Avian predation upon a mixed community of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*)

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Summary. Pellets of diurnal avian predators (mainly kestrels and buzzards) were analysed to prove the hypothesis of selective predation for a mixed population of small rodents. It was found that voles heavily predominated as prey over mice (up to a factor of 19 during winter). Within both prey species, predation focussed on distinct parts of the populations: during winter the heaviest specimens were preferentially captured, during summer the subadults were in an exposed position. In the voles, an additional predominance of males occurred (up to a factor of 5.2 during summer). These findings verify the assumption of Errington (1956) that specimens of a low social rank are susceptible to the highest risk of predation.

Key words: Pellet analysis – Selective avian predation – Small rodent populations – Social rank – Varying vulnerability

The influence of predation upon small mammal populations has been under discussion for a long time (see Huffaker 1971), particularly following the basic considerations of Errington (1946). Many investigations deal with the aspect of whether this factor is necessary or at least of some importance for the fluctuation of vole populations (e.g. Pearson 1966, Hansson 1984). Erlinge et al. (1983) on the other hand suppose predation to be responsible for the suppression of cyclicity in southern Sweden. One of the most important matters of discussion is the possibly differing vulnerability of specific prey groups. Errington (1956) framed the hypothesis that individuals of a low social rank are selectively taken by predators. From field data, this assumption was sometimes verified and sometimes questioned, so the factual situation remains uncertain. The problem, however, is of keen interest: if non-random predation could be proved correct, this would imply that predators affect the population structure of their prey in a subtle manner, and that the total impact of predation would be of lesser importance.

It was our aim to scrutinize Erringtons assumption for one distinct predatory group, i.e. the diurnal avian predators. The survey was carried out in a reclaimed area of the Rhineland lignite district near Cologne, which was characterized by young afforestations and some grassland. The population dynamics of the two dominant small mammal species, *Microtus arvalis* and *Apodemus sylvaticus*, were well-known from an extensive investigation on the small

rodent ecology in this area (Halle 1987). In addition, the density and hunting habits of the raptors were carefully examined (Schnitzler 1987). With this background, the analysis of pellets, which is the source of this paper, offers the chance to elucidate the situation thoroughly. It centres on two questions: 1. Do predators preferentially select one of the two species, and if so, what are the reasons for this? 2. Does the comparison of population structure and prey spectrum furnish evidence for disproportional vulnerability within the rodent populations?

Methods and material

Collecting and examination of pellets

Pellets were collected for the first time in late March 1984 (with a total of 1060 pellets) and a second time in November of the same year (with a total of 611 pellets). This was done by examining the preferred roosts like pales, posts and stakes in an area of about 400 ha. Some freshly released pellets were deposited in the field and controlled at regular intervals. They kept solid for half a year at the most, so it was certain that the first collection represents the winter aspect and the second the summer aspect of predation.

After air-drying of some weeks, pellets were measured and the associated avian predators were identified after März (1972). Pellets of kestrels (*Falco tinnunculus*) and buzzards (*Buteo buteo*) were mainly found, and during the winter period some pellets of hen harriers (*Circus cyaneus*) were present as well. For further evaluation, pellets of the various species were not segregated. They were carefully dissected and the contents were identified by bones and, for the small mammals, by dentition. Pairs of upper incisors were taken to count the number of individuals.

Estimation of body weight

The cranium of 10 males and 10 females of *M. arvalis* and *A. sylvaticus* with different body weights were skeletonized and measured. It was found that the correlation between the upper jaw diastema length and body weight was good for both species (*M. arvalis:* $r = 0.87$, *A. sylvaticus:* $r = 0.89$); this was therefore taken for body weight estimation. Sebek (1959) also recommended this measurement as being suitable for age determination in *M. arvalis*. It was of additional advantage that the maintenance of this part of the cranium was frequently good in the pellets.

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Whenever possible, the diastema in the skull remains was measured with a vernier caliper accurate to 0.1 mm. This could be done for 1357 *M. arvalis* (winter: 930, summer: 427) and 168 *A. sylvaticus* (winter: 97, summer: 71). The approximate body weight of each specimen was then estimated using the calibration graph for the associated species. In order to evaluate the distribution of weight-classes, the number of same-sized remains was plotted as a percentage of the total.

Estimation of sex ratio

If possible, the remains of the pelves were measured as described by Brown and Twigg (1969). The material contains 1186 pelves of *M. arvalis* (winter: 849, summer: 337) and 471 pelves of *A. sylvaticus* (winter: 252, summer: 219). According to Brown and Twigg (1969), males and females were distinguished by graphical analysis. The accuracy of the discrimination was then tested for the 10 males and 10 females of both species which were skeletonized for body weight estimation. Those ranges of the graph where overlapping seemed possible and where the determination would therefore be ambiguous were excluded. The sex ratio was calculated separately for left and right ossa coxae, and the average was then taken.

Data from rodent populations

For the comparison between the spectrum of captured specimens and the rodent populations, data from a detailed perennial investigation on population dynamics in the same biotope were used (Halle 1987). Findings are based on 224 catches of *M. arvalis* (winter: 116, summer: 108) and 733 catches of *A. sylvaticus* (winter: 358, summer: 375), which occurred from monthly live-trapping with the "Oos-Drahtgitterfalle". Only a rough survey is required for the purpose mentioned here, so the average of weight-class distribution (summarized for classes of 4 g) and sex ratio for both species were evaluated for the winter and the summer periods.

In order to assess the different risk of predation for the two species, the pattern of above-ground activity was determined by trap catches. In the month of October, a grid of 100 live-traps was controlled every 30 min for 48 h. For each species the number of catches within one time interval were summarized for both days and expressed as a percentage of the total.

Results

Spectrum of prey

In Table 1, the spectrum of the prey is represented as it was found in the pellets of the raptors. During both seasons, *M. arvalis* was by far the most frequent prey. It was followed by *A. sylvaticus*, which obviously was of much less importance. Owing to the numerical proportions of determinable rodents, it is reasonable to suppose that most of the unidentified Myomorpha (remains which could not be classified as Arvicolidae or Muridae) were also specimens of *M. arvalis*. Other prey items could almost be neglected, only *M. agrestis* and birds were of slight importance during winter.

This result does correspond with the occurrence of the species in the investigated area as determined by trap

Table 1. Numbers of definitively identified individuals in pellets of diurnal avian predators (mainly kestrels and buzzards). Pellets were collected twice a year in a reclaimed area of about 400 ha. The first collection in late March encompasses prey captured during the winter, the second in November prey captured during the summer

	Winter		Summer	
	N	%	*N*	%
Microtus arvalis	1082	67.8	687	67.6
Microtus agrestis	25	1.6	7	0.7
Microtus sp.	192	12.0	100	9.8
Clethrionomys glareolus	2	0.1	1	0.1
Arvicola terrestris	2	0.1	2	0.2
Apodemus sylvaticus	171	10.7	174	17.1
Rattus norvegicus	3	0.2	1	0.1
unidentified Myomorpha	80	5.0	29	2.9
Muscardinus avellanarius	0	0	1	0.1
Sorex araneus	8	0.5	4	0.4
Crocidura leucodon	1	0.1	1	0.1
unidentified Soricidae	3	0.2	0	0
Aves	25	1.6	9	0.9
Pisces	1	0.1	0	0
sum total	1595	100	1016	100

Table 2. Proportions of the genus *Microtus* and the genus *Apodemus* as ascertained by live-trapping in the field (=population) and by analysing the prey items (=pellets). The factor of *Microtus* predominance referes to the frequency of voles found in the pellets relative to those found in the population

	Proportion of Microtus to Apodemus		Factor of Microtus predominance
	Population	Pellets	
Winter	0.4:1	7.6:1	19.0
Summer	0.5:1	4.6:1	9.2

catches. *M. arvalis* and *A. sylvaticus* were numerous in the young afforestations, while the other species were present only in older parts and on the outskirts (Halle 1987).

Different vulnerability of voles and mice

When the proportions of the genus *Microtus* and the genus *Apodemus* as a prey were compared with their abundance, a crude bias towards the voles became obvious (Table 2). During both seasons, mice outnumbered voles by about two to one in the field (Halle 1987). In the pellets, however, 7.6 or 4.6 voles were found per one mice during winter and summer respectively. The factor of predominance amounted to 19.0 during winter and 9.2 during summer. As an annual average, voles were about 14 times more exposed to predation than mice.

The reasons for this striking result became plain when the patterns of above-ground activity were taken into consideration (Fig. 1). In the trap-catches, *A. sylvaticus* appeared as a strictly nocturnal species, while *M. arvalis* exhibited considerable daylight activity: during the two days of trapping, all the 298 catches of *A. sylvaticus* occurred during the night, but 37 out of the 165 catches of *M. arvalis* (=22.4%) were during daylight. Therefore, the availability
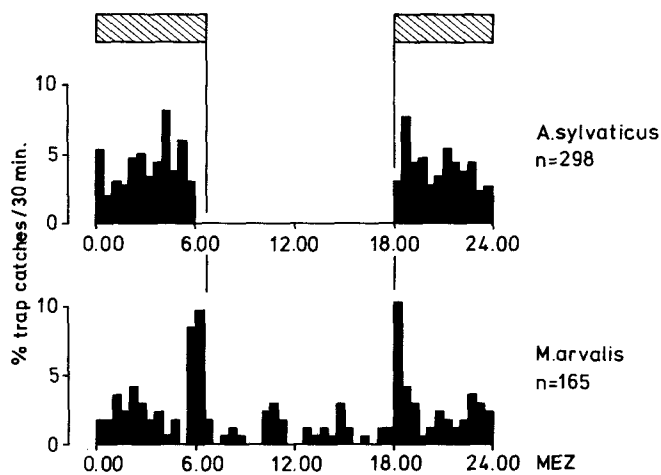
Fig. 1. Activity patterns of *A. sylvaticus* and *M. arvalis* as determined by live-trap catches. For each 30 min interval of the 24 h day, the number of catches are expressed as a percentage of the total during the two days of examination ($n = 100\%$ for each species). Vertical lines indicate times of sunrise and sunset

Fig. 2. Comparison of weight-class distribution as found in the population (shaded columns) and as prey (solid lines) for *M. arvalis*. The approximate body weight of prey specimens was estimated from the length of the upper jaw diastema (accurate to about 1 g). The numbers of same-sized remains were plotted as percentages of the total. The population structure was evaluated from weight-classes of 4 g; for each class, the percental amount was therefore divided by 4 to achieve comparable dimensions

to diurnal avian predators differed considerably, which explains the bias of the prey proportion.

The much higher vulnerability of voles during winter (c.f. Table 2) is likely to be an effect of the changing vegetation cover. During winter, when the grass is flat and the trees have lost their leaves, voles are much easier to perceive, especially when they move above the snow cover. An additional factor could have been a phase-shift of activity towards daylight during winter, which for *Microtus* species was described by Ostermann (1956), Erkinaro (1961) and Bäumler (1975). Nevertheless, results from new registration methods recently casted doubts upon the phenomenon as a regular annual process (Halle and Lehmann 1987). The diminished shelter, therefore, remains the most probable explanation for seasonal differences.

Selective predation upon the rodent populations

During winter voles with a body weight of 15–23 g were found to be the preferred class of prey (Fig. 2). In the population, however, specimens of 10–14 g constituted the most frequent weight-class during this period. This discrepancy could have been somewhat overestimated because of habitat heterogeneity: the population under survey inhabitated a young afforestation, which was found to be a suboptimal biotope for *M. arvalis* with unstable populations and extremely low body weights of overwintering animals (Halle 1987). Schnitzler (1987), however, ascertained that the few grass-grown plots in the area were favoured hunting grounds for both kestrels and buzzards. In such biotopes, which offer optimal conditions for voles, slightly higher body weights of overwintering animals were found. At all events, it could nevertheless be stated that during winter, predation focussed on the heaviest specimens of *M. arvalis*.

This pattern changed for the summer period. The curve of favoured prey was obviously shifted to lower weight-classes and voles of about 15–20 g prevailed in the pellets. The weight-class distribution reflected the population structure during the reproductive season. The classes of juveniles and young subadults (up to 14 g) as well as the class of heavy adults (above 22 g) were present in typical amounts.
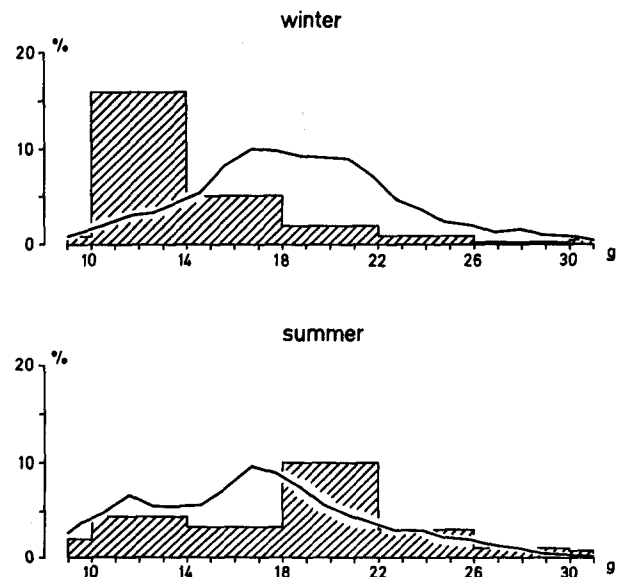
The class of 18–22 g was mainly formed by non-pregnant females. A remarkable fact is the unexpectedly low proportion of the weight-class 14–18 g. This could have been a consequence of intensive predation, which was particularly high in this class. The point will be discussed again later on.

For *A. sylvaticus*, the results were principally equal (Fig. 3). During winter, specimens of the two weight-classes 18–22 g and 22–26 g were found most frequently in the pellets, although animals of 18–22 g were twice as common in the population as the heavier class. An extremely high proportion of prey was formed by specimens above 26 g, which in the population during winter were represented in very small numbers only. These were old animals, especially females, which had overwintered the year before and which for the most part disappeared from the population in late autumn and early winter (Halle 1987).

During summer the spectrum of *A. sylvaticus* as a prey was characterized by a shift towards lower body weights. On the whole the curve followed the weight-class distribution of the population, with the one exception of the class 18–22 g. This class was extremely exposed to predation, which again could be the explanation for its relatively low proportion in the population.

In Table 3, the sex ratios as found in the population and in the pellets are compared. During winter the sex ratio of the voles was nearly balanced, whereas females distinctly prevailed during the reproductive season. During both seasons males predominated in the pellets. This bias was especially high during summer, when the factor of male predominance yielded 5.2. For the mouse population, an overweight of males was observed all the year round, equal proportions being found in the pellets. So for *A. sylvaticus*, no sex predominated as prey at any season.
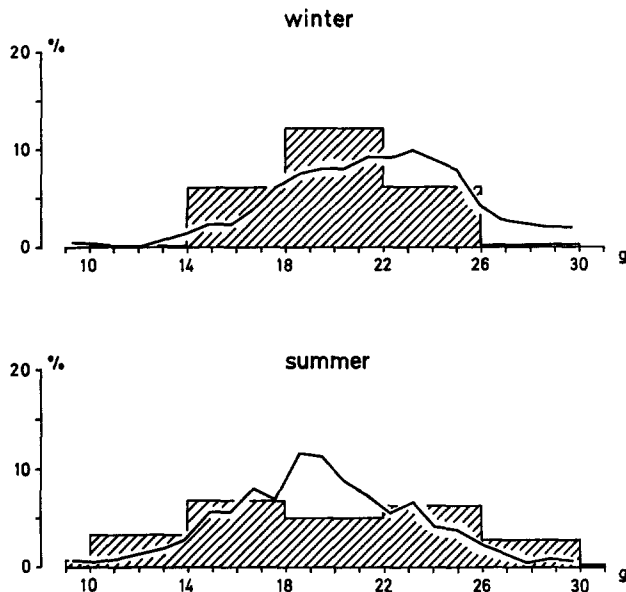
winter

summer

Fig. 3. Comparison of the weight-class distribution as found in the population (shaded columns) and as prey (solid lines) for *A. sylvaticus*. The style of diagram is in accordance with Fig. 2

Table 3. Sex ratio (males to females) of voles and mice as ascertained by live-trapping in the field (=population) and by measuring pelves remains of the prey (=pellets). The factor of male predominance refers to the frequency of males found in the pellets relative to those found in the population

		Sex-Ratio (♂♂:♀♀)		Factor of male predominance
		Population	Pellets	
Microtus	Winter	1.2:1	1.9:1	1.6
	Summer	0.6:1	3.1:1	5.2
Apodemus	Winter	1.6:1	1.8:1	1.1
	Summer	1.7:1	1.6:1	0.9

Discussion

Owing to the higher degree of digestion, it is much more difficult to identify prey items from pellets of diurnal raptors than from those of owls. Duke et al. (1975) suppose that greater bone corrosion in Falconiformes is a consequence of higher acidity of the gastic juice. So, pellets of buzzards normally contain a few teeth and skeleton remains, and the identification of prey species is only rarely possible (Uttendörfer 1939; Melde 1983; Glutz von Blotzheim et al. 1971). Descriptions of the skeleton maintenance in kestrel pellets, however, vary in wide ranges. During an experimental investigation with one caged individual, Yalden and Yalden (1985) found that on the basis of skeleton remains only 26% of known prey animals could be identified to the genus, not even to the species. Therefore they suggested that analyses of kestrel pellets are burdened with inevitable uncertainties. On the other hand, Uttendörfer (1939) and Piechocki (1970) reported a type of kestrel pellets, in which the maintenance of the bones is of comparable quality as in owl pellets. In our material, most kestrel pellets contained skeleton remains in exellent condition, in a few cases even inclusive of ribs and phalanges.

The reasons for this uncommon finding are speculative. It seems possible, however, that on the basis of good nour-

ishment (as given in the investigation area, Schnitzler 1987), kestrels released pellets more often and the bones were therefore exposed to high acidity for shorter times than usual. Such a relation between nourishment, "meal to pellet interval" and "thoroughness of digestion" was demonstrated by Duke et al. (1980) for barred owls (*Strix varia*). Nevertheless, the good maintenance in our material had the welcome effect that prey species could easily be identified and the amount of uncertain items kept to a low level.

The investigation of Boonstra (1977) with tagged *Microtus townsendii* has shown that "the majority of voles eaten by predators were subsequently deposited on the study area itself." So, we could be fairly sure that the analysis mainly reflects the predatory habits in the area where the pellets were collected. This was additionally confirmed by the spectrum of prey species, which in the main resembled the distribution of small mammals in the afforestations.

There was, however, one substantial difference: the genus *Microtus* was found to be the most frequent prey, whereas in the field *A. sylvaticus* was the dominant species. The fact that especially *M. arvalis* is under extremely high predatory pressure is well-known (e.g. Uttendörfer 1939, 1952). Nevertheless, the degree of *Microtus* predominance, which amounted up to a factor of 19 during winter, is of course remarkable. This finding, which could obviously be explained by different activity patterns of the two rodent species, is of some interest in connection with biological pest control. *M. arvalis*, which can cause severe damage in young afforestations, are exposed to much more intense predation than the harmless mice, a differentiation which is not fulfilled by common rodenticides (Frank 1952). It is probable that this factor was one of the reasons for the very low rate of damage in the area, which was found to be not more than about 0.4% of the standing growth per year (Halle 1987).

The most important question regarding the assumption of Errington (1956) is whether predation focusses on distinct classes of the prey species. This could quite definitely be confirmed from our material for both species under survey. During winter months, the heaviest voles and mice were in an exposed position. During summer, however, the situation became much more indicative: in both species the subadults were the class with the highest vulnerability. As Errington (1956) put forward, they are characterized by a low position in the social system. Subadults are normally not provided with established home-ranges and therefore have to move in unknown terrain more often. Metzgar (1967) and Amrose (1972) have shown by experiments, that this would increase the risk of predation.

Furthermore, for *M. arvalis* males predominated as prey to a great extent. It is well-known from common vole populations that there is a surplus of subadult males, which disappear in some way from the populations (Frank 1953; Stein 1953, 1958). From our data, it could be emphasized that predation is one important factor for this occurrence. Our findings are, therefore, in absolute agreement with the results of Beacham (1979), who investigated avian predation during the decline phase of *M. townsendii*. He stated that "smaller males tended to be the animals most likely selected by avian predators, whereas larger females were the least likely" and that this "may also partially account for the deficiency of males which often characterizes resident vole populations". It should not be suppressed that particularly this mechanism was dismissed for *M. arvalis*

by Becker (1954), who found no predominance of males in the pellets of owls. Brown and Twigg (1969), however, commented that the mensural method of Becker gave imprecise separation of the sexes. Nevertheless, Boonstra (1977) also found no confirmation for non-random predation in *M. townsendii*, although body weights of the prey tended to be lower than in the population. The situation therefore is not as plain as it seemed to be initially.

A real effect of predation on the population structure of the prey is difficult to prove, because of the mutual influence upon each other. It is almost impossible to distinguish rigorously whether predation causes the low numbers of a specific class within the prey population, or whether predation focusses on a class, which is for some other reason not so numerous. For the data presented here, however, the first possibility seems reasonable. During both summer and winter, those classes which were known to disappear from the populations within the corresponding period, were overproportionally found in the pellets. Additionally, a higher vulnerability could partly be explained by social and behavioural peculiarities.

Although an influence on the population structure was obviously present, there is some question as to whether or not the population dynamics itself was affected by predation. Subadults, and especially subadult males of *M. arvalis*, are a real "surplus" of the population, whose most important task is to guarantee supply for the functional group of reproductive adults. Those specimens which cannot ascend to the higher social rank are without importance for the reproductive output of the population. Their thankless role could be seen in diverting predation from their breeding congeners, which indeed is of advantage for the population as a whole.

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