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Feeding habits of Great Grey Shrike *Lanius excubitor* wintering in north-eastern Poland: does prey abundance affect selection of prey size?

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Diet composition and prey selection of wintering Great Grey Shrike (*Lanius excubitor*) were studied at two sites in north-eastern Poland: in the Mazurian Lakeland and at Białowieża Glade. The feeding habits of shrikes were recorded on the basis of 1582 prey items found in 1220 pellets, collected in years 1998–2003. Live-trapping of small mammals showed that in both habitats, *Microtus* voles predominated in rodent communities, with higher densities of the Common Vole (*M. arvalis*) in the Mazurian Lakeland, and the Root Vole (*M. oeconomus*) in Białowieża. At both sites, the two main shrike prey groups were small mammals and insects, with a lesser contribution of other prey (passerines, lizards and frogs). Voles comprised between 69 and 86% of consumed food biomass, while other small mammals comprised only 5–13% of prey biomass. Shrikes selectively hunted the Common Vole, especially in the habitat with a lower abundance of this species. On the other hand, in the habitat with a higher abundance of Common Voles, shrikes selected smaller individuals from this population, a feature that was not recorded in the habitat where the Root Vole was predominant. Therefore, intra- and inter-specific prey selection appears to be interrelated and dependent on prey abundance. The prey stored (here, prey impaled on thorns and spikes) by shrikes differed from the prey consumed. The Root Vole was not stored but occurred in the shrike diet. Frogs, newts and lizards were more often stored than consumed. Analysis of the proportion of skulls, pelvises and thigh-bones in pellets, suggests that at the end of winter and in early spring when voles numbers decline, shrikes consumed more whole vole bodies compared to the autumn.

1. Introduction

According to optimal diet theory, fitness is related to the quantity and quality of food gathered by an animal (Stephens & Krebs 1986). Food resources for predators typically include various types of prey characterized by different morphological and ecological parameters such as body mass, mobility and preferred habitat. The utility of these various types of prey depends on the level of energy intake in relation to the time spent searching for and handling the prey (Stephens & Krebs 1986). Accord-

ing to optimal foraging theory, when the time spent searching for or handling prey increases, the intake-rate (i.e., the body mass of prey selected by the predator) should increase too. Furthermore, with increasing abundance of higher value prey (i.e., larger in size), their use should increase, while lower value (smaller) prey should be dropped from the diet (Pulliam 1974, Charnov 1976, Stephens & Krebs 1986).

However, the strength of this generalization is questionable because the predictions of the optimal diet theory concern only a part of the process of predator diet preferences, i.e., active choice, and ignores two important phases of the predatory sequence: capture success and consumption probability (Sih & Christensen 2001). Those two phases are unimportant if prey is characterized by slow mobility and predator is much larger than prey.

Many predators hunt very mobile prey, and some of them may kill prey larger than their own body size. In these cases, the hunting success of predators decreases with the development of anti-predator behaviour, increased mobility and body size of the prey (Stephens & Krebs 1986, Longland & Jenkins 1987, Jędrzejewski *et al*. 1992). Therefore, predators should 'prefer' the less mobile type, with lower escape success, from two alternative prey types of similar body size (Christensen 1996). Predators hunting for relatively larger prey may have very low hunting success (e.g., Creel & Creel 2002) because, for example, prey may show active defence which may increase the probability of predator injury (Newton 1986, Hayward & Kerley 2005). Furthermore, as the predator might be unable to consume a large prey in a short time, the probability of scavenging by other animals increases (Selva *et al*. 2005). In such cases, predators often hide freshly-killed prey for later consumption (Grakov 1970, Cerveny & Okarma 2002), although a larger prey is more difficult to transport to such storage place and conceal. All these restrictions create an upper limit for prey size hunted by a predator, so that the most profitable prey are not the largest ones but rather medium-sized prey with good availability.

The Great Grey Shrike *Lanius excubitor* is a thrush-sized bird (body mass 67–70 g) that breeds in large part of the Holarctic region (Cramp & Perrins 1993). In winter, part of the North European population overwinters on the breeding sites, while another part migrates (Olsson 1984a). In Poland, most of the breeding population is sedentary, some birds are nomadic, and regular winter immigration from the north is observed (Tomiałojć & Stawarczyk 2003). Shrikes usually hunt in semi-open habitats with short vegetation, using a 'sit-and-wait' strategy (Olsson 1984b, Tryjanowski *et al*. 1999). In southern Europe, where the abundance of invertebrates is high, shrikes feed predominantly on orthopterans and beetles (Nikolov *et al*. 2004). In Northern and Central Europe, shrikes also capture mammals and birds (Hernández 1995a, Hromada & Krištín 1996, Karlsson 1998, 2002). They often hunt for shrews and Harvest Mice *Micromys minutus* (Huhtala *et al*. 1977, Karlsson 2007) which weigh 5 to 10 g; however, their main prey are voles, primarily the Common Vole *Microtus arvalis* and Field Vole *M. agrestis* (Hernández 1995a, Hromada & Krištín 1996, Gorban 2000, Karlsson 2002) which weigh about 20–30 g (in Lithuania, mean body mass of adult *M. arvalis* and *M. agrestis* are 30.07 g and 33.91 g, respectively; subadults of both species weigh about 20 g [Balčiauskien *et a*l. 2004]). Thus, voles can weigh as much as 40 to 50% of the body mass of a shrike individual, which makes the Great Grey Shrike one of the smallest predators that regularly hunts these rodents. This minor weight difference between predator and prey may be a reason why shrikes may sometimes select smaller individuals from the vole population (Hernández 1995a). The Root Vole *M. oeconomus* is much heavier than other vole species, with mean body mass of adults ca. 45 g (Balčiauskien *et a*l. 2004); due to its size it seems an unlikely prey for shrikes. However, in some open habitats (e.g., river valleys), Root Voles predominate among the rodent communities and the encounter rate with predators is likely to be high. Therefore, according to optimal diet theory, this species should be included in the shrike diet at a high frequency.

In the present study, we investigated the effects of prey community structure on the diet composition and prey-size selection of the Great Grey Shrike. We compared the shrike diet at two sites with different rodent communities: one dominated by the Common Vole (smaller species) and the other by the Root Vole (larger species). We predicted that (1) shrikes prefer less agile and smaller

rodent species (e.g., voles over mice); (2) in a site with higher abundance of the Root vole (the largest vole species), the proportion of this prey in the shrike diet should increase; and (3) at both sites, shrikes should select smaller individuals from the Common Vole population.

2. Material and methods

2.1. Study area

The study was conducted at two sites in north-eastern Poland: in the Mazurian Lakeland and in Białowieża Primeval Forest. The Mazurian Lakeland study site extends along the eastern bank of the Lake Łuknajno (53°49' N, 21°38' E), covering over 2 km^2 of fallow areas. The site is adjacent to a large mixed forest. The area includes several small water bodies that attract amphibians during the spawning season, but despite the close vicinity of the Lake Łuknajno, the majority of the area is covered by dry and sandy hilly grassland. The area was cultivated up until 1991. In the plant succession, the abandoned fields were initially overgrown with grasses and herbs, and later also with shrubs, mainly Pear *Pyrus communis*, Dog Rose *Rosa canina* and Common Hawthorn *Crataegus monogyna*.

In the Białowieża Primeval Forest, the study was carried out in the Białowieża Glade (13 km^2) and the river valley of Narewka (2 km^2) (52°43' N, 23°54' E). Białowieża village, situated in the central part of the glade, is surrounded by ploughed fields, pastures, fallow areas and meadows. Some of the meadows are regularly mown, but those bordering the Białowieża National Park are included in the protected zone and natural succession of the forest is ongoing in this area. Single trees, shrubs or groups of trees (mainly birches) scattered around pastures and on field/meadow banks are present all over the Białowieża Glade. Low-lying areas and river valleys are covered by natural open wet habitats (sedge meadows, moist meadows, marsh, macro-forbs).

2.2. Rodent and insectivore availability

The availability of small mammals was estimated by live-trapping at sites of pellet collection. Due to the differences in habitat composition and structure between the study areas, different trapping regimes at the areas were applied. In the more homogenous habitats of the Mazurian Lakeland, rodents were trapped during one-week trapping sessions in October and April in two (in one year at five) 1-ha plots by placing 100 live traps (wooden-box traps; Pucek 1981) per 1 ha. To estimate densities of insectivores, 50 cone traps (a cone-shaped pitfall trap; Pucek 1981) were used in each 1-ha plot in July in years 1999–2007. In the more heterogeneous habitats of the Białowieża Glade, rodents and insectivores were trapped in October and April–May, during 5-day trapping sessions at 7, 1,300 m^2 plots of different types of open habitat, each with 8 live and 2 cone traps.

2.3. Pellet collection and diet analysis

The analysis of diet composition was based on prey remains in pellets regurgitated by shrikes. In the Mazurian Lakeland, 899 shrike pellets with 1250 recognized prey specimens were collected from December 1999 to April 2003. Collections were made regularly each month from October to April over three years of study. In Białowieża, 321 pellets with 332 prey specimens were collected between April 1998 and March 2003. In this area, the collection of pellets was more extensive and occurred 3–4 times per year. Prey remains were identified according to Pucek (1981), März (1987) and the authors' personal reference collection. All prey specimens from pellets were counted, if possible, according to the presence of quantitative body parts such as skulls, beaks, jaws and mandibles. The composition of the shrikes' diet was expressed in two ways: as the percentage of specimens of a given taxon in the total number of prey individuals, and as a percentage of mean prey wet weight. The biomass of prey consumed was calculated by multiplying the number of individuals by the mean body mass of a prey item. The mean body mass was estimated on the basis of samples of particular prey species collected by live trapping. The sampling period was divided into three seasons: autumn (October–November), winter (December–February) and early spring (March–April). The results are presented for each of these seasons,

although for Białowieża only winter and spring data were available. Due to the sample size, multiannual comparisons of the shrike diet were analyzed only for the Mazurian Lakeland. Log-linear likelihood tests were used on the frequency-percentage data to look for dietary differences between seasons and sites (Sokal & Rohlf 1995). Owing to the large number of comparisons (12 dietary categories) the level of significance was adjusted to 0.0042 with a Bonferroni correction. Preference of particular rodent species by the Great Grey Shrike in autumn and spring was evaluated by calculating the Ivlev electivity index (Jacobs 1974) for rodent communities of the two areas.

To estimate the possible body-size based selection of Common Voles by the shrikes, a correlation between vole body mass and the length of mandibular tooth row was calculated using measurements taken from 58 dead voles from Mazurian Lakeland and 86 from Białowieża. The allometric relationship between body size and tooth row length was significantly different between the two areas; therefore, we used different equations for Mazurian Lakeland ($Y = 0.006X^{4.425}$, $R^2 = 0.63$, $p < 0.001$) and Białowieża ($Y = 0.024X^{3.883}$, $R^2 = 0.58$, $p < 0.001$). The body sizes of Common Voles estimated from shrike pellets were compared to body size estimates obtained from trapping. In Białowieża, the number of Common Voles captured during spring was low; therefore, we used additional data from the Mammal Research Institute PAS on the body mass of Common Voles trapped in the same study area in years 1960–2000. For this purpose, the autumn body mass of Common Voles trapped in these two periods (1960–2000 versus the present study, i.e., 1997–2002) were compared. These values were not significantly different: the average body mass 1960–2000 was 17.28 g ($N = 277$) and for 1997–2002 was 17.52 g ($N = 62$; 1-way ANOVA, $F = 0.115$, $p > 0.05$). Therefore, we assumed no differences in the spring body masses of Common Voles.

Apart from collecting pellets and recognizing prey remains, thorny shrubs were searched from October until April during 1999–2006 and prey stored by shrikes were collected in the Mazurian Lakeland. Altogether 342 prey specimens, both intact or partly consumed, were found. To estimate the efficiency of vole consumption for different seasons, the proportion of skulls to other bones (pelvises and thigh-bones) in pellets was compared as an index of utilisation of hunted common voles.

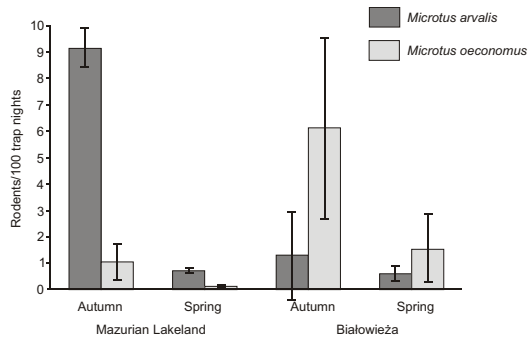

Fig. 1. Spring and autumn abundance (± SD) of Common Vole and Root Vole in the two study areas. Data from the Mazurian Lakeland combined for 2000–2002 and that from Białowieża for 1997–2002.

3. Results

3.1. The abundance of small mammals

In total, 791 rodents and 202 shrews were trapped at the Mazurian Lakeland from spring 2000 to autumn 2002, and 393 rodents and 234 shrews were trapped in Białowieża from April 1997 to October 2002. The Common Vole and Root Vole were the dominant rodent species at both sites. The mean number of both vole species trapped in autumn did not differ between the Mazurian Lakeland and Białowieża (10.1 and 7.4 voles/100 trapping nights, respectively; Mann-Whitney $U = 15$, $p = 0.12$). The density of both species for the two areas fluctuated seasonally, with peaks in autumn and the lowest densities in early spring (Fig. 1). The spring densities of voles were up to ten-fold lower compared to those in the autumn. In the autumn, the Common Vole was more numerous in the Mazurian Lakeland than in Białowieża (Fig. 1). In contrast, the Root Vole predominated in Białowieża. In both areas, the mean autumn densities of Striped Field Mouse *Apodemus agrarius*, Yellow-necked Mouse *Apodemus flavicollis* and Harvest Mouse *Micromys minutus* were lower than the

Table 1. Seasonal and between-site variation in the diet of the Great Grey Shrike in the Mazurian Lakeland and in Białowieża in north-eastern Poland in 1998–2003. Diet composition was calculated as the percentage frequency (%). Other insects = Odonata, Heteroptera, Cerambycidae and undetermined species.

	Mazurian Lakeland			Białowieża	
Prey type	Autumn	Winter	Spring	Winter	Spring
Microtus arvalis	16.2	35.0	30.5	48.6	35.7
M. oeconomus	0.2	3.4	1.7	1.4	8.1
Microtus spp.	0.2	1.3	3.1	2.7	0
Myodes glareolus	0	2.1	1.4	0	0
Micromys minutus	1.6	4.0	0.6	2.7	0.8
Apodemus agrarius	0.4	1.1	0	0	0.8
Sorex araneus	2.5	7.5	3.6	1.4	2.3
S. minutus	2.1	3.4	1.7	4.0	1.9
Birds	1.6	3.4	1.4	4.0	1.9
Lizards	0.8	0	7.8	1.4	2.7
Frogs	1.0	1.6	2.3	2.7	0.4
Insects, total	73.4	37.2	45.9	31.1	45.4
Carabidae	15.6	28.6	14.0	39.1	42.6
Curculionidae	2.4	2.1	29.9	0	3.4
Dytiscidae	2.1	0.7	16.5	8.7	6.0
Scarabaeidae	8.2	7.1	1.2	4.3	12.8
Silphidae	9.2	1.4	6.1	8.7	1.7
Coleoptera, undet.	7.7	13.6	11.0	26.1	19.6
Orthoptera	19.3	9.3	0.6	0	0
Hymenoptera	21.6	9.3	7.3	0	3.4
Dermaptera	9.2	7.9	1.8	0	0.9
Arachnida	2.1	14.3	6.1	13.1	2.6
Other insects	2.6	5.7	5.5	0	7.0
N prey items	516	377	357	74	258

combined densities of Common and Root Voles (3.7 mice/100 trapping nights in the Mazurian Lakeland and 3.3 mice/100 trapping nights in Białowieża). Other rodent species were occasionally trapped.

3.2. Seasonal and area-dependent variation in the shrike diet

In both areas, the diet of wintering Great Grey Shrikes mainly consisted of small mammals and insects, with lesser contribution by other prey such as passerines, lizards and frogs. Small mammals, predominantly the Common Vole, were captured at a frequency similar to insects (mainly Coleoptera; Table 1). Due to the much lower body mass of insects, however, they may be less important than mammals in the shrike diet (Fig. 2).

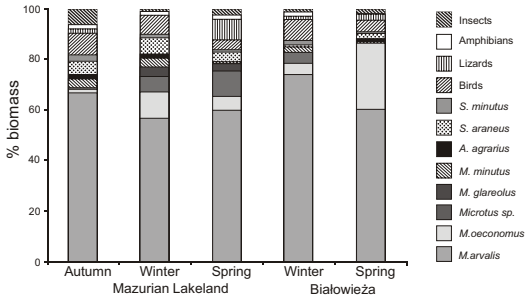

Fig. 2. Seasonal variation in percent biomass of food items in the diet of the Great Grey Shrike at the two study areas; for sample sizes, see Table 1.

Overall, the shrike diet composition considerably varied between seasons and the two areas (Tables 1–2, Fig. 2). The significant interaction with season and area for the Common Vole implies that the frequency of this species in the diet

Table 2. Summary of log-linear likelihood tests for the variation in the diet of Great Grey Shrike during three seasons at two areas in north-eastern Poland.

Prey type	Effect	df	χ^2	*p*
M. arvalis	Season	2	25.88	0.0000
	Site	1	10.68	0.0011
	Season × Site	2	24.73	0.0000
M. oeconomus	Season	2	18.97	0.0001
	Site	1	9.15	0.0025
	Season × Site	2	2.39	0.3023
M. minutus	Season	2	6.95	0.0310
	Site	1	2.06	0.1510
	Season × Site	2	8.62	0.0134
Sorex spp.	Season	2	11.21	0.0037
	Site	1	6.01	0.0142
	Season × Site	2	5.67	0.0587
Birds	Season	2	1.66	0.4362
	Site	1	0.01	0.9212
	Season × Site	2	6.25	0.0439
Lizards	Season	2	50.53	0.0000
	Site	1	9.85	0.0017
	Season × Site	2	2.45	0.2943
Frogs	Season	2	2.22	0.3295
	Site	1	0.02	0.9012
	Season × Site	2	6.04	0.0489
Coleoptera	Season	2	17.30	0.0002
	Site	1	14.42	0.0001
	Season × Site	2	14.68	0.0007
Orthoptera	Season	2	78.78	0.0000
	Site	1	25.29	0.0000
	Season × Site	2	6.82	0.0331
Hymenoptera	Season	2	54.36	0.0000
	Site	1	15.61	0.0001
	Season × Site	2	8.39	0.0151
Dermaptera	Season	2	20.73	0.0000
	Site	1	10.20	0.0014
	Season × Site	2	5.17	0.0755
Arachnida	Season	2	4.78	0.0915
	Site	1	2.24	0.1343
	Season × Site	2	10.27	0.0059

was lower in winter in the Mazurian Lakeland than in Białowieża, but was similar at both areas in spring (Tables 1–2). Consumption of Root Voles and shrews varied between seasons but not between areas. Lizards were more frequently eaten by shrikes in the spring and in the Mazurian Lakeland. Harvest Mice, birds and frogs were hunted at a constant frequency in all seasons and in both areas. Orthoptera, Hymenoptera and Dermatoptera were consumed significantly more often in the Mazurian Lakeland than in Białowieża, and in autumn than in spring. The significant interaction between the frequency of Coleoptera in the diet, area and season showed that these insects were less frequent in the diet in winter especially in the Mazurian Lakeland.

Diet composition, expressed as consumed prey biomass, showed that from the beginning of October until the end of April, rodents made up the bulk of shrike diet (Fig. 2). Despite the fact that the vole densities were lower in spring than in autumn each year, Common Voles constituted on average 57–75% of the biomass of shrike diet for both seasons (all years pooled).

Two extremes, the pooled *Microtus* voles comprised 69% of autumn food biomass in the Mazurian Lakeland and 86% of spring food biomass in Białowieża. Other species of small mammals were of minor importance and together comprised less than 5–13% of prey biomass in any season. Small passerine birds and lizards each represented up to about 8% of prey biomass in some seasons (Fig. 2). Insects on average only constituted 6% of the prey biomass in autumn and considerably less in the other seasons.

3.3. Year-to-year variation in diet composition

Inter-annual variation in the diet composition of shrikes was negligible in the Mazurian Lakeland. Voles constituted the majority of prey biomass, ranging from 60% to 84% of total prey biomass. The relatively high consumption of Harvest Mice and Striped Field Mice in the autumn and winter 2001/2002 (Fig. 3A) reflected the high observed densities of these two species in October 2001. In mid-winter 2001/2002, birds, insectivores and mice constituted almost 40% of the hunted prey biomass (of these, approx. 50% were passerines), while in the next year this figure was only about 16%. In the early spring the most important supplementary prey were lizards; however, their contribution to prey biomass varied considerably, from about 3% to 25% in different years.

In the Mazurian Lakeland, year-to-year variation of insects in the shrike diet was more pronounced than that of vertebrates. Each winter arthropods comprised 32–43% of prey items, while in spring the variation was between 32% and 67%.

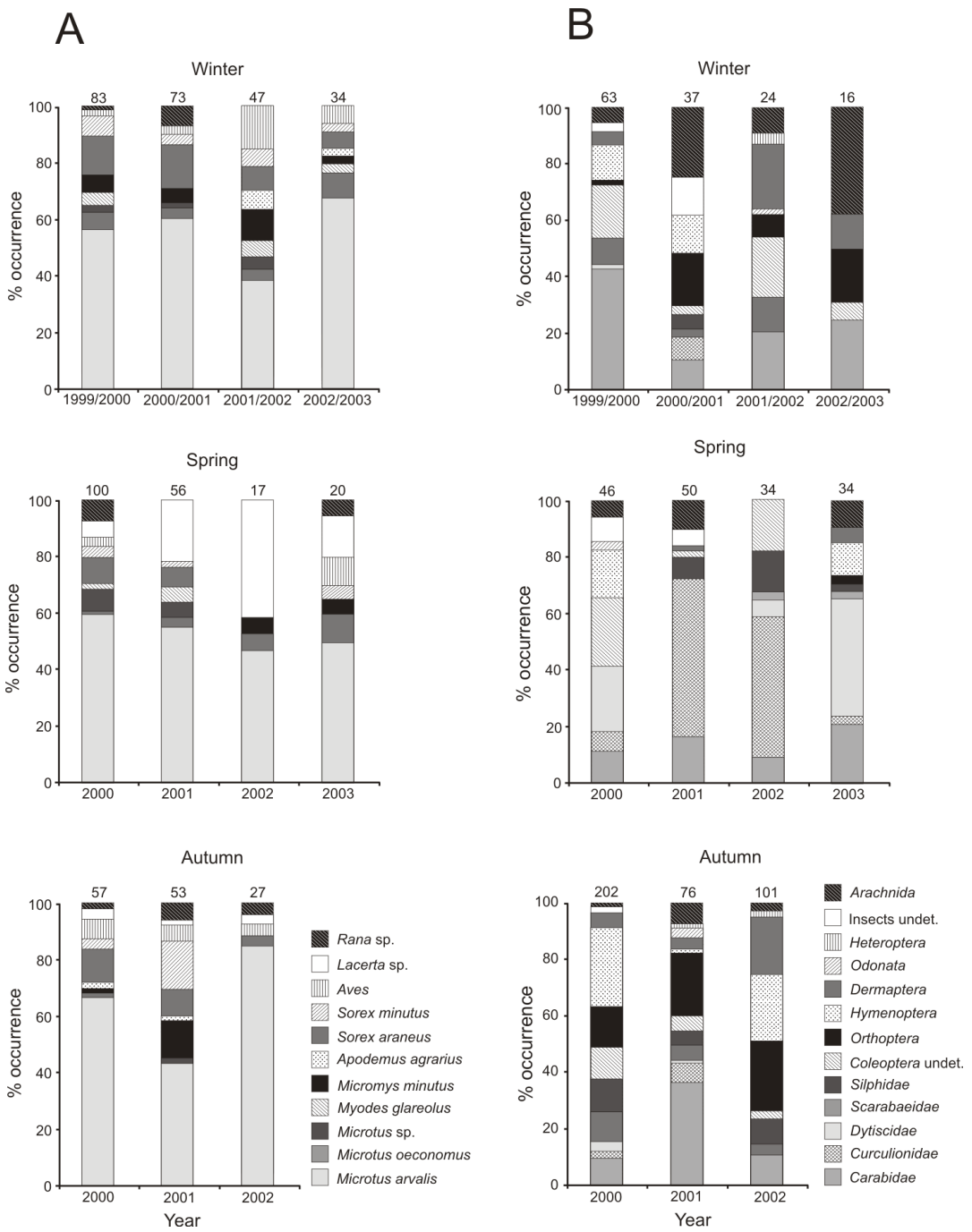

Fig. 3. Year-to-year and seasonal variation in the occurrence of vertebrates (A) and invertebrates (B) in the Great Grey Shrike diet in the Mazurian Lakeland. Values above bars indicate the number of prey items.

The consumption of arthropods by shrikes was highly variable according to year and season, and did not show any clear pattern (Table 1, Fig. 3B). In general, Coleoptera were the most frequently captured arthropods, particularly the families Carabidae, Curculionidae, Dytiscidae and Scarabae-

Table 3. Preference of Great Grey Shrike for rodent species in autumn and spring at two study areas. Preferences were calculated using the Ivlev electivity index (D; Jacobs 1974). Species with a proportion of less than 0.03 in the rodent community at both study sites are not included. Rod = rodent community; Prey = shrike prey; D = electivity index.

	Mazurian Lakeland						Białowieża		
	Autumn			Spring			Spring		
Prey species	Rod	Prey	D	Rod	Prey	D	Rod	Prey	D
Microtus arvalis	0.65	0.88	0.60	0.57	0.89	0.72	0.07	0.82	0.97
Microtus oeconomus	0.06	0.01	–0.73	0.03	0.05	0.21	0.46	0.14	–0.67
Apodemus agrarius	0.09	0.02	–0.63	0.26	0.00	–1.00	0.14	0.01	–0.85
Apodemus flavicollis	0.12	0.00	–1.00	0.13	0.00	–1.00	0.05	0.00	–1.00
Myodes glareolus	0.01	0.00	–1.00	0.00	0.04	1.00	0.15	0.00	–1.00
Micromys minutus	0.06	0.08	0.14	0.00	0.02	1.00	0.07	0.03	–0.47

idae. Seasonal comparisons showed that, Curculionidae and Dytiscidae were most frequently consumed in early spring, although not in all years of the study, while Orthoptera, Hymenoptera and Dermaptera were most frequently taken in autumn, but again with high year-to-year variation (Fig. 3B).

3.4. Prey selection from the rodent and shrew community

At both sites, the Common Vole was more often found in shrike pellets than could be predicted from its relative abundance in the rodent community (Table 3). Due to the low densities of Common Vole in Białowieża, selective predation on this species by shrikes was more pronounced there than in the Mazurian Lakeland. The Root Vole and Bank Vole *Myodes glareolus* were taken by shrikes less often than expected from their abundance in the rodent community, except in spring in the Mazurian Lakeland. Yellow-necked Mice and Striped Field Mice were avoided in both areas, while the Harvest Mouse was taken in similar proportions to its occurrence in the rodent community in the Mazurian Lakeland but was avoided in Białowieża.

The contribution of different shrew species in the shrike diet was proportional to their densities in the Mazurian Lakeland. There, the Common Shrew *Sorex araneus* was twice as numerous as the Lesser Shrew *Sorex minutus* (proportions in the shrew community were 67.3% and 32.7%, respectively), and was in turn eaten twice as often by shrikes, with the average proportion of all shrews over multiple years being 64.3% to 35.7%, respectively. In Białowieża, Lesser Shrews were more often selected by shrikes than could be expected by their proportional abundance in the field: there, 53.3% of shrews in pellets represented this species, but only 18.6% collected in the cone traps.

3.5. Selection of different-sized Common Voles by the shrikes

In the Mazurian Lakeland, selective choice of Common Vole body mass classes by shrikes occurred in autumn and in early spring, being more pronounced in spring. In the autumn, the mean body mass of consumed Common Voles was 12.1 (± 2.18 SD) g, while the mean body mass of captured voles was 14.9 (± 3.89 SD) g (1-way ANOVA; $F = 19.797$, $p < 0.001$). In spring, shrikes consumed Common Voles with a mean body mass of 13.9 (± 3.38 SD) g, whereas the mean body mass of voles trapped in that season was 18.0 (± 4.57 SD) g (1-way ANOVA; $F = 25.717$, $p < 0.001$). In Białowieża, the average body mass of Common Voles eaten by shrikes in winter and spring was 18.7 (± 2.96 SD) g, and the mean body mass in the vole population for the same winter and spring seasons was 19.8 (± 4.93 SD) g, but this difference was not statistically significant (1-way ANOVA; $F = 1.791$, $p > 0.05$).

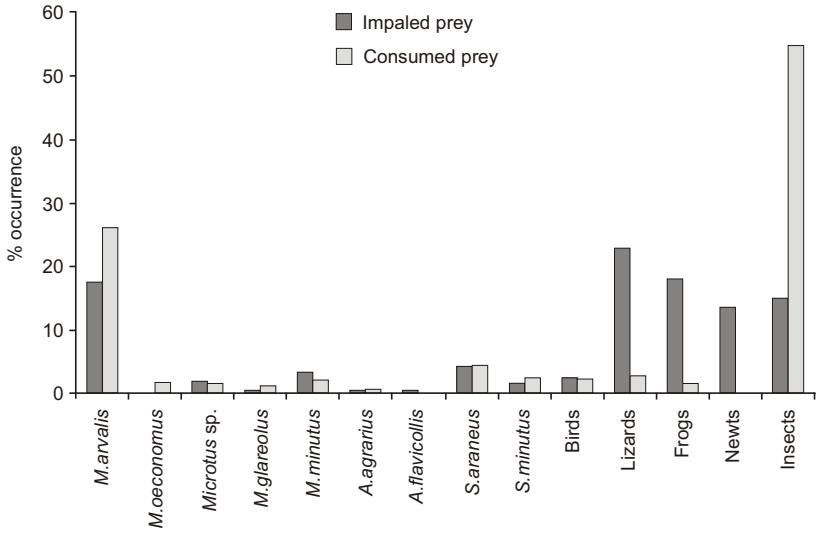

Fig. 4. Comparison of prey stored (impaled on thorns and spikes; 342 items) and consumed (1250 items) by the Great Grey Shrike in the Mazurian Lakeland.

3.6. Prey storage and utilisation

In the Mazurian Lakeland, the prey stored by shrikes differed from that identified in the shrike pellets (Fig. 4). The Root Vole was the only prey category that occurred in the shrike diet but was not stored. The Smooth Newt *Triturus vulgaris* was among the prey most often stored by shrikes (13.4%), but its remains were not found in pellets. Other main groups of prey which were more often stored than consumed were lizards and frogs. Insects as a whole comprised over 50% of prey individuals consumed by shrikes, but their contribution to the total of stored animals was only about 15%. Apart from caterpillars (see below), only three insect taxa were stored: Scarabaeidae, Dytiscidae and Orthoptera. The latter was represented as a stored insect prey more often than could be expected from their contribution to the total number of insects consumed (76.5% versus 12.7% of all insects, excluding caterpillars, respectively). Caterpillars were not found in the diet and, due to their high digestibility and the low likelihood of detecting their remains, were excluded from these calculations.

Among the carcasses of Common Voles stored by the shrikes, 63.4% were headless. In the Mazurian Lakeland, 325 skulls of Common Voles were identified in shrike pellets over the whole study, while vole thigh-bones comprised 61.2% and pelvises 46.5% of the total number of skulls found (Table 4). In Białowieża, thigh-bones comprised 70.3% and pelvises 57.0% of the total skull number (128). These proportions varied among seasons (log-linear models for thigh-bone: $\chi^2 = 8.62, p = 0.013$; pelvis: $\chi^2 = 8.53, p = 0.014$) but not between the two areas (thigh-bone: $\chi^2 = 0.89, p = 0.346$; pelvis: $\chi^2 = 0.62, p = 0.427$; Table 4). The contribution of pelvises and thigh-bones increased from autumn to spring, which indicated that in autumn, shrikes more often consumed only heads, whereas in winter and spring other parts of the body were also eaten.

4. Discussion

4.1. Seasonal and habitat-dependent variation in the diet composition

This study demonstrated seasonal and geographic variation in diet composition of the Great Grey Shrike in Central Europe. The two study areas differed in terms of land management and landscape heterogeneity. The Mazurian Lakeland exclusively consisted of fallows, whereas in Białowieża, shrikes inhabited a mosaic of fallow areas, pastures, meadows and cultivated fields. Furthermore, the Białowieża Glade contains a greater proportion of wetlands, whereas the study site in the Mazurian Lakeland is mainly composed of dry, sandy hills, overgrown with grassland. At both ar-

eas, the structure of small mammal communities (mainly the proportion of Root and Common Voles) reflected these differences. Nevertheless, the similarity of the shrike diet in both areas was very high, suggesting similar foraging strategies and prey selection.

In our study, *Microtus* voles were the predominant prey of the Great Grey Shrike throughout the winter, and the Common Vole was the most frequently hunted species, results similar with other studies from temperate Europe (Mester 1965, Grönlund *et al*. 1970, Haensel & Heuer 1970, Straka 1991, Wagner 1994, Hromada & Krištín 1996). Shrikes consumed more Root Voles in Białowieża than in the Mazurian Lakeland, reflecting the relatively low densities of the Common Vole in the former area. Habitat composition, season, climate and prey availability may shape the local shrike diet. The geographical variation in food eaten by the Great Grey Shrike, at least if expressed as consumed biomass (pellets), may not be considerable (but see Nikolov *et al*. 2004). The bulk of the diet of the Great Grey Shrike mostly comprises voles; the foraging strategy is thus markedly adapted to preying on these rodents. Shrikes use UV cues to gain information on vole location and abundance (Probst *et al*. 2002), which helps in hunting. However, morphological features associated with killing prey are apparently less efficient in shrikes than in many raptors and owls (beaks, talons and body size). Therefore, shrikes may need longer time to handle prey than do owls and raptors; indeed, Olsson (1984b) reported that the act of killing a vole by a Great Grey Shrike may take as much as a minute. Atkinson and Cade (1993) showed that the predation success of shrikes is considerably higher on arthropods than on small mammals (over 90% versus 56%). Karlsson (2001) recorded even lower (25%) hunting success of shrikes in winter. Hromada *et al.* (2003) analyzed the relationship between Great Grey Shrike phenotype and the choice of prey, and found that some morphological traits may affect dietary preferences. However, these findings concerned mainly different groups of insects but not *Microtus* voles, supporting the "universal ability" of shrikes to catch voles.

In both study areas, vertebrates other than mammals were consumed by shrikes as a supplementary food, but their contribution to the shrike diet was generally low. In mid-winter, small passerine birds were occasionally hunted in both areas, a finding similar to previous studies (Haensel & Heuer 1970, Wagner 1994, Bocca 1999, Nikolov *et al*. 2004). The low proportion of birds in the shrike diet is probably due to difficulties in hunting this mobile prey. However, in both areas the proportion of small birds in the shrike diet peaked in mid-winter, which suggests that passerines represent an important alternative prey when snow cover reduces the availability of rodents, as has been observed in north Europe (Karlsson 2002). In support of this suggestion, Lorek *et al*. (2000) also found that the number of avian prey taken by the Great Grey Shrike varied seasonally and peaked in December–January. Amphibians and reptiles are hardly available in mid-winter when the temperature drops below 0^{o}C, but in autumn and spring they were very numerous in both study areas. In early spring, probably due to the low densities of Common Vole, lizards (mostly *Lacerta vivipara* and the less frequently consumed *L. agilis*) constituted a more significant part of the shrike diet. Grönlund *et al*. (1970) in Finland and Bocca (1999) in Belgium showed that lizards may represent the majority of vertebrates consumed by shrikes during spring and summer, but similarly to our findings they were unimportant in autumn and winter.

Invertebrates, mainly insects, were numerically the most important prey of the Great Grey Shrike, but the contribution of particular taxonomic groups to the shrike diet appeared variable. Little is known about the selective choice of insects as prey. The availability of invertebrates depends on the season and habitat type, and may affect the diet composition of shrikes. For example, Haensel and Heuer (1970) found that Staphylinidae beetles represented nearly half of all invertebrates consumed by wintering shrikes in eastern Germany, and Bocca (1999) recorded Dermaptera to be the most frequently eaten insects in winter in Belgium. However, the most common insect prey for shrikes may actually be Carabidae, Hymenoptera and Orthoptera (Grönlund *et al*. 1970, Straka 1991, Atkinson & Cade 1993, Hromada & Krištín 1996). All these, and additionally Curculionidae and Dytiscidae, were the most frequently consumed invertebrates in the Mazurian Lakeland; on the other hand, in Białowieża the composition of

Table 4. The occurrence of skulls (*N*), and thigh-bones and pelvises (% of the recorded skulls) of the Common Vole in the pellets of Great Grey Shrike. The two study areas and different seasons are shown separately.

	Mazurian Lakeland			Białowieża	
Bone type	Autumn	Winter	Spring	Winter	Spring
Skull *(N)*	84	132	109	36	92
Thigh-bone%	54.8	61.4	66.1	52.8	77.2
Pelvis%	38.1	43.2	56.9	50.0	59.8

the shrike diet was more homogenous, with beetles, particularly Carabidae, being predominant.

The diet composition of shrikes did not well correlate with the composition of stored prey, because some stored prey was often not consumed. Birds and small mammals were exceptions, as the contribution of these in pellets was similar to their contribution in the stored prey. In Spain, the prey most often stored but frequently left unused by shrikes were reptiles and insects (mainly Orthoptera) and over one-third of all stored prey was not eaten (Hernández 1995b). Similarly, in the Mazurian Lakeland many stored invertebrates, newts, frogs and lizards were not consumed, and the stored voles were only partly utilized. This partial consumption of stored voles was supported by approximately two-thirds of all carcasses being headless, and the higher proportion of skulls than pelvises or thigh-bones found in pellets (see also Straka 1991). The proportion of wasted parts of prey body decreased from autumn to spring, suggesting that declining vole densities forced shrikes to utilize their prey more efficiently. The difference between consumed and stored amphibians and reptiles along with the partial consumption of voles suggest that, at least in late autumn, shrikes are not short of food in the study areas. These observations may also result from the fact that stored prey can be robbed by other birds (corvids) and mammals (canids), although there was no evidence for such behaviour in the study areas.

4.2. Inter- and intraspecific selection of prey

Optimal foraging theory suggests that a predator prefers the most profitable prey available to maximize energy gain in relation to that expended during foraging. However, the suitability of prey depends not only on its energetic profitability (body size) but also on its accessibility, manageability and hunting success (Stephens & Krebs 1986, Sih & Christensen 2001). Therefore, selection of rodent species by shrikes can be related to size, mobility and habitat selection of the prey.

The Common Vole seems to be the optimal mammalian prey to be handled and killed by shrikes; this species was preferred over other rodents in the present study. In other regions, however, shrikes may prefer smaller species and even avoid larger rodents. In contrast to our findings, Hernández (1995a) reported that in Spain shrikes more often selected *Microtus lusitanicus* and *M. agrestis* than could be expected, whereas the Common Vole was avoided. However, *M. lusitanicus* is smaller than the Common Vole. Root Voles were the most abundant rodents in Białowieża but were avoided by shrikes probably because of their large size. Lorek *et al*. (2000) also reported a preference of smaller (avian) prey: over 82% of hunted passerines were less than 30 g. The Harvest Mouse and both shrew species seem to be small enough to be easily killed, and indeed these are the main mammalian alternative prey if *Microtus* voles are scarce (Karlsson 2002). At both present study areas, Harvest Mice and in the Mazurian Lakeland shrews were hunted by shrikes in proportion to their availability. Although shrikes preferred Lesser Shrews over the larger Common Shrews in Białowieża, it seems that among very small vertebrates, selection of prey based on size may not be common.

Shrikes may commonly hunt voles because voles generally move slower than mice and shrews, such as the very small Striped Field Mouse. Indeed the present results indicated that

this mouse was avoided by shrikes. These results are consistent with previous studies that have shown Muridae to be a minor component in the shrike diet (Haensel & Heuer 1970, Straka 1991, Wagner 1994). Shrikes hunt on open areas with low vegetation (Yosef & Grubb 1993, Tryjanowski *et al*. 1999) which are preferred also by *Microtus* but not by Bank Voles. The Bank Vole, similar in size and mobility to the Common Vole, inhabits forest edges, shrub land and small, wooded patches within agricultural landscapes but avoids open areas (Pucek 1983), making it generally unavailable to shrikes. Hence, Bank Voles were only rarely consumed by shrikes. Apart from differences in body size and movement ability, habitat preferences may also explain why shrikes preferred *Microtus* voles in their diet. In both study areas, Common Voles were more abundant in dry, open habitats with lower vegetation, whereas Root Voles preferred meadows or fallow areas with thicker and taller vegetation. Vegetation cover may be an important factor affecting rodent availability and in turn shrike hunting success, and differences in detectability between *Mirotus* species could affect their share in the diet of Great Grey Shrike. However, in winter and in early spring, vegetation cover is generally sparse in habitats preferred by Common Vole and Root Vole. Consequently, during this period the habitat preferences of different vole species not affect their availability to shrikes.

The present study also demonstrated the shrikes to be able to select their prey intra-specifically. In the Mazurian Lakeland, the proportion of smaller Common Vole individuals in the diet was higher than could be expected by their share in the local rodent population. Likewise, in Spain, Common Voles consumed by shrikes weighed on average 19.6 g, whereas in the vole population the average weight was 23.9 g (Hernández 1995a). Similar results have been obtained for owls that appear to select particular size classes in prey species that otherwise are too large to be easily killed (Zalewski 1996). The present results demonstrated that intra-specific selection of prey of certain size may also be related to the community structure and relative abundance of the prey community. In the Mazurian Lakeland, where the abundance of Common Voles was higher than in Białowieża, shrikes selectively hunted small individuals of this species. In Białowieża, the preference of Common Voles over other rodent species was evident but the preference of small individuals was far less pronounced. The pattern may be explained by the low density of this species as compared to the Root Vole. Due to the scarcity of Common Voles in Białowieża, shrikes could be forced not only to take larger-than-preferred Common Voles but also to hunt other larger prey, such as the Root Vole. Consequently, in Białowieża the selection between Common and Root Voles as a process was similar to the preference of smaller Common Vole individuals in habitats with relatively high densities of this rodent. Due to the small number of Root Vole remains in the pellets, we were not able to analyze the selective choice of body mass within populations of this species. However, due to its larger body size shrikes may select smaller individuals even more strongly than in the case of the Common Vole.

The selective choice of rodent size by raptors is usually related to the raptor size; smaller individuals are preferred over larger if the prey is on average relatively large for the size of the predator (Zalewski 1996). The Great Grey Shrike is among the smallest predators that can hunt voles; thus, the selection of small prey species and smaller individuals can be pronounced in this species. The present study indicates that the selection of prey species by the shrike operates at the level of prey community (inter-specific selection of particular prey/vole species) but also at the population level (intra-specific selection of individuals of particular size within a prey species). The selection intensity varies, and optimal foraging by shrikes among various rodent communities includes interrelated selection at both levels in relation to the abundance of smaller vole species. Therefore, selection of particular prey size should be analyzed not only for particular prey species but for ecologically similar groups of species. However, on the inter-specific level of prey selection many other factors contribute to differences in the choice of prey, such as prey availability resulting from their habitat associations.

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Isolepinkäisen talviaikainen ravintokäyttäytyminen Koillis-Puolassa: vaikuttaako ravinnon saatavuus saaliin kokoon?

Ravinnon koostumusta ja saaliinvalintaa tutkittiin talvehtivilla isolepinkäisillä (*Lanius excubitor*) kahdella alueella Koillis-Puolassa: Masurian järvialueella ja Białowieżan aukeilla. Lepinkäisten ruokailutottumushavainnot perustuivat 1582 tunnistettuun ravintokohteeseen kerättynä 1220 oksennuspallosta, jotka kerättiin 1998–2003. Pikkunisäkkäiden elävänä pyynnit osoittivat, että kummallakin alueella *Microtus*-suvun myyrät dominoivat ja että Masurian alueella kenttämyyrä (*M. arvalis*) ja Białowieżassa lapinmyyrä (*M. oeconomus*). Molemmilla alueilla lepinkäisten pääravintoa näyttivät olevan pikkunisäkkäät ja hyönteiset ja vähemmässä määrin muu saalis (varpuslinnut, liskot ja sammakot). Myyrät muodostivat 69–86 % ja muut pikkunisäkkäät vain 5–13 % ravinnon biomassasta. Lepinkäiset saalistivat valikoivasti kenttämyyriä erityisesti paikoilla, joilla tätä saalista oli vähän. Toisaalta paikoilla, missä kenttämyyrää oli enemmän, lepinkäiset valikoivat pienimpiä yksilöitä, mitä ei havaittu niillä paikoilla, joilla lapinmyyrä oli runsain myyrä. Ilmeisesti lajinsisäinen ja lajienvälinen saaliin valikoivuus on kytköksissä ja riippuu saaliskohteen saatavuudesta.

Lepinkäisten varastoima ravinto erosi niiden syömästä. Lapinmyyriä ei havaittu keihästetyn, mutta niitä löytyi syödystä ravinnosta. Sammakoita, vesiliskoja ja liskoja oli varastoitu suhteessa enemmän kuin syöty. Kallon-, lantio- ja reisiluiden analyysi viittasi siihen, että lopputalvesta ja varhaiskeväällä, kun myyrämäärät laskevat, lepinkäiset söivät myyriä useammin kokonaisina kuin syksyllä.

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