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Seasonal changes in the food of the Tengmalm's owl *Aegolius funereus* in western Finland

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Seasonal changes in the food of the Tengmalm's owl during the first half of the year were studied in western Finland from 1973 to 1985. In peak vole years the proportion of the most preferred prey (*Microtus* voles) in the food peaked at the end of March but after the middle of April their number was relatively constant. In other years their proportion was highest in winter and thereafter it decreased continually. In good vole years, bank voles were most often taken at the turn of April–May but in other years as early as the end of March and the beginning of April. The proportions of shrews and birds in the diet increased as the breeding season proceeded. Nestlings and young birds formed an important prey group in June. The results showed that the Tengmalm's owl reacts opportunistically to the changes in the availability of prey. These changes were caused by variation in the snow and vegetation cover, and in the abundance and behaviour of prey animals. Foraging theory predicts that a predator should widen its food niche when the preferred prey types become scarce, and shrink it when they become abundant. This was observed in the Tengmalm's owl during the breeding period.

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1. Introduction

In birds of prey using voles as their staple food, breeding generally occurs relatively early in the spring, although vole numbers peak in the autumn, long after the nestling phase of predatory birds. Yet the highest clutch size and reproductive output is observed in the earliest breeding pairs rather than the latest, e.g. in the kestrel *Falco tinnunculus* (Cavé 1968), the long-eared owl *Asio otus* (Wijnandts 1984) and the Tengmalm's owl *Aegolius funereus* (Korpimäki 1981, 1987a, b).

The Tengmalm's owl is the earliest breeder among North European birds of prey; for example, half of the females start to lay before 4 April in South Ostrobothnia, western Finland (Korpimäki 1981, 1987b). During egg production, voles are generally near their seasonal low phase (Korpimäki 1987b) and the mean snow depth in the study area is about 35 cm (Solantie 1975), which reduces the availability of small mammals. Later in spring, marked changes in snow conditions and vegetation cover occur, changing the hunting opportunities available to owls.

Taking into account the above aspects, the aims of the present paper are to describe seasonal changes in the food of the Tengmalm's owl, both before and during the breeding season, and to relate these changes to vole dynamics, snow conditions and vegetation cover.

2. Material and methods

The study was carried out from 1973 to 1985 in South Ostrobothnia, western Finland (63°N, 23°E). Initially, the study area was about 200 km^2 in extent, containing a total of 99 nest-boxes and holes suitable for the Tengmalm's owl. Thereafter the study area was gradually extended, reaching 1300 km^2 at the end of the study period and including 450 nest-sites. Further details have been described in earlier papers (Korpimäki 1981, 1984, 1985a).

Tengmalm's owls use boxes and holes in trees for resting and eating outside the breeding season (Sulkava & Sulkava 1971, Korpimäki 1981). Pellets and other food remains that accumulate on the bottom of the boxes and holes in the period 1 January–15 March were sampled when checking nest-sites at the end of March (57 samples in 1973–85).

Food samples were carefully examined and all bones and feathers were separated. As a single examination usually reveals only 50-70 % of the bones significant for identification (Korpimäki 1981), the pellets were checked three

times, a procedure which reveals 80–100 % of the bones of even small prey items, such as shrews. Small mammals were identified by diagnostic features according to Siivonen (1974) and the number of individuals was determined by counting mandibles. Birds were mostly identified with the aid of the humeri, by comparing the bones with reference material from museum collections. In some cases beaks, legs, metacarpals and feathers were also used in the determination (for further details, see Korpimäki 1981, 1985b, c).

Nest-holes of the Tengmalm's owl regularly contain a store of prey animals, especially during the egg-laying, incubation and hatching periods (Korpimäki 1981). On nest visits these prey items were identified in order to collect data on changes in food composition in the breeding season (total number of prey items 3429 in 1973–85). To avoid counting any individual in a food store twice, the tails of small mammals and the claws of birds were cut off; Tengmalm's owls always begin to eat their prey starting with the head (Scherzinger 1971, Korpimäki 1981 and unpubl.).

Diet breadth (diet diversity) was calculated using Levins' (1968) formula:

$$B = 1 / \Sigma p_i^2$$

where p_i is the proportion of prey taxon i in the diet. This index renders values ranging from 1 to n. For the calculations the specific (if possible), or sometimes the generic, level of prey identification was used, since the ordinal level of prey identification consistently underestimates diet breadth (Greene & Jaksîc 1983).

During 1973–85 small mammals were snap-trapped in May and early June (spring catches) and in late August and early September (autumn catches), at four sample quadrats (in a cultivated field, an abandoned field, a pine forest and a spruce forest) (a total of 24 440 trap nights, see Korpimäki 1981, 1986 for further details).

3. Results

Based on snap-trap captures (Korpimäki 1986 and unpubl.), breeding seasons of Tengmalm's owls were classed as peak vole years (1973, 1977, 1982 and 1985) or as other years (1974–76, 1978–81 and 1983–84). Note that in this study area only *Microtus* voles (*M. agrestis* and *M. epiroticus*) show pronounced year-to-year fluctuations (Korpimäki 1986); so peak years are characterized by high abundances of these microtines. By contrast, the bank vole *Clethrionomys glareolus* has a seasonally fluctuating pattern, with low numbers in the spring and high numbers in the autumn (Korpimäki 1986).

3.1. Peak years

The diet of the Tengmalm's owl changed markedly during the first half of the year, since in peak vole years the diet composition differed significantly between successive time periods – apart from between the second half of May and June (Table 1). In good vole years *Microtus* voles were the most frequent prey group, comprising 52.4 % of prey items. Their proportion in the diet peaked at the end of March but after mid-April their number was relatively constant. Bank voles were most often taken during the second half of April and during the first half of May. In the breeding season (16 March–30 June), the proportion of shrews (the most common species being the common shrew *Sorex araneus* and the pygmy shrew *S. minutus*) increased nearly continually but before the breeding season their percentage was also high. Birds were most frequently caught in winter (1 January–15 March) and at the end of the nesting season (16–31 May and June) but there were few of them in the diet between mid-March and late April. In June nestlings and young birds also played an important role in the food. There was only irregular variation in the small percentage of murids (harvest mouse *Micromys minutus* and house mouse *Mus musculus*). The diet breadth was highest in winter and at the end of the breeding season.

3.2. Other years

When vole populations were not at a peak, bank voles were the most important prey, followed by shrews, *Microtus* voles and birds (Table 2). The diet composition differed significantly between successive time periods (apart from between 16 March–15 April and 16–30 April, and between 16–31 May and June). The proportion of *Microtus* spp. was highest in winter and decreased continually during the breeding season. The number of bank voles in the diet peaked at the beginning of the nesting period and decreased markedly as the breeding season proceeded. The reverse was evident for shrews but the capturing of murids varied only irregularly. Adult birds were the second most common prey group in winter, and in May and June their proportion was also high. Especially at the end of May and in June, nestlings and young birds formed an important prey group, since they were the second most frequent prey after shrews. The diet diversity was highest in winter, and in May and June.

Table 1. The seasonal changes in the food composition (as percentages by number) of the Tengmalm's owl during the first half of the year in peak vole years (pooled data from 1973, 1977, 1982 and 1985). The statistical significance of the differences between consecutive time periods was examined using χ^2-tests.

Prey groups	Time periods							Total
	1 Jan.–15 March	16–31 March	1–15 April	16–30 April	1–15 May	16–31 May	1–30 June	
Shrews	17.3	2.4	4.6	15.9	10.5	15.8	20.0	11.8
Water vole	–	–	–	–	0.2	–	–	0.1
Bank vole	17.3	11.2	15.5	34.0	34.1	27.2	20.0	27.7
Microtus spp.	34.7	84.0	74.0	46.6	49.0	45.1	48.0	52.4
Murids	6.7	2.4	5.5	2.8	5.6	–	–	4.1
Birds, adults	24.0	–	0.5	0.7	0.7	12.0	8.0	3.9
nestlings and young	–	–	–	–	–	–	4.0	0.1
total	24.0	–	0.5	0.7	0.7	12.0	12.0	4.0
No. of prey items	150	125	219	427	602	184	25	1732
Diet width	9.04	2.49	3.12	4.02	3.98	5.15	4.25	
χ^2	45.80	26.38	65.39	13.64	54.80	5.49		
df	4	4	5	5	5	4		
$P<$	0.001	0.001	0.001	0.05	0.001	ns		

Table 2. The seasonal changes in the food composition (as percentages by number) of the Tengmalm's owl during the first half of the year when vole populations were not at a peak (pooled data from 1974–76, 1978–81 and 1983–84). Statistical analysis as in Table 1.

Prey groups	Time periods						Total
	1 Jan.–15 March	16 March–15 April	16–30 April	1–15 May	16–31 May	1–30 June	
Shrews	11.9	17.1	26.0	24.0	36.8	45.8	25.2
Red squirrel	–	0.3	–	–	–	–	0.0
Water vole	–	0.3	0.3	0.2	–	0.6	0.2
Bank vole	9.9	51.6	46.5	42.3	19.6	14.5	35.4
Microtus spp.	42.9	25.1	23.1	18.8	7.7	4.2	21.8
Murids	1.4	4.8	3.2	3.6	4.2	–	3.2
Birds, adults	34.0	0.9	1.0	11.2	26.7	18.7	12.3
nestlings and young	–	–	–	–	4.9	16.3	1.9
total	34.0	0.9	1.0	11.2	31.6	34.9	14.2
No. of prey items	294	351	624	421	285	166	2141
Diet width	8.18	3.05	3.24	3.95	5.20	4.13	
χ^2	222.10	9.02	50.47	84.56	6.28		
df	5	5	5	5	4		
$P<$	0.001	0.10	0.001	0.001	ns		

3.3. Bird prey

The bird species in the diet showed great seasonal variation. In winter the most important birds were tits *Parus* spp. (*P. major*, *P. montanus* and *P. cristatus*), bullfinch *Pyrrhula pyrrhula*, yellowhammer *Emberiza citrinella* and crossbills *Loxia* spp. (*L. curvirostra* and *L. pytyopsittacus*) (Table 3). All these birds generally overwinter in the study area. At the end of March and in April prey birds were either wintering species (such as bullfinch and yellowhammer) or the earliest migratory species (chaffinch *Fringilla coelebs*). In May, migratory birds, especially thrushes *Turdus* spp. and chaffinch emerged as the most common birds in the diet. In June, nestlings and juveniles of e.g. thrushes, chaffinch and yellowhammer formed an important prey group.

Table 3. The seasonal changes in the bird prey (as percentages by number of all prey items) of the Tengmalm's owl during the first half of the year (pooled data from 1974-76, 1978-81 and 1983-84).

Bird prey items	Time periods					
	1 Jan.-15 March	16 March-15 April	16-30 April	1-15 May	16-31 May	1-30 June
Parus spp.	15.3	-	-	0.4	1.9	0.6
Turdus spp., adults	2.0	-	-	3.8	3.2	3.6
nestlings and young	-	-	-	-	2.5	6.0
Erithacus rubecula, adults	-	-	-	0.5	1.1	-
nestlings and young	-	-	-	-	-	2.4
Phylloscopus spp.	-	-	-	0.2	1.4	3.0
Carduelis spp.	1.0	0.3	-	0.2	0.7	-
Pyrrhula pyrrhula	4.8	-	0.2	0.2	0.4	-
Loxia spp.	2.0	-	-	-	-	0.6
Fringilla coelebs, adults	1.0	-	0.2	4.0	11.6	9.0
nestlings and young	-	-	-	-	-	2.4
Emberiza citrinella, adults	2.4	0.6	0.5	1.2	3.2	1.8
nestlings and young	-	-	-	-	-	3.0
No. of prey items	294	351	624	421	285	166

4. Discussion

4.1. Reasons for seasonal changes in the food

The present results show that the Tengmalm's owl reacts opportunistically to the changes in the availability of prey (for characteristics of opportunistic forager, see Wiens & Rotenberry 1979). The reasons for these changes are the variation in the snow and vegetation cover, and in the abundance and behaviour of prey animals. Because changes in the food were nearly similar both in the peak and other years, they were not caused by the higher proportions of shrews and birds in late nests during low vole years (Korpimäki 1981). However, there is one other factor that may affect the seasonal differences. It is possible that, at the beginning of the breeding season, the high proportion of *Microtus* spp. in the diet is due to the fact that hunting occurs in the fields. Later in the season Tengmalm's owls may turn to hunting more in forests, which could cause the increased proportion of bank voles and birds in their diet. Since there are no data on changes in hunting habitat utilization during the breeding period, the assessment of this possibility is difficult in this case.

In general, the depth of the snow layer increases from the beginning of January to the middle of March, after which the snow usually begins to melt. The deep snow cover protects small mammals against aerial predators (Korpimäki 1985c). This protective effect probably explains the lower proportion of *Microtus* voles and the higher proportion of birds in the winter diet than in the breeding season, even in good vole years. Bank voles tend to move more above the snow than *Microtus* spp., because they often climb trees in winter (see e.g. Pulliainen & Keränen 1979), and the snow cover in forests is shallower and more discontinuous than in open areas. These factors increase the catchability of bank voles in comparison to *Microtus* voles and probably cause the higher proportion of the former in the winter diet.

In late March and in April, the snow melts most rapidly in open habitats. The vegetation of the previous summer has been pressed down on to the ground and no new vegetation has grown up. The melt water forces *Microtus* voles to leave their holes and winter nests, and to come out into the open where they are easy to catch. This is the likely reason for the high proportion of *Microtus* spp. in the diet at that time (Tables 1 and 2). In May the vegetation starts growing in the fields, decreasing the availability of microtines in this habitat. At that time the snow has just melted in the forests, forcing bank voles to come up out of the ground, and increasing their risk of getting caught. At the end of May and beginning of June, the vegetation in forests also becomes denser as the leaves of bushes and bilberries develop. This reduces the availability of bank voles in the forests, and thus birds nesting above the ground and their young become the easiest prey to hunt (Korpimäki 1981). Moreover, the maturity of shrews begins in April

(Skarén 1973, 1979, Heikura 1984). This increases their mobility and makes them more accessible for predation by the Tengmalm's owl. Shrews are much more vociferous than microtines, especially in the spring (pers. obs., see also Heikura 1984). Therefore Tengmalm's owls, which locate their prey by hearing, can hunt shrews even in May and June when the dense vegetation cover protects voles against aerial predators.

In the present study area, *Microtus* voles are the most preferred prey of Tengmalm's owls (Korpimäki 1981). Assuming that there is no winter reproduction (but see Hansson 1984), the abundances of these microtines in the field likely become reduced from their seasonal peak in autumn to their next reproductive season, which in South Ostrobothnia usually starts in late May (Korpimäki & Norrdahl unpubl.; see also Myllymäki 1977, Heikura & Lindgren 1979). This decrease is reflected as a decreasing number of *Microtus* spp. in the food of the Tengmalm's owl. Among alternative prey, bank voles are more preferred than shrews and birds (Korpimäki 1981). When the availability of *Microtus* spp. decreased, Tengmalm's owls firstly switched to catch bank voles, and when their availability became reduced at the end of May, the owls finally moved over to capturing shrews and birds. The availability of birds increased especially in June when there were plenty of nestlings and juveniles which were easily caught by Tengmalm's owls (Korpimäki 1981).

The catchability of small mammals differs according to sex and season (Smith et al. 1975). All small mammal species stored in the nests of Tengmalm's owls show a clear male predominance (Korpimäki 1981 and unpubl.), probably because of the greater activity of this sex in spring. This intersexual difference is also evident in the diets of breeding tawny owls *Strix aluco* (Lagerström & Häkkinen 1978) and kestrels (Korpimäki 1985d). The greater activity of small mammal males in spring obviously increases their catchability for birds of prey. This may explain why Tengmalm's owls are able to capture so many voles early in the season and possibly also why they can lay so early in otherwise adverse environmental conditions.

4.2. Comparison with other investigations

The present results were consistent with the earlier investigations on birds of prey in which a decrease in small mammals and an increase in birds during the breeding period was observed. This trend has been reported in the sparrowhawk *Accipiter nisus* (P. Sulkava 1972), pygmy owl *Glaucidium passerinum* (Kellomäki 1977) and kestrel (Korpimäki 1985b, d) in Finland, and in the long-eared owl in South Sweden (Nilsson 1981) and in the Netherlands (Wijnandts 1984).

Seasonal changes in the food of the kestrel in South Scotland (Village 1982), of the long-eared owl in South Sweden (Nilsson 1981) and in the Netherlands (Wijnandts 1984) were studied throughout the year. In all these studies the proportion of *Microtus* voles decreased continually during the first half of the year. The occurrence of birds was largely confined to the June–July period. The most striking difference was that the number of *Microtus* spp. in the present study was lower in winter than in the breeding season. This dissimilarity was due to the much deeper snow cover in western Finland in comparison to the above, more southern areas.

4.3. Optimal foraging

Optimal foraging theory (e.g. Pyke et al. 1977, Pyke 1984) predicts that a predator should widen its food niche when the preferred prey types become scarce, and shrink it when they become abundant. This was observed in the Tengmalm's owl during the breeding period, since the diet width increased from 16 March to 31 May with decreasing abundances of *Microtus* voles, but in peak years the diet diversity seemed to decrease in June, probably due to the rapid offspring production of microtines at that time (see above). A similar decrease was also found in other years when predation by Tengmalm's owls in June was mainly biased towards shrews and birds, and this might decrease the diet width. Despite the higher abundance of voles and lower density of birds in winter than in the breeding season, the diet diversity was greatest in winter. This was likely caused by the low availability of voles in that season. This suggests that both prey abundance and availability (or vulnerability) may be important when studying the diets of predators in the field, since they utilize relatively scarce food resources compared, for instance, with herbivores. Recently Krebs et al. (1983) have concluded that the difficulty of measuring the availability of prey could be a reason for the relatively low success of the

above prediction of foraging theory in the field. This difficulty also applies to the Tengmalm's owl.

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