut. Pair 2A nested in a box situated in a 20-ha clear-cut (Sonerud et al. 1987). The nesting habitats were thus open, and typical of Hawk Owls in SE Norway (see Sonerud 1985a).

Pellets were collected at intervals of 1–21 days, with an average of 6.0 days (SD=5.7, n=35). For pair 1A they were collected 20 times during 18 March – 10 June (average interval 4.4 days (SD=5.7, n=19)), for 1B 7 times during 9 April – 10 June (average interval 10.3 days (SD=6.9, n=6)), and for 2A 11 times during 20 April – 24 June (average interval 6.4 days (SD=3.9, n=10)). Pellets were collected from below roosting trees at the nest sites of all three pairs, and also from below hunting perches of the male of pair 1A.

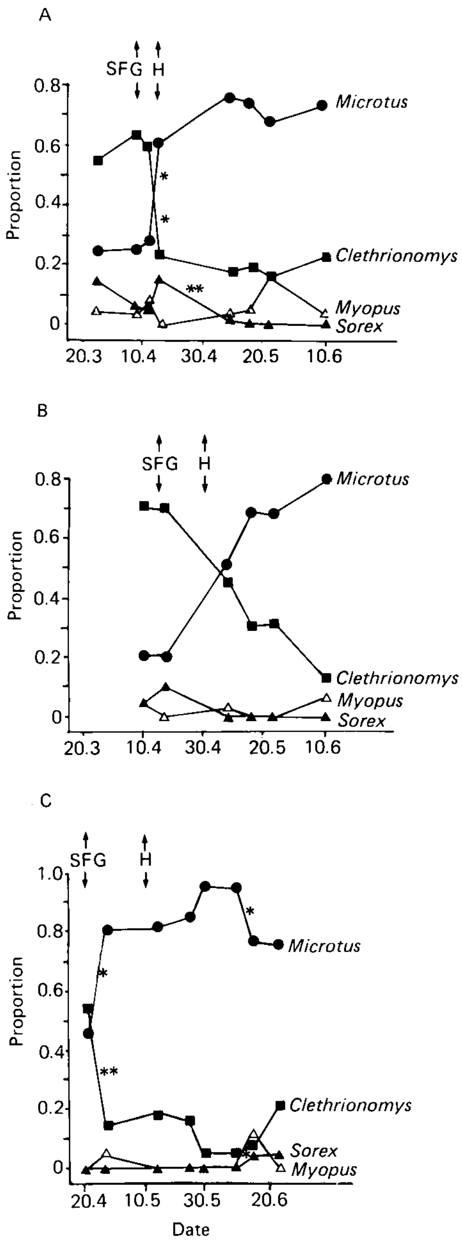

Fig. 1. Proportions of small mammal species in the diet of three Hawk Owl pairs during the breeding season (A = pair 1A, B = pair 1B, C = pair 2A). Date of first patch of snow-free ground in the home range of the Hawk Owls (SFG), and date of hatching of the Hawk Owl nestlings (H) indicated. Asterisks denote significant differences (* = P<0.05, ** = P<0.01) in the proportion of Bank Voles *Clethrionomys glareolus* and *Microtus* spp. voles between successive periods (χ^2 tests).

The pellets were analysed as described by Sonerud (1986), and the prey individuals found numbered 423 (1A), 203 (1B), and 242 (2A). The frequency of prey species consumed by Hawk Owls is not necessarily that of the prey species in their pellets, because digestion of cranial parts may vary with the age of the owls, and with the prey species and their age (for a further discussion see Sonerud (1986)). However, we dealt with changes in the diet of the same adult owls throughout the sampling periods, so this bias was unlikely to affect our results. Some consecutive samples were pooled because of the low sample size, and are represented by their average sampling date. Differences in the composition of prey species between periods were tested for significance with the χ^2 test, although not all successive captures were independent, since the owls' search was influenced by where the last prey animal was captured (Nybo & Sonerud unpubl., cf. Sonerud 1985b).

The occurrence of small mammal prey was measured soon after the snow had disappeared (from 8 to 16 May in area 1, and from 24 to 28 May in area 2) by putting out snap-trap lines in clear-cuts (about 60 traps in area 1 and 230 in area 2) and mature stands (about 60 traps in area 1 and 80 in area 2), and checking the traps daily for four days (see Sonerud 1986, 1988).

3. Results

A total of 868 prey items were found, of which 99.2% were mammals, 0.6% birds and 0.2% insects. Among the mammals, microtines made up 97.2%, shrews 2.7%, and the weasel *Mustela nivalis* 0.1%.

The composition of the Hawk Owls' diet changed dramatically during the breeding season (Fig. 1). When snow covered the ground, the Bank Vole was the most frequent prey of all three pairs, but a few days after the appearance of snow-free ground, *Microtus* voles (Field Voles *M. agrestis* only in area 1, Field Voles and Root Voles *M. oeconomus* pooled in area 2) began to predominate in the diet. The change was probably even more rapid than indicated by Fig. 1 because pellets from the period with complete snow cover may have been hidden in the snow and collected when the snow had disappeared. Among small mammals in the diet, the proportion of Bank Voles was significantly smaller when the ground was snow-free than when it was snow-covered (χ^2=79.0 (1A), χ^2=27.5 (1B) and χ^2=26.5 (2A), P<0.001), while the proportion of *Microtus* voles was significantly larger (χ^2=95.4 (1A), χ^2=40.3 (1B) and χ^2=20.4 (2A), P<0.001). Snow-free ground is defined as starting seven days after the first appearance of a snow-free patch. The proportion of the Wood Lemming *Myopus schisticolor* did not change significantly when the snow disappeared (χ^2=0.005, P>0.9 (1A), χ^2=0.91, P>0.1 (1B), and χ^2=0.43, P>0.5 (2A)). The proportion of shrews *Sorex* spp. (Common Shrew *S. araneus* only for pair 1B and 2A, Common Shrew and Lesser Shrew *S. minutus* pooled for pair 1A) was significantly smaller when the ground was snow-free than when it was snow-covered in area 1 (χ^2=7.77, P<0.01 (1A), and χ^2=4.42, P<0.05 (1B)), but not in area 2 (χ^2=0.21, P>0.5).

In both study areas the habitat distribution differed between Bank Voles and *Microtus* voles trapped in May (Fig. 2). The former were found exclusively in mature stands, while the latter were found exclusively in clear-cuts. This difference was significant for both study areas (P=0.001 in area 1 and P=0.008 in 2, Fisher's exact probability test).

In area 1 the winter and spring populations of microtines were larger in 1984 than in the previous and the succeeding year (Bondrup-Nielsen & Ims 1986), while in area 2 the winter and spring populations increased from 1983 to 1985 (Sonerud 1988). Hence, microtine density was higher in area 1 than in area 2 during our study. In area 1 the trapping index (number of individuals taken per 100 trap nights) of shrews and microtines combined, as recorded in mid-May, was 6.6 in mature stands and 1.3 in clear-cuts, and in area 2, as recorded in late May, 1.3 in mature stands and 0.8 in clear-cuts.

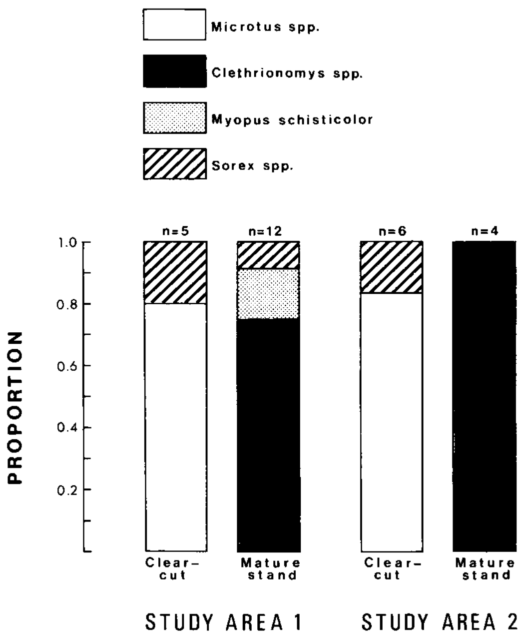

Fig. 2. Proportions of small mammal species trapped in clear-cuts and mature forest stands within the home range of the Hawk Owls in May; n = number of trapped specimens.

4. Discussion

Among the prey items found in the present study, 99% were shrews and microtines. This is similar to the results of earlier studies on the diet of Hawk Owls during peak densities of microtines (Hagen 1952, Mikkola 1972, Pulliainen 1978, Ims 1982, Sonerud 1986).

The diet changed rapidly from a preponderance of Bank Voles when the ground was snow-covered to mainly *Microtus* voles when the ground was snow-free. Both Bohlin (1985) and Sonerud (1986) found the same trend during the breeding season (April–June), but were unable to observe or time any sudden change, due to the long intervals between successive pellet samplings. In central Norway, Bank Voles made up 97% of the microtines in the diet of Hawk Owls during winter (January–April) (Hogstad 1986). Tengmalm's Owls *Aegolius funereus* nesting sympatrically with Hawk Owls also took increasingly more *Microtus* voles than Bank Voles when snow-free ground appeared (Sonerud 1986, Jacobsen 1989).

When based on prey density alone, the prediction of a change in the composition of the diet did not hold true, while the prediction based on different availability of prey in the two main habitats during periods with and without snow cover was fulfilled. Therefore, prey density as measured by trapping is not a satisfactory predictor of the diet of Hawk Owls during periods of rapid changes in the environment (cf. Nilsson 1981, Korpimäki 1986a,b). Prey availability, as influenced by the ground cover, must be employed in models constructed to predict the optimal diets of raptors.

In both study areas, Bank Voles were found solely in mature stands, while individuals of the two *Microtus* species were confined to clear-cuts. This confirms the habitat preferences of these species reported earlier in Fennoscandia (e.g. Henttonen et al. 1977, Larsson & Hansson 1977, Hansson 1978, 1983, Sonerud 1986). Trails of small mammals on top of the snow cover are more frequent in mature stands than in clear-cuts (Hansson 1982, Sonerud 1986). Hawk Owls rely mainly on vision when searching for prey (Nybo 1986, Sonerud 1986, Norberg 1987), and in our studies were observed to capture only visually exposed prey (Sonerud 1986, J. O. Nybo pers. obs.). Therefore, when the ground is snow-covered, the availability of their prey is higher in mature stands than in clear-cuts (Sonerud 1986). As the snow disappears, prey availability increases in both these habitats, but most in clear-cuts, because individuals of *Microtus* move less on top of the snow-cover than do Bank Voles (Sonerud 1986). The rapid change in diet thus suggests that the Hawk Owls changed their major foraging habitat from mature forest to clear-cuts when patches of snow-free ground appeared. In Tengmalm's Owls, a similar diet change during spring coincided with a change in foraging habitat from mature forest to clear-cuts, as revealed by radiotelemetry (Jacobsen 1989).

Hawk Owls forage both by day and by night (Huhtala et al. 1987, J. O. Nybo and G. A. Sonerud pers. obs.). Thus, the rapid change in diet during the snow-melt cannot be explained by a change in the diel activity pattern of the prey species .

Microtines sometimes reproduce when the ground is still snow-covered, especially in years of increase (Hansson 1984). Such winter breeding is more common in *Microtus* species than in the Bank Vole (Hansson 1984), and may lead to an early termination of the spring decline and start of the summer increase. This might have been the reason for the increase in the proportion of the largest prey type (*Microtus*) in the Hawk Owls' diet during spring, but our data do not support such an explanation. First, most of the increase in the proportion of *Microtus* in the Hawk Owls' diet occurred within a short period following the appearance of snow-free ground; only a minor increase occurred thereafter. Second, the microtines trapped did not include any juveniles (body mass of Bank Voles 17–27 g, and of Field Voles 24–51 g). The trapping took place up to a month after the switch in the owls' diet (in area 1 trapping on 8–16 May and diet switch on 13–16 April (pair 1A) and on 19 April – 16 May (pair 1B), in area 2 trapping from 24–28 May and diet switch on 20 April – 2 May). Thus, if the microtine population had been increasing during the time when the major switch in diet occurred, juvenile microtines should have been found among the specimens trapped. Third, the pattern of the change in diet was the same in the two study areas, although the microtine populations were at a peak in area 1 and in an increase phase in area 2. Moreover, in the peak microtine year of 1981, Hawk Owls also increased the proportion of *Microtus* voles in their diet and decreased that of Bank Voles when the ground became snow-free in area 2 (Sonerud 1986, 1988). Thus, we conclude that the major diet switch of the Hawk Owls was not due to an increase in the microtine prey populations.

Sonerud (1986) suggested that in Fennoscandia the snow cover lowers prey availability to avian vole predators more in open grassland, than in closed forest, and imposes a stronger selection for migration to snow-free areas in predator species dependent upon hunting in grassland (e.g. Short-eared Owl *Asio flammeus* and Long-eared Owl *Asio otus*) than in those able to hunt in forest (the remaining owl species). The results of the present study support the basis of this explanatory model.

Hansson & Henttonen (1985) found that the cyclicity indices of Fennoscandian populations of the Bank Vole and the Field Vole increased with increasing duration and thickness of the snow cover. They attributed this pattern to a decreasing buffering effect of generalist predators that shift from microtines to other prey types, e.g. birds, when snow accumulates. The present study and that of Sonerud (1986) show that avian specialist predators may switch from one microtine species to another when the ground becomes snow-covered. Thus, there is reason to believe that the population dynamics of sympatric Bank Vole and Field/Root Vole populations are differently affected by the snow cover, owing to different degrees of supranivean exposure to avian predators.

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Sammanfattning: **Snötäckets betydelse för årstidsmässiga förändringar i hökugglans diet**

Dieten hos tre hökugglepar undersöktes genom analys av de vuxna ugglornas spybollar, insamlade var sjätte dag under häckningsperioden. Dieten jämfördes med smågnagarförekomsten i hökugglans två huvudhabitat, barrskog och kalhyggen. Bytet utgjordes i huvudsak av ängssork *Clethrionomys glareolus* så länge marken var snötäckt, men av åkersork *Microtus agrestis* och mellansork *M. oeconomus* efter snösmältningen. Förskjutningen skedde snabbt i samband med uppträdandet av barmark. Ängssork förekom endast i skog, fältsorkarna (*Microtus* spp.) enbart på hyggen. Hökugglorna bytte därför sannolikt jakthabitat från skog till hygge vid snösmältningen. Tidigare undersökningar har visat att så länge marken är snötäckt är smågnagarna lättare tillgängliga i skog än på kalhyggen. När snön försvinner ökar därför fältsorkarnas både relativa och absoluta tillgänglighet. Däremot minskar den absoluta mängden smågnagare under våren. Denna undersöknings resultat överenstämmer därför med förutsägelser baserade på teorin för optimalt näringssök endast om bytesdjursfrekvensen ersätts med bytesdjurstillgänglighet för hökuggla i relation till snötäcket. Undersökningen visar att snöförekomsten kan inverka olika på ängssorkens och fältsorkarnas populationsdynamik genom förändring i tillgängligheten för smågnagarjagande rovfåglar.

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