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Connections between Predatory Birds and Mammals and Their Prey [1]

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Goszczyński J., 1977: Connections between predatory birds and mammals and their prey. Acta theriol., 22, 30: 399—430 [With 13 Tables & 8 Figs.].

An analysis was made of the diet, numbers and penetration of study area by a group of predators typical of the agrocenoses of the Wielkopolska region of Poland. There was distinguished a group of predators highly specialized in capture of the common vole. This group includes species for which the vole forms the most important component of their food, which react very markedly in respect of their numbers to variations in the density of this rodent and which obtain their food chiefly in fields and meadows. Estimates are given of the extent of pressure exerted by predators on field and forest rodents, and means of counteracting mass irruption of field rodents discussed.

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1. INTRODUCTION

The study presented in this paper forms a continuation of earlier studies on predators and their prey carried out in the Department of Agroecology at Turew (see: Ryszkowski *et al.*, 1971; Ryszkowski *et al.*, 1973; Goszczyński, 1974; Goszczyński *et al.*, 1976; Goszczyński, 1976a; Truszkowski, 1976).

The purpose of the study was to examine the functional connections between predators and their prey and to estimate the effectiveness of biocenotic control of rodent populations by a group of predators. In order to carry out this task it was necessary simultaneously to make studies of the group of predators and their prey (primarily small rodents). In view of the very great significance of *Microtus arvalis* (the chief herbivorous species in the group of vertebrates of the agrocenoses analyzed), the studies covered the period of the full cycle of variations in numbers of this rodent. In order to define the effect of predators on populations of small rodents it was first necessary to obtain estimates of a large number of population and bioenergetic parameters. Amongst the

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most important characteristics were: (1) Estimates of the number of rodents and predators present during the study period in the study area obtained from information on variations in densities, average length of life, etc. (2) Degree of predators' food specialization defined by the composition of their diet and its seasonal variations (3) Amount of daily food requirements of predators (4) Intensity of penetration by predators of the habitats in the area investigated.

The studies made on the pressure exerted by the group of predators permitted of treating the role of these animals in biocenotic control of rodents as a whole, while at the same time it became possible to trace how variations in the density of one species indirectly (through pressure of predators) affect other species in the group of prey examined.

2. STUDY AREA

The studies were concentrated round Turew (52°04'N, 16°48'E) within a radius of about 5 km from the building of the Department of Agroecology, Institute of Ecology, Polish Academy of Sciences. Estimates of the density of predators and their prey applied to the immediate area, covering about 32 km². The material used for evaluating predators' food was collected in a similar way from the same area. It was only when determining the diet of *Tyto alba* that pellet material was collected from stations situated at slightly greater distances (up to 20 km) from Turew.

The Turew district in the Kościan plain area belongs to the group of very sparsely wooded regions; the area covered by forests forming only 12%. Arable land, orchards, meadows and pastures decidedly predominate in this area, of which they occupy 80%. Arable land is used chiefly for growing winter cereals, spring plants and root crops (respectively: 24.1, 17.5, 19.7% of the area of the whole region). Long-term crops such as alfalfa, clover and meadows jointly form about 16%.

The large number of shelterbelts and roadside rows of trees or copses give variety to the landscape, and the mosaic character of the habitat provides good conditions for shelter, rest and rearing young for birds and game, and also for predators.

Roedeer *Capreolus capreolus* (Linnaeus, 1758) and hares *Lepus europaeus* (Pallas, 1778) are numerous in this area. Birds frequently encountered are the partridge *Perdix perdix* (Linnaeus, 1758). Other game species encountered are wild boar (*Sus scrofa* Linnaeus, 1758), rabbits *Oryctolagus cuniculus* (Linnaeus, 1758) and pheasants (*Phasianus colchicus* Linnaeus, 1758).

Among predators the fox *Vulpes vulpes* (Linnaeus, 1758) occurs in large numbers; with the slightly rarer species: pine martens *Martes martes* (Linnaeus, 1758) and stone martens *Martes foina* (Erxleben, 1771), and badgers *Meles meles* (Linnaeus, 1758). The domestic cat *Felis catus* (Linnaeus, 1758) is a predator often found in fields and also the weasel *Mustela nivalis* Linnaeus, 1766. The above species were included in the studies; but on account of their rare occurrence the following have been, omitted from the estimates: the stoat (*Mustela erminea* Linnaeus, 1758) and polecat (*Mustela putorius* Linnaeus, 1758).

Among predatory birds the most numerous are buzzards: *Buteo buteo* (Linnaeus, 1759) and the species occurring during the winter period *Buteo lagopus* (Brümich, 1762). Studies also included three species of owls: *Strix aluco* Linnaeus, 1758, *Tyto alba* (Scopoli, 1769) and *Asio otus* (Linnaeus, 1758). *Circus aeruginosus* (Linnaeus, 1758), *Accipiter gentilis* (Linnaeus, 1758) and *Accipiter nisus* (Linnaeus, 1758), which very rarely nest in this area, were omitted, as were also migratory predators such as, for instance, *Circus cyaneus* (Linnaeus, 1758).

Among the rodents of forests and shelterbelts the most numerous species is the bank vole, *Clethrionomys glareolus* (Schreber, 1780), accompanied by the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) and striped field mouse *Apodemus agrarius* (Pallas, 1771). The last two species also occur in cultivated fields, chiefly in spring and summer. The common vole *Microtus arvalis* (Pallas, 1779) decidedly predominates in all cultivated fields, chiefly occupying long-term crops (alfalfa, meadows and clover).

Additional information on the area discussed above is to be found in previously published studies (Ryszkowski *et al.*, 1971, 1973).

3. METHODS

3.1. Estimates of Density

3.1.1. The Common Vole

The methods described in the study by Ryszkowski *et al.* (1973) consisting in pouring water into the burrows of these rodents and catching the animals as they emerge, were used for estimating the density of the common vole. Samples from an area 625 m^2 in extent were taken at random from various crops, allowing for corrections due to the fact that some of the rodents remained in the burrows even when water was poured into them. Samples from different sites were taken three times a year: in spring (April, May), summer (July, August) and autumn (October, November). Since the participation of the given station in the crop structure in the study area was known, the density of the common vole was estimated each time per average hectare of area. Attempts at estimating the density of voles occupying grass boundaries between fields, roadside verges and ditches proved unsuccessful, as the burrows were so branched that it was impossible to flood them all with water.

3.1.2. Forest Rodents

Trapping of rodents was carried out in the Obryda wood which was taken as representative of the neighbouring wooded areas. Trapping took place over the study period in three stations in this wood, using trapping areas 135×135 m in extent, over which coloured bait was distributed in a 15 m grid, using a different colour in the middle of the grid and another on its edges. Bait was prepared in accordance with Hološova's method (1968). After laying out bait for 3 days snap traps were set and rodents caught for a further three days. An estimate of density, allowing for entry of animals into the area, was made using Ryszkowski's method (1971), consisting in comparing places of capture of differently marked individuals. In addition to trapping in the Obryda wood, in 1972 and 1973 two series of trappings were made in the park surrounding the Department of Agroecology at Turew. The above three forest stations and one park station were used to assess density per average ha of wooded land.

For estimates in relation to the species *A. agrarius* and *A. silvaticus* living either permanently or periodically in fields, their density in treeless areas was also taken into consideration on the basis of results of flooding burrows in field habitats.

3.2. Composition of the Diet of Predators

3.2.1. Material Used to Determine Diet and Ways of Presenting Diet

On account of the continuous character of the studies estimates of diet were based on *in vivo* methods. Analysis of excrement collected in the area was used to compare the diet of predators, and analysis of

Table 1

Material used for comparison of the diet of predatory birds and mammals.

Species	Number of pellets or portions of faeces analyzed
Strix aluco	492
Asio otus	1675
Tyto alba	1286
Buteo sp.	1321
Buteo buteo	1235 [1]
Mustela nivalis	121
Martes sp.	835
Meles meles	195
Vulpes vulpes	1090
Felis catus	56 [2]

[1] Number of prey carried to nests; [2] Number of stomachs analyzed.

pellets to define the composition of food consumed by predatory birds, including owls. It was only in the case of the cat that analysis of stomach contents had to be carried out. The amount of material used for determining diet is illustrated in Table 1.

In order to render the diet of different species of predators comparable it was converted to percentage by weight, *i. e.*, defined by the percentage formed by the weight of the given prey in the predator's diet.

3.2.2. Food Preferences of Predators in Relation to Voles of Different Weight

In order to examine possible preferences of predators for individuals of *M. arvalis* of different weight it was necessary to take measurements of bone elements remaining after consumption of prey as a basis.

The experiments made by Raczyński & Ruprecht (1974) and Goszczyński (1976a) indicate that different elements of the skeleton of small rodents are not uniformly thoroughly digested by

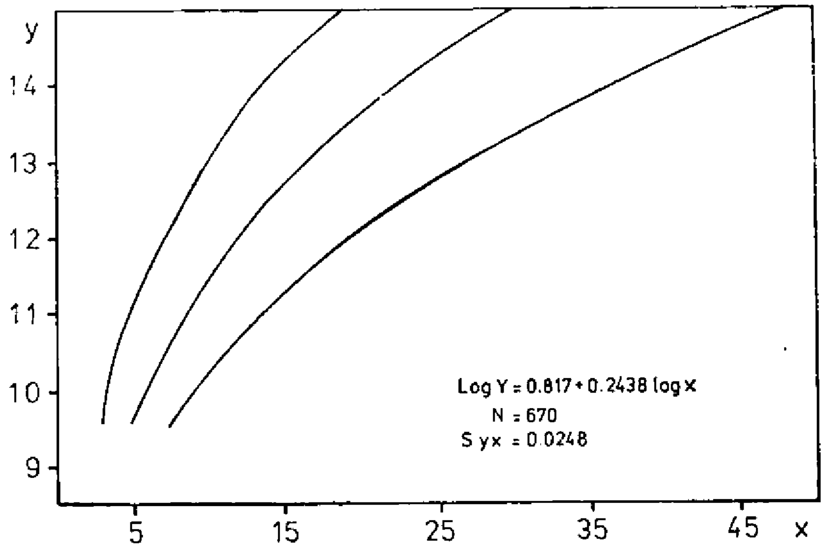

Fig. 1. Correlation between length of mandibular incisor in *M. arvalis* and weight of vole.
x, length of mandibular incisor in *M. arvalis* (mm); y, weight of individual (g); lateral lines indicate range of variations from average.

owls. The mandible is best preserved, although the angular and rostrate processes of the mandible were often broken off or digested, and molars had often fallen out. As the damage most frequently occurring to the mandible of *M. arvalis*, due to consumption of this species by predators, was known, measurement of mandible length was accepted as a measure of the voles' body weight.

Control measurements were made on the mandibles of voles belonging to the following weight classes: 5.1—10.0, 10.1—15.0, 15.1—20.0, 20.1—

25.0, 25.1—30.0 and over 30.1, using a vernier caliper (accuracy — 0.1 mm). Gestating females were excluded in measurements, as periodical increase in body did not affect the size of the bony element analyzed. The relation between mandibular incisor length and weight of the vole was defined and the range of variations in weight, with the given incisor length, estimated in accordance with the equation given by Simpson *et al.* (1960) and cited in the paper by Dapson & Irland (1972) (Fig. 1).

The error in estimating body weight on the basis of mandibular incisor length is considerable as from the class 25.1—30.0 g, and therefore it is possible to allocate individuals to classes 5.1—10.0, 10.1—15.0, 15.1—20.0, 20.1—25.0 and over 25 g (Table 2). Since there were no voles weighing less than 5 g in the experiments made, and they frequently fall prey to foxes and badgers, the upper limit of the first class (5.0 g) was determined from the equation (Fig. 1).

Table 2

Estimate of error connected with division of *M. arvalis* into weight classes on basis of length of mandibular incisor.

Weight class, g	Agreement of theoretical (*NT*) and empirical (*NE*) estimates according to measurements of length of mandibular incisor		
	Theoretical numbers (*NT*)	Empirical numbers (*NE*)	Error: $\frac{(NT-NE)}{NE} \times 100$
5.0—10.0	154	171	10
10.1—15.0	139	165	16
15.1—20.0	90	106	15
20.1—25.0	124	113	10
25.1—30.0	112	75	49
>30.0	33	40	18

The vole incisors separated from pellets and excrement were measured and allocated to one of the weight classes defined above. Measurements were made over the course of the three-year study period. In all a total of 3500 vole incisors distinguished in the pellets of *Asio otus* were measured, and about 3200 incisors of voles eaten by *Tyto alba*. Less num erous material was collected from *Strix aluco* (about 400 measurements). In addition 230 incisors of voles eaten by foxes and about 160 incisors of voles caught by badgers were measured. Only 20 measurements were made for prey caught by martens.

3.2.3. Food Requirements of Predators

The amount of the daily food requirements of predators has been estimated in several cases by means of feeding experiments (cf. Ryszkowski *et al.*, 1973) and in other cases data in literature were used.

3.3. Methods for Estimating of the Area by Predators

The following methods were used for estimates of predators' penetration of the area:

(a) Estimate of the composition of food eaten by predatory birds and mammals. Studies on the degree of residence and activity of different species of small rodents have shown that the bank vole is an animal most closely connected with forests and shelterbelts and practically speaking does not move any great distance away from wooded land (Truszkowski — pers. commun.). The common vole is a species occurring primarily in treeless area. The ratio of these two species in the diet of predators forms a good indicator of differences in the degree to which forests and fields are used as hunting grounds.

(b) Winter tracking in snow (cf. Ryszkowski *et. al.*, 1973) consisting in inspection of one-hectare plots in different cultivated fields. Length of the predator's tracks on the surface of the plot was recorded and also the number of attacks on voles, in order to discover the relation between intensity of penetration of the habitat and capture of field rodents.

(c) Night and daytime censuses. When night censuses were made the number of predators seen in the light of a strong lamp attached to the side of a car or motorcycle, observed in the path of light obtained was counted. This method was used to estimate density of predators by Joslin (1970) and Kaškarov & Zakirov (1971). The length of the station inspected and the predators encountered were recorded (either using the car meter or by direct measurement). Duration of a census varied from one to four hours. During the growing season a journey was usually made round whole fields of known area, recording the animals encountered on them. In this way inspection was made of 19 km² of the area in the winter of 1971/72, 8 km² in the early spring of 1972, 19 km² during the winter of 1972/73 and 33 km² during the growing season of 1973. A total of about 80 censuses were made by means of this method, in order to estimate penetration of the area by cats, foxes and owls.

Daytime censuses made from a car consisted in observing cats along a 100 m path. Such censuses were made from September 1972 to November 1973, inspecting a total area of approx. 220 km² of the area.

Table 3

Variations in density of voles in different crops, individ./ha. Range of variations in average value in percentages, with $P<0.05$, given in brackets.

Crop	Autumn 1970	Spring 1971	Summer 1971	Autumn 1971	Spring 1972	Summer 1972	Autumn 1972	Spring 1973	Summer 1973	Autumn 1973
Alfalfa and Clover	44 (± 90.0)	112 (± 66.0)	1412 (± 55.4)	1450 (± 51.4)	125 (± 67.0)	139 (± 57.5)	82 (± 38.0)	4 (± 100.0)	32 (± 100.0)	25 (± 47.2)
Winter crops	5 (± 100.0)	22 (± 55.4)	84 (± 41.0)	84 (± 38.3)	40 (± 37.0)	20 (± 35.4)	0	0	3 (± 65.0)	0.1 (± 100.0)
Winter rape	20 (± 100.0)	41 (± 63.5)	131 (± 40.0)	204 (± 14.2)	44 (±53.0)	10 (± 69.0)	5 (± 100.0)	1 (± 100.0)	46 (± 48.0)	1 (± 100.0)
Spring crops	*	0	79 (± 50.3)	*	0	25 (± 33.3)	*	0	0	*
Root crops and maize	*	*	0	*	*	0	*	*	0	*
Average hectare of cultivated fields	11 (± 91.0)	32 (± 65.6)	333 (± 53.8)	332 (± 48.2)	42 (± 54.8)	40 (± 50.0)	17 (± 41.2)	1 (± 100.0)	9 (± 88.9)	5 (± 52.0)

* Crop did not occur in sowing structure during given period acc. to Ryszkowski *et al.* 1973 and Truszkowski (unpubl.).

Application of these two methods was restricted by development of plant cover, so that in order to grasp variations in the size of the area accessible for the purpose of the censuses the height of plants and time of agrotechnical operations were recorded (grain harvest, mowing green crops and rape, hay harvest in meadows and alfalfa, ploughing etc.).

4. VARIATIONS IN NUMBERS OF SMALL RODENTS

4.1. Common Vole [3]

Extremely great variations in numbers of voles were observed during these studies. Maximum density was found in the summer and autumn of 1971 (over 300 animals/ha) and minimum in the spring of 1973 (1 individual/ha), cf. Ryszkowski *et al.*, 1973 and Table 3.

Alfalfa and clover, in which density of voles was greatest, determine the course taken by variations in numbers in the study area (Table 3). On account of the group distribution of the vole, the range of variations of the average density per hectare of the given crop (Table 3). As rodents occupying grass boundaries, roadside ditches and haystacks were omitted from the estimates, their real numbers are slightly higher than the ones estimated only in relation to cultivated fields.

4.2. Forest Rodents

Average density per hectare of wooded land varied from a few to over fifty individuals, but the range of variations from year to year was slight in comparison with those of the vole. As a rule maximum density was found during the autumn period. During the winter, unlike the vole, forest rodents were not observed to reproduce.

The most numerous species during the study period was the bank vole, and the least numerous — field mice. The latter species, usually never caught in summer in wooded areas, occurred during this time in low densities together with the wood mouse, in cultivated fields (Table 4).

5. DIET OF PREDATORS

5.1. Size of the Predator and Size of Its Preferred Prey

Considerable variation in weight existed within the group of predators examined. The smallest of the predatory mammals — the weasel — weighs from 50 to 150 g, whereas foxes weight from 4 to 7 kg. Among predatory birds also differences in body weights are considerable (from

[3] The data discussed here were taken from the paper by Ryszkowski *et al* 1973 and from unpublished material by J. Truszkowski.

Table 4

Density of forest rodents from 1970—1973, individuals/ha. *C.g.* — *Clethrionomys glareolus*, *A.f.* — *Apodemus flavicollis*, *A.a.* — *Apodemus agrarius*, *A.s.* — *Apodemus silvaticus*.

Habitat (station)	Species	Autumn 1970	Spring 1971	Summer 1971	Autumn 1971	Spring 1972	Summer 1972	Autumn 1972	Spring 1973	Summer 1973	Autumn 1973
Young pinewood	*C.g.*	28.0	10.3	13.7	31.6	12.3	22.0	4.5	1.4	9.2	12.5
	A.f.	14.3	2.5	0.6	11.6	4.9	4.4	3.4	1.7	1.2	11.2
	A.a.	3.5	0.3	0.0	5.6	0.6	0.0	0.0	0.0	0.0	1.6
Mixed forest	*C.g.*	16.5	7.3	5.3	24.8	12.0	18.6	13.1	2.0	10.5	17.6
	A.f.	14.8	2.7	1.1	8.9	3.2	4.9	4.2	1.0	1.4	1.4
	A.a.	5.1	0.0	0.0	11.7	0.3	0.0	0.0	0.0	0.0	1.1
Oak forest	*C.g.*	0.4	0.0	0.0	1.2	2.3	1.5	1.5	0.0	3.1	4.3
	A.f.	9.4	1.1	0.1	12.7	3.0	0.8	0.0	0.0	0.6	5.1
	A.a.	5.0	0.0	0.0	16.8	2.0	0.0	0.0	0.0	0.0	7.9
Park	*C.g.*	—	—	—	—	—	—	8.0	1.6	—	—
	A.f.	—	—	—	—	—	—	7.7	1.0	—	—
	A.a.	—	—	—	—	—	—	0.0	0.0	—	—
Wooded land (weighed avg.)	*C.g.*	16.1	6.3	6.8	20.7	9.4	15.1	7.1	1.3	7.9	12.1
	A.f.	13.1	2.2	0.6	11.0	3.7	3.6	3.7	1.0	1.1	5.6
	A.a.	4.5	0.1	0.0	11.0	0.9	0.0	0.0	0.0	0.0	3.3
Cultivated fields	*A.a.*	—	0.5	0.5	—	—	—	0.5	0.1	—	—
	A.s.	—	—	—	—	—	—	—	—	0.1	0.6

— Lack of estimates during given period.

300 g for *Asio otus* up to 1 kg for buzzards). Comparison of the diet of various predatory species (comparison of weights of their prey was limited to mammals, on account of accuracy of identification) shows that the food of larger animals is more varied in respect of body weight of the prey caught than that of small predators (Table 5). Foxes and martens often catch hares in addition to small rodents, the percentage formed by hares in the diet of foxes being greater than in the diet of martens. Buzzards and tawny owls supplement their diet by hunting for moles, rats, *Arvicola terrestris* and squirrels, that is, prey, the body weight of which comes within the 51—500 g class. Small predators, however, usually base their diet on small rodents weighing from 11—50 g (Table 5).

Table 5

Percentage by weight of mammals of different weight in the diet of predators.

Species	Weight of predator, kg	Classes of weight of prey in g <10	11—50	51—100	101—500	>500
Asio otus	0.30	0.45	99.27	0.0	0.28	0.0
Tyto alba	0.30—0.35	9.64	88.48	0.17	1.71	0.0
Strix aluco	0.48—0.52	0.91	90.66	1.94	6.49	0.0
Buteo sp.	0.73—1.10	0.23	74.63	18.66	2.96	3.53
Mustela nivalis	0.05—0.13	0.0	95.46	0.0	4.54	0.0
Martes sp.	1.00—2.00	0.82	85.10	0.65	1.13	12.29
Vulpes vulpes	4.50—7.00	0.25	67.22	0.38	0.96	31.19

5.2. Relation of Predators to the Common Vole

5.2.1. Specialization of Predators in Capture of Voles

When comparing the average percentage formed by voles in the diet of different species of predators it is possible to distinguish species with different degrees of food preferences (Fig. 2). If we agree to take 50%

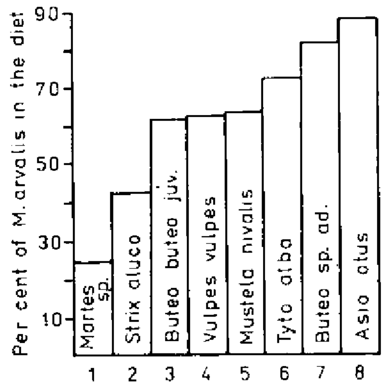

Fig. 2. Average long-term participation of *M. arvalis* in predators' diet (data for *Buteo buteo* juv. and *Buteo* sp. ad. after Truszkowski, 1976).

as the extreme limit for the percentage of voles in predators' diet, then *Asio otus, Tyto alba, Buteo buteo* and the weasel must be regarded as highly specialized species. These species fed chiefly on voles throughout the whole study period. Tawny owls and martens, in the diet of which the vole forms on a average a small percentage, subject to frequent fluctuations, constitute a second group. These species make use of voles primarily when the density of the latter is high. The fox occupies a separate position among the predators examined, since althought it is a specialized predator of rodents it changes to different food when the density of voles becomes extremely low (cf. Goszczyński *et al.*, 1976).

5.2.2. Selective Effect of Predators on Voles of Different Weight

The data collected show that there are significant differences between the predatory species examined in the extent to which they prey on voles of different weight. Owls as a rule catch individuals weighing more than 15 or even 20 g (Fig. 3), whereas they do not hunt voles at all in

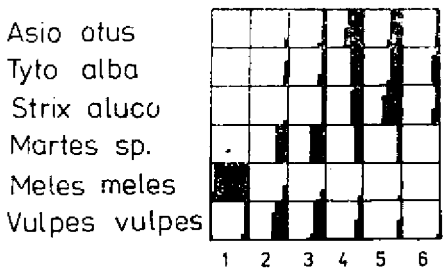

Fig. 3. Capture of voles differing in weight by predators. Degree of shading of each square corresponds to participation in percentages of voles in the given weight class.
Weight classes (in g) of voles: 1, below 5.0; 2, 5.1—10.0; 3, 10.1—15.0; 4, 15.1—20.0; 5, 20.1—25.0; 6, over 25.1.

the lowest class (up to 5 g), which is not astonishing since they are either animals still living on their mother's milk or animals which have not yet left the burrow. The classes from 5.1—10.0 and 10.1—15.0 are represented only to a slight degree, individuals of this size being most often caught by barn owls. It would appear that these owls, which as a rule more often catch smaller prey, *e. g.* shrews, than other owls, make more effective use of small voles. Analyses of the food of young buzzards, to which the parents bring voles weighing above the average for the local population (Ryszkowski *et al.*, 1973) also show that predatory birds hunt chiefly heavier and older voles.

Foxes as a rule catch small individuals, from 5 to 15 g. Individuals in the class up to 5 g are animals caught directly in the nests. Particularly intensive hunting by foxes for young voles, combined with digging up earth and destroying nests, takes place during the summer-autumn period, when vegetation does not hinder movements or access to nests. In alfalfa fields and stubble numerous traces of foxes having dug up burrows were observed during this period, the place where the fox had begun to dig being directly above the nesting chamber, as was shown by the remains of nests in places where the earth had been dug away. Over 90% of the total number of voles caught by badgers were individuals up to 5 g in weight, which is evidence that during its hunting activities badgers aim chiefly for small voles, and only sporadically caught heavier animals (Fig. 3). The small amount of material representing voles caught by martens limited accuracy of conclusions, but it would appear that martens mostly catch individuals up to 15 g in weight. Martens also are capable of digging up rodents' burrows and destroying nests, this being observed in the summer of 1973.

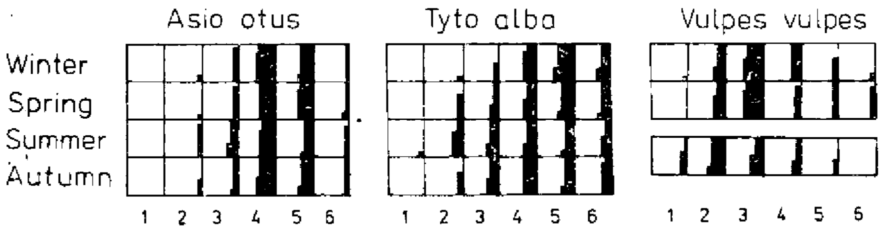

Fig. 4. Seasonal variations in capture of voles of different weight (in g) by predators.

Degree of shading of each square corresponds to participation in percentages of voles in the given weight class. 1, below 5.0; 2, 5.1—10.0; 3, 10.1—15.0; 4, 15.1—20.0; 5, 20.1—25.0; 6. over 25.1.

The cat's diet was compared on the basis of analysis of the stomach contents of animals shot in fields. In many cases the rodents were disintegrated or slightly digested, which made it difficult to determine the size of the prey eaten. A group of stomachs was, however, distinguished in which whole and undigested animals were found and the number of these voles was counted. 219 voles dried on filter paper jointly weighed 3584 g, and thus the average weight of one individual was approx 16.5 g. As they were weighed after taking them from the formalin in which the stomachs had been stored, and in view of the fact that the weight of animals and their organs fixed in formalin increases (L u s k & P o k o r n y, 1964; P u c e k, 1967), it would appear that the true weight of an average vole was in fact even smaller. It may therefore be considered that cats catch voles weighing less than the average for the population (average weight of a vole was estimated on the basis of about 3000 measurements as 18.4 g — cf. Ryszkowski *et al.*, 1973), but which have emerged from the burrows on to the surface of the area. Very small individuals were not observed in cats' stomachs.

Comparison of the weight of individuals caught by predators at different seasons of the year points to the modifying effect of the age structure of a population on capture of voles of different weight (Fig. 4). Foxes react far more strongly than owls to variations in population structure. Owls more often catch smaller voles in summer and autumn, although the basic part of their diet consists of individuals weighing more than 15 g, whereas foxes concentrate their hunting activities on

Table 6

Seasonal differences in capture of voles of different weight by tawny owls and badgers (%).

Period covered by estimate	Weight of voles consumed, g					
	< 5.0	5.1—10.0	10.1—15.0	15.1—20.0	20.1—25.0	> 25.0
			Strix aluco			
Winter	0.0	0.6	8.9	26.9	49.7	13.9
Growing season	0.0	1.0	14.6	34.0	37.9	12.6
			Meles meles			
Early spring	87.2	5.1	2.6	0.0	5.1	0.0
Summer-autumn	93.2	3.4	2.6	0.8	0.0	0.0

small individuals in summer and autumn. The differences between the winter and summer diet form evidence of the high degree of adaptability of this species. Seasonal differences in the range of weight of voles consumed were also observed in the case of the tawny owl and badger (Table 6).

5.3. Relation of Predators to Other Prey

Our observations showed that in years when numbers of voles were low small predators specializing in catching voles (barn owl, long-eared owl, weasel) changed their diet only slightly, as they are able to make use of even single isolated colonies of voles (Goszczyński, unpubl. data).

During the same period larger predators (buzzards, foxes) balance the deficiency of field rodents by catching other prey more frequently

(G o s z c z y ń s k i, 1974; G o s z c z y ń s k i *et al.*, 1976; P i e l o w s k i, 1976; T r u s z k o w s k i, 1976), while polyphagous predators (martens, tawny owls) decidedly change to different food (G o s z c z y ń s k i, 1976b).

6. VARIATIONS IN NUMBERS PREDATORS

Variations in numbers of predators generally speaking exhibit connection with the state of rodents in fields. In the first place the easily accessible food caused increase in intensity of hunting by predators. The number of cats penetrating the crop clearly increased (from a few to over 50) (Table 7). Analysis of their stomachs showed that during this period cats hunted almost exclusively for voles. The remains of »domestic« food showed that they had left farm buildings during the hunting period. Increase in the numbers of these predators is directly connected with access to food and penetration of areas which normally are rarely visited. The number of hunts made in fields rapidly rises with increase in density of their prey and equally rapidly drops when numbers of rodents decrease (Table 7).

Table 7

Number of predators in whole study area (31 km²). In different periods variations in numbers are given.

	15.X.'70— 31.III.'71	1.IV.'71— 31.X.'71	1.XI.'71— 31.III.'72	1.IV.'72— 31.X.'72	1.XI.'72— 31.III.'73	1.IV.'73— 31.X.'73
Strix aluco	14	14—18	13	11—15	12	13—14
Asio otus	4	4	6	5—10	9	4
Tyto alba	6	6—10	10	8—12	3—5	5—10
Meles meles	6	6	6	5—6	5—6	6
Martes sp.	7	7—14	8	14—7	7	10—5
Vulpes vulpes	18	18—32	20	20—56	18—30	17—42
Felis catus *	0—6	6—62	62—36	36—16	16	16—22
Buteo sp.	15	15—60	48	14—38	30	10—27
Mustela nivalis	78—68	68—207	121	77—171	77—20	20—142

* Numbers in cultivated fields and meadows.

Considerable numbers of voles also caused migration from other areas of predators specializing in hunting rodents, for instance migrating individuals of *Buteo buteo* and *Buteo lagopus* readily stay in places with an abundant supply of voles. During the autumn-winter period of 1970 the number of buzzards in the study area was 15, but after mass occurrence of voles, that is, in the late autumn and winter of 1971 their numbers were 60—48 and during the subsequent two autumn-winter seasons respectively 38—30 and 27 (Table 7). Variations in numbers of migratory buzzards in the study area reflected (of course on a different scale) variations in numbers of voles. In 1971 single individuals of long-eared owls were recorded in places in which they had not previously appeared. In the same year at a distance of about 11 km from Turew a group of about 15 long-eared owls was observed in the shelterbelt adjoining the alfalfa field.

In the second place variations in density of voles affect the breeding of predators forming the stock in the given area. This is manifested in, for instance, variations in the number of litters and broods. Species specializing in hunting voles react to increase in density of these animals by increased reproduction. The rapidity of their reaction depends in this case on the predator's biology, *e. g.* foxes exhibited maximum reproduction during the year following mass irruption of voles (Table 7). In 1971 3 foxes' earths with young were found within an area of 30 km², while the following year the number was 6 and a year later 4. Common buzzards reacted slightly more rapidly to increase in numbers of voles, although in their case also reproduction was observed to shift to the year following mass occurrence of rodents. The number of nests with young was as follows for this species in successive years: 1970 — 3, 1971 — 7, 1972 — 7, 1973 — 4 (Truszkowski, 1976). Barn owls reacted quickly by hatching broods in 1971 itself.

In the case of weasels reproduction was not estimated directly but judging by the far higher winter density in 1971/72 than in the preceding and subsequent year, particularly intensive reproduction must have taken place in 1971. This is also indicated by their high numbers during the growing season of 1971 (cf. Table 7) and decrease in the two subsequent years.

Species not highly specialized in catching voles, *e. g.* martens and tawny owls, maintain their numbers on an even level (Table 7). In the case of tawny owls the number of young reared changes in sussessive years (in 1971 and 1972 with high and medium density of voles tawny owls reared 5 and 4 nestlings and in 1973 with deficiency of both voles and forest mice only 1 nestling), although the number of pairs is constant from year to year. The degree to which this species is resident is outstandingly high and the same pairs occupy the same territories for many years. During the autumn period young owls usually disperse. For these predators, which have a wide food spectrum, abundance of rodents (both field and forest) may favour production of young, but deficiency of mice and voles is not a basic limiting factor.

7. PENETRATION OF THE AREA BY PREDATORS

7.1. Hunting Penetration of Wooded and Treeless Areas

The studies made over a period of four years on the composition of the diet and the comparison of the ratio of *C. glareolus* (a typically forest species) and *M. arvalis* (a field species) in the food of predators showed that there were significant differences in the degree to which wooded areas were used by different predators (Table 8). Direct observations (tracks on snow) of the migrations of martens over the area showed that this species avoids open areas and catches voles within the immediate vicinity of shelterbelts and forests. The high percentage of voles in the tawny owl's diet indicates that the distribution of hunting activities is similar to that of martens. This owl catches voles chiefly during a period of their mass occurrence.

Table 8

Number of common and voles caught by predators as index of penetration of forests and fields.

Species of predator	Species of prey		$\frac{C.g.}{M.a.} \times 100$
	C. glareolus	*M. arvalis*	
Tyto alba	7	2531	0.28
Buteo sp. ad.			0.61 *
Vulpes vulpes	14	1089	1.28
Buteo buteo juv.			1.29 *
Asio otus	71	4504	1.58
Strix aluco	104	855	12.16
Martes sp.	18	88	20.45

* After Truszkowski, 1976.

Forests form the place where buzzards, foxes and long-eared owls rear their young and rest, but are not their hunting grounds, as is shown by the negligible percentage of voles in their diet.

The barn owl must also be considered as among birds obtaining the greater part of their food in treeless areas, despite the fact that this species hunts near and inside farm buildings for house mice and sparrows during periods of low numbers of field rodents.

7.2. Differences in Penetration of Cultivated Fields and Meadows and Their Causes

Daytime and night censuses showed that both cats and foxes are most often encountered in alfalfa fields, meadows and rape fields. They are far less often recorded as found on ploughed land, root crops or spring cereals (Table 9). If we assume that there are no factors causing concentration of predators and that potential prey are distributed uniformly in the area, then the number of predators recorded in the given station would be in proportion to the size of the area occupied by this station. Comparison between a theoretical distribution of this kind and results

Table 9

Number of foxes and cats in different crops.

Crop (observation area in ha)	Predator	Number of predators per unit of crop (individ./km²) Winter 1972	Spring 1972	Winter 1973	Spring 1973	Summer 1973	Autumn 1973
Alfalfa	Fox	4.0	0.9	2.3	1.0	1.8	0.6
(1721)	Cat	3.5	2.6	1.6	1.3	2.0	1.2
Meadows	Fox	0.0	—	3.9	0.9	0.5	0.8
(716)	Cat	1.2	—	1.9	0.9	1.0	1.5
Winter crops	Fox	0.4	—	1.0	0.3	0.7	0.9
(2703)	Cat	2.1	—	0.3	0.3	1.1	0.5
Ploughland	Fox	0.3	—	0.4	0.0	0.0	0.0
(1763)	Cat	1.0	—	0.4	0.8	0.8	0.8
Root crops and maize	Fox	*	*	*	0.4	0.4	0.4
(277)	Cat				0.4	0.4	0.4
Spring crops	Fox	*	*	*	0.0	0.7	*
(170)	Cat				1.1	1.1	
Winter rape	Fox	—	—	2.2	2.2	2.2	2.2
(271)	Cat	—	—	3.7	3.7	3.7	3.7

* Crop does not occur in sowing structure during given period; — Lack of estimates during given period.

obtained during estimates and winter tracks made using the χ^2 test show that the difference ($P<0.001$) between empirical distributions and anticipated distributions is significant (Table 10). On spring and winter crops and ploughed land the number of predator recorded per unit of area is usually significantly smaller than the number anticipated, which points to their avoidance of these crops. The probability of encountering

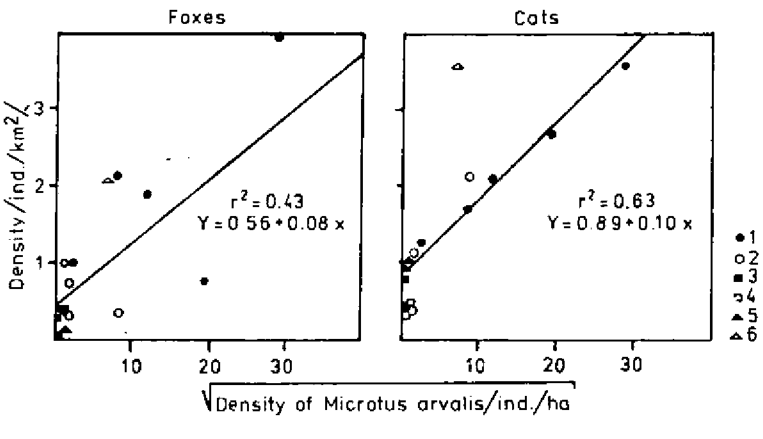

Fig. 5. Correlation between density of cats and foxes and density of the common vole in different crops.

1. alfalfa; 2, winter wheat; 3, ploughed land; 4, root crops; 5, spring cereals; 6, winter rape.

a predator in these habitats which is not engaged in hunting but for instance only passing through the crop is greater than for alfalfa or rapes occupying a far smaller area. Very similar results were also

Table 10

Intensity of penetration (in %) of different stations by predatory mammals and owls *.

	Al-falfa	Mead-ows	Winter crops	Spring crops	Plough-land	Root crops	Rape	$\sum$	χ^2
Winter									
1971, Fox, A	13.1	38.1	25.4		21.0		2.4	100	66
1972, Fox, A	16.4	30.7	29.3		17.7		5.9	100	53
1972, Fox, B	52.0	0.0	27.0		21.0		0.0	100	296
1972, Cat, B	16.0	10.0	50.0		24.0		0.0	100	22
1973, Fox, B	13.4	39.6	30.2		12.3		4.5	100	81
1973, Cat, B	16.2	38.6	15.7		21.3		13.2	100	126
1973, Cat, C	54.5	27.3	9.1		9.1		0.0	100	363
Theor.	7.4	12.9	38.3		38.8		2.6	100	
Growing season									
1973, Fox, B	19.4	27.7	26.6	6.0	0.0	8.9	11.4	100	93
1973, Cat, B	12.5	21.2	13.5	10.8	28.2	4.4	9.4	100	28
1973, Cat, C	19.3	32.3	32.3	3.2	3.2	6.5	3.2	100	69
Theor.	7.8	17.5	20.1	9.1	32.8	10.3	2.4	100	
Whole Year									
1973, Fox, B	16.4	34.9	28.3	2.8	5.2	4.1	8.3	100	74
1973, Cat, B	13.2	23.7	16.2	7.6	25.6	3.2	10.5	100	42
1973, Cat, C	28.5	30.9	26.2	2.4	4.8	4.8	2.4	100	99
1973, Owls, B	40.0	20.0	16.0	4.0	10.0	5.0	5.0	100	171
Theor.	7.7	15.9	26.1	6.1	34.8	6.9	2.5	100	
Attitude of predator to station	P	P	A	A	A	A	P		

Theor. — theoretical estimates, assuming that distribution of penetration is random
A, B, C — empirical estimates on basis of: tracks on snow (A); night censuses (B); daytime censuses (C).
P — preference; A — avoidance.

obtained for owls (Table 10). The reason for such difference penetration of the area by predators is the density of small rodents. Comparison of the number of cats and foxes recorded per unit of crop and numbers of voles points to the significant correlation of these two variables (Fig. 5).

During the growing season a considerable number of cats were recorded as encountered on wasteland, which indicates that the cats had either abandoned or limited their hunting activities in places with greatly developed vegetation (Table 11). During the first period following cereal and rape harvests the numbers of predators reflected the intensity of their searches in these crops. If the density of voles in these habitats was low, then the numbers of predators rapidly decreased (*e. g*, on rape the greater part of the predators, 66% of all foxes and 87% of cats were recorded during the first three days).

Table 11

Penetration of wasteland (grass boundaries, ditches, roads through fields etc.) by cats with different states of plant cover.

		Night censuses	Daytime censuses
Sept., 1972—March, 1973	Length of census path, km	18.7	103.4
	N of cats	3	5
	N of cats per 1 km of census	0.160	0.048
April—August, 1973	Length of census path, km	22.3	89.3
	N of cats	19	8
	N of cats per 1 km of census	0.852	0.089

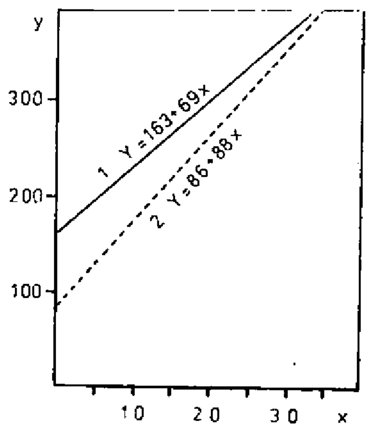

Fig. 6. Relation between length of foxes tracks and number of attacks on rodents, with different densities of the voles. Data for long-term crops.

1. Average density of voles — 80 individuals/ha
2. Average density of voles — 800 individuals/ha

x, number of attacks on rodents (per ha per day); y, length of foxes tracks per 1 ha per day (m).

In the case of the fox it was possible to show, by means of the winter tracking carried out, that intensity of capture of voles is correlated with the density of these rodents (Fig. 6). Frequency of attacks on voles increases with increase in their density (cf. Fig. 6).

7.3. Effect of Abiotic Factors on Penetration of the Area by Predators

7.3.1. Climatic Factors

A sudden drop in temperature during the winter period combined with snowfall limit the number of cats penetrating crops (Fig. 7).

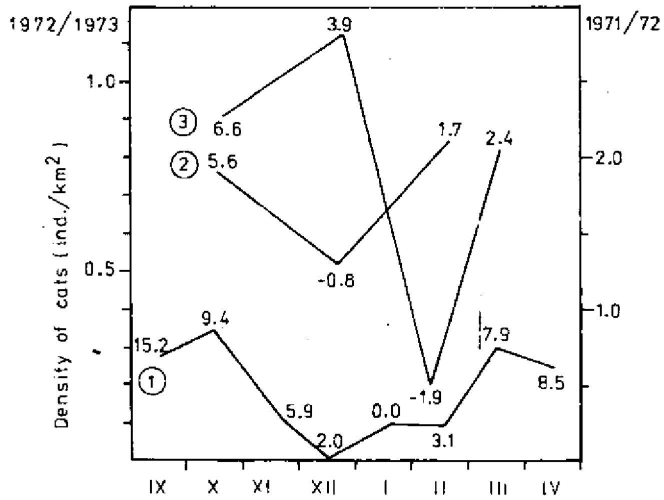

Fig. 7. Number of cats penetrating crops during winter period.
1, daytime estimates (1972/73); 2, night estimates (1972/73); 3, night estimates (1971/72). Temperatures for study periods given near successive lines: for daytime estimates average temperature at 13,00 for night estimates average temperature at 21,00

In addition snow cover of varying depth and different degree of freezing hinders access of predators to small rodents. Winters with heavy snowfall contribute to a decrease in the percentage of voles in the diet of foxes and greater use of substitute food (Goszczyński, 1974).

7.3.2. Agrotechnical Operations in Fields

Intensification of field work as from May limits the daytime penetration of crops by cats. The presence of a large number of people and agricultural machines is a factor frightening cats away at this time. It is not until after the harvest (beginning of August) that the number of

Table 12

Daily variations in range of cats' wanderings.

Distance from buildings, m	Percentage of cats encountered	
	During day (N=63)	At night (N=49)
1— 100	63.5	16.3
101— 250	11.1	24.6
251— 500	11.1	34.6
501—1000	11.1	20.4
>1000	3.2	4.1
Average distance on basis of accurate measurements, m	250.0	430.0

cats searching for food in fields increases. Agrotechnical operations do not, however, limit the nocturnal activities of these predators, but in fact stimulate their increase (Fig. 8). This is easy to understand since the operations taking place one after another render areas which had previoulsy been protected by tall plants accessible to predators and the peaceful night time makes hunting easier. Differences in the extent of nocturnal and daytime wanderings of cats must probably be explained by the considerable activity taking place throughout the day in fields (Table 12).

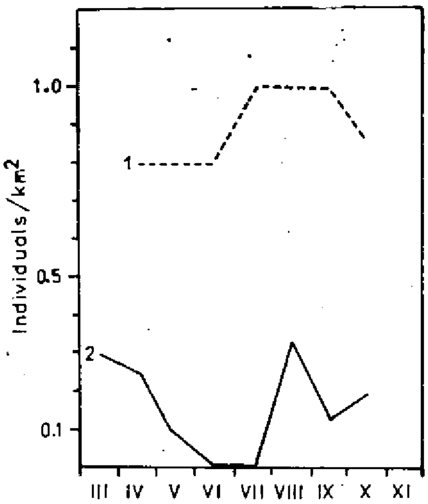

Fig. 8. Numbers of cats in crops during season 1973.
1, Estimates on basis of night censuses; 2, Estimates on basis of daytime censuses.

The fact of increase in percentage of small rodents (chiefly the vole) in the foxes' food during the summer-autumn period is evidence of the important part played by agrotechnical operations in the composition of this predator's diet. When fields are cleared of their plant cover the voles are deprived of convenient shelter and forced to migrate, which makes it far easier for foxes to catch these rodents (Goszczyński, 1974).

8. PRESSURE OF PREDATORS ON POPULATIONS OF SMALL RODENTS

8.1. Small Rodents as a Potential Source of Food for Predators

In order to estimate the number of rodents present during the studies and to assess their mortality use was made of the method suggested in the paper by Ryszkowski *et al.*, 1973. In the case of the vole, an account of their great tendency to congregate in groups the range of variations in numbers of voles present and range of variations in their mortality were defined.

8.2. Consumption of Rodents by Predators

In order to estimate the number of rodents consumed by predators the following equation was used

$$\text{Number of rodents consumed} = \frac{\text{Number of predator-days} \times \text{Daily portion of food eaten by a predator} \times \text{Percentage by weight of prey in diet (\%)}}{\text{Average weight of prey} \times 100}$$

In the case of the cat and badger the number of rodents consumed was calculated by multiplying the number of predator individuals by the number of rodents eaten daily.

8.3. Participation of Predators in Reduction and Mortality of Small Rodents

Rodents present during a given period of time in fields and in forests form potentional food for predators. The estimate made additionally of total mortality of both forest and field rodents permitted of defining more exactly the pool from which predatory animals took their prey.

The participation of predators in reduction (ratio of number removed by predators to the number of potentially accessible rodents) and total mortality of the vole is subject to wide fluctuations (Table 13). With

Table 13

Pressure of predators on rodents.
1, Forest rodents; 2, *M. arvalis;* Calculated on basis of average (A) and maximum (B) densities of rodents per 1 ha of area.

Study period		Percentage of predators in total mortality of rodents, %		Reduction of rodents present in study area by predators, %	
		A	B	A	B
15.X.1970—	1	74.4		55.8	
31.III.1971	2	78.8	48.0	47.4	28.3
1.IV.1971—	1	33.2		18.2	
31.X.1971	2	20.4	10.2	13.1	8.2
1.XI.1971—	1	41.2		28.0	
31.III.1972	2	10.7	8.3	9.4	7.1
1.IV.1972—	1	41.7		33.5	
31.X.1972	2	76.5	50.7	68.3	45.5
1.XI.1972—	1	95.3		74.8	
31.III.1973	2	89.4	62.6	86.6	59.9
1.IV.1973—	1	96.6		49.3	
31.X.1973	2	>100.0	88.9	>100.0	73.2

high densities of the vole the total pool of potentially accessible prey is reduced only to a slight degree by predators. Although predators base their diet on the vole, they make use of only a small part of the population of this prey. Other causes of mortality than those due to predators intensify in vole populations. The capacity for adaptation of the predators examined is insufficient during this period to balance the enormous natality of their prey, which, owing to their high reproduction potential, reach very great numbers within a relatively short time.

A different situation occurs when density of voles is low. Reduction by predators of the number of rodents present usually exceeds 50% of the head of population and the participation of predators in total mortality of their prey is over 75%.

During the growing season of 1973 the estimated number of individuals consumed exceeded the average number of prey accessible to predators. The range of error in the average shows, however, that consumption of rodents by the group of predators was lower than the upper limits defining the range of variations in the mean number of individuals present and average mortality of rodents (Table 13). During periods of numerical depression of voles, or when their densities are moderate, reduction of the prey population is undoubtedly higher than reduction during the period of peak numbers (Table 13). Predators make more effective use of the population and play, if not the most important, at least one of the chief roles in total mortality of this prey.

Similar regularities were observed in the case of forest rodents. The small degree of participation in reduction of numbers and total mortality, with high numbers of forest rodents, is more a secondary effect due to increased pressure by predators on *M. arvalis* (Ryszkowski *et al.*, 1973). Maximum numbers of forest rodents occur during the period of mass irruption of voles, the density of which is several times greater than the density of mice of the genus *Apodemus* and other forest rodents. The vole is a far more accessible prey under such conditions. The fact that there is a decrease in the percentage of forest rodents in predators' diet (despite considerable increase in the numbers of forest rodents in the area) suggests that this is the mechanism operating during a period of mass irruption of voles. In years when the numbers of voles are low, however, the effect of predators on forest rodents is distinct.

9. DISCUSSION

The results set out in this paper make it possible to form an opinion in respect of the questions: definition of the types of correlations between predators and their prey and estimate of the effectiveness with which the group of predatory birds and mammals affects populations of their prey.

9.1. Types of Correlations between Predators and Their Prey

On the basis of the results obtained it is possible to distinguish from among the group of predators examined, a certain group of species particularly closely connected with the common vole, segregating them on the strength of: a) the predator's diet, b) effect of the prey on numbers of the predator (manifested in variations in the predator's reproduction or migrations, c) the way in which the predator penetrates the area. Since studies on predators lasted for several years, the three categories distinguished are not burdened with error due to seasonal or annual variations in the estimated parameters.

The long-eared owl, barn owl, buzzards, foxes, cats and martens were allocated to the group of predators specializing in capture of the vole, on the basis of analysis of their diet. These predators react strongly in respect of their numbers to variations in the number of voles. An increase in the numbers of voles is usually accompanied by increase in the numbers of predators, taking place as the result of immigration or increased reproduction. The typical hunting grounds of these species are treeless areas, as is shown by the minimum amount of food originating from forests and shelterbelts.

It is to be expected that under conditions of common food, increase in numbers during periods of mass irruptions of voles or after them, use of treeless areas for hunting purposes, intensive competition for food occurs between the various species of predators. It was found, however, that during a period of mass occurrence of voles the density of this rodent reaches so high a level that even if the stock of predators were several times more numerous than that observed, the situation in which one or several species could exert (through catching prey) pressure on another predator species would never occur. During a period of mass irruption of their prey the predators consume only a negligible part of the food available to them. This has been emphasized previously by Chitty (1938), Kadočnikov (1953) and Pearson (1971). This induced us to accept the opinion that during mass occurrence of rodents, the pressure of predators on a population of their prey is inconsiderable, which eliminates the possibility of interspecies competition for food occurring.

The situation changes when the numbers of prey decrease. The participation of predators in mortality and reduction in the number of individuals present reaches a high level. Under such conditions the possibility of »tensions« between different species is reduced by changes in diet and wider use of substitute foods. The studies by Rosenzweig (1966), Marti (1969) and Beusekom (1972) on sympatric species of predators show that even slight differences in composition of diet weaken competition for food and make the coexistence of different predators possible. Changes in diet do not of themselves ensure against »crossing« of the food requirements of different species. It would seem that removal by capture of individuals of different weight from within the prey populations may be of certain significance. Even during periods of numerical depression of prey the various species of predator have lesser opportunities of affecting each other than would appear to be the case from analyses alone of the composition of diet and amount of pressure.

A separate group is formed by the remaining predatory species (tawny owl, martens, badgers). Analysis of their diet shows that these are polyphagous animals. Increased consumption of voles was observed in their case only during a period of mass irruption of voles (see section 5.2), while when the numbers of field rodents were low they make use of a wider variety of food. Data in literature also confirm the polyphagous character of the diet of these species; cf. data on the diet of martens (Lockie, 1961; Rzebik-Kowalska, 1972), of badgers (Andersen, 1954; Skoog, 1972) and tawny owl (Southern, 1954; Smeenk, 1972). Martens and tawny owls catch a large number of their prey in forests and shelterbelts. Badgers most often penetrate fields, but their movements are not closely connected with hunting and catching rodents. Excursions made by badgers into fields and meadows are often connected with obtaining plant food, earthworms or insects.

Tawny owls and martens, on account of their connection with forests and shelterbelts, play an important role in reduction of forest rodents (they catch about 20% of all the rodents eaten by predators). The important participation in mortality and reduction of the number of forest rodents present of species specialized in catching voles (particularly foxes) also merits emphasis. When numbers of voles decrease these species change to catching forest rodents as substitute food. The reverse situation, *i.e.* inclusion of martens, badgers and tawny owls in the group of predators feeding on voles, takes place, as mentioned above, when mass irruptions of this rodent occur. The participation of these predators in reduction of voles is, however, slight (they catch about 9% of all voles caught by predators).

9.2. Effectiveness of the Action Exerted by the Group of Predators on Populations of Voles and Other Prey

Before discussing the pressure exerted by predators on vole populations it is necessary to throw light on the question of accumulation by predators of stores of food, or consuming only certain parts of the body (*e.g.* heads) of the prey they catch. If this process reached any great extent then the numbers of rodents removed would be underestimated on account of the method used. The fact that weasels accumulate stores has been reported by, *e. g.* Heptner *et al.* (1967). In the study area a case of rodents killed by weasels being stored was observed in the winter of 1971/72. The »store« was situated in a haystack and consisted of harvest mice, house mice and field mice. It is interesting that despite the considerable density of the common vole, this species was not represented in the composition of the »store«. If rodents are not eaten from »stores«, then estimates of pressure by weasels based on composition of diet and daily food requirements are underestimated. Tarnowski (1972) has, however, shown that weasels and stoats gradually eat rodents which they had previously killed. Czarnecki *et al.*, (1955) and Czarnecki (1956) have emphasized in their studies that during mass irruptions of voles owls may eat only the head of the rodents they catch, but these authors do not state if they themselves observed such facts or whether they refer to the earlier observations made by *e. g.* Taczanowski. During the course of my studies I frequently inspected haystacks, places used by owls to rest during the daytime, and places in which these birds ate the prey they had caught, and encounterded this phenomenon three times only. I am thus inclined to assume, on the basis of my own observations, that consumption by owls of the heads of voles they catch is only a sporadic phenomenon. It would not thus appear that this fact could exert any important influence on the estimate of the number of voles destroyed by long-eared and barn owls.

Predators treated as a group most strongly affect small voles (weighing from 5 to 15 g). This is shown chiefly by the activities of foxes and cats hunting primarily animals of this size. Particularly strong influence is exerted during periods of numerical depression of the vole, when the part played by predators in reduction and mortality of this species reaches considerable dimensions (see section 8.3). Heavier and older voles (weighing over 15 g) are caught primarily by buzzards and owls. Reduction caused by predatory birds and owls is, however, smaller in extent than reduction of young individuals by foxes and cats, while the pressure exerted by predators on nestlings and very small individuals weighing less than 5 g is negligible.

It is only badgers, foxes and probably also weasels which can make use of animals of this size (see section 5.2.3). Since, however, badgers do not play an important part in total mortality and the percentage of nestlings among all voles caught by foxes is about 10%, the conclusion is obvious that only a negligible part of the nest mortality of these rodents is caused by direct capture by predators. It is of course possible that predators exert an indirect influence on nestlings by catching lactating females, but it would seem that the greater part of mortality in the early stages of development is due to other factors.

When the effect of predators on vole populations is considered as a whole it is necessary to emphasize the particularly strong pressure occurring at the time when the numbers of this rodent are low. It may be that capture of individuals by predators during such a period is a factor modifying the rate of reconstruction of population numbers. This kind of situation would be in agreement with the hypothesis put forward by Pearson (1971), who states that the level of pressure by predators with low states of pery population defines the amplitude and time limits of the cycle. On the basis of the results obtained it is, however, impossible to ascertain whether this hypothesis is correct. Without trying to solve this problem I should like to draw attention to the fact that under conditions in which numbers of voles are maintained on a moderate level or when the structure itself of the agrocenosis (small percentage of long-term crops and meadows in the total cultivated area) hinders the development of vole populations, predators may, by means of selective pressure on different groups in the population, limit the effective reproduction of their prey.

Even if predators could for a certain time modify reproduction of their prey, they are not able to maintain vole populations on a constant defined level. The fact itself of the occurrence of mass irruption of the vole in the study area is the best proof of this. The disproportion in the reproductive potential and relation of biomass of predator and prey is so great that predators are unable to affect the general course taken by variations in numbers of their prey in the agrocenoses examined, especially since particularly strong development of the vole population takes place during the period of luxuriant development of the plant cover, which hinders the hunting activities of predators. Under such circumstances establishment of a state of dynamic balance between predator and prey is never reached, which is typical of, for instance, large predatory animals feeding on wild ungulates (Estes & Goddard, 1967; Pimlott, 1967; Schaller, 1972 and others).

Analyses of the extent of pressure also show that predators are not responsible for the decrease in numbers of voles immediately after a mass irruption. Causes of mortality other than those due to predators intensify in the population at that time (see Ryszkowski *et al.*, 1973).

The effect of predators on populations of forest rodents presents a different picture. Populations of these species do not exhibit the fluctuations in numbers characteristic of the vole. Although the pressure of predators is, as in the case of vole populations, slight whedensities are high, this state of affairs is due to predators abandoning their hunting activities as soon as a more attractive prey — the vole — appears. Even tawny owls, martens and badgers, which often catch forest rodents, switch to catching voles. Thus large numbers of voles increase the forest rodents' chances of survival. In a period of numerical depression of the vole predators switch to other food, and make intensive use of populations of forest rodents. This is a typical example of indirect action (through variations in extent of pressure by predators) of one species of prey on another.

Similar indirect action takes place between vole and hare populations. Low numbers of voles cause intensification of pressure by foxes on hares, and mass irruptions of this rodent greatly reduce the pressure and increase the hares' chance of survival.

Vole populations therefore exert, through the group of predators feeding on this species, either a negative or positive effect on populations of other species of prey, altering the conditions for their survival.

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REFERENCES

1. Andersen J., 1954: The food of the Danish badger. Danish Rev. Game Biol., *3:* 1—76.
2. Beusekom C. F., 1972: Ecological isolation with respect to food between Sparrowhawk and Goshawk. Ardea, *60,* 1—2: 72—96.
3. Chitty D., 1938: A laboratory study of pellet formation in the short-eared owl (*Asio flammeus*). Proc. zool. Soc., Lond., *108* A: 267—287.
4. Czarnecki Z., 1956: Obserwacje nad biologią sowy uszatej (*Asio otus* L.). Pozn. Tow. Przyjaciół Nauk, *18,* 4: 1—38.
5. Czarnecki Z., Gruszczyńska J. & Smoleńska E., 1955: Badania nad składem pokarmu płomykówki *Tyto alba guttata* (C.L.Br.) w latach 1950—1952 w województwie poznańskim. Pozn. Tow. Przyjaciół Nauk, *16,* 3: 3—35.
6. Dapson W. R. & Irland M. J., 1972: An accurate method of determining age in small mammals. J. Mammal., *53,* 1: 100—107.
7. Estes R. D. & Goddard J., 1967: Prey selection and hunting behaviour of the African wild dog. J. Wild. Manage., *31:* 52—70.
8. Goszczyński J., 1974: Studies on the food of foxes. Acta theriol., *19,* 1: 1—18.

9. Goszczyński J., 1976a: Estimation of daily food ratio of *Tyto alba* Scopoli under natural condition. Pol. ecol. Stud., *2*, 1: 95—102.
10. Goszczyński J., 1976b: Composition of the food of martens. Acta theriol., *21*, 36: 527—534.
11. Goszczyński J., Ryszkowski L. & Truszkowski J., 1976: The role of the European hare in the diet of predators in cultivated field systems. [In: »Ecology and management of the European hare populations«. Eds. Pielowski Z. & Pucek Z.] Państw. Wyd. Roln. i Leśn.: 127—133. Warszawa.
12. Heptner V. G., Naumov N. P., Jurgenson B. P., Sludskij A. A., Čirkova A. F. & Bannikov A. G., 1967: Mlekopitajušče Sovetskovo Sojuza. Izd. Vysšaja Škola, *2:* 1—1004. Moskva.
13. Holišova V., 1968: Marking small mammals by means of coloured admixtures to bait. Small Mammal Newslet., *2*, 3: 36—40.
14. Joslin P., 1970: Conserving the Asiatic lion. IUNC Publis. New. Ser. *18:* 24—33.
15. Kadočnikov N. P., 1953: O vzaimnootnošenii hiščnych ptic i obščestvennoj polevki v stepnom Azerbajdžanie. Zool. Ž., *32*, 6: 1222—1233.
16. Kaškarov D. J. & Zakirov A., 1971: Opyt učeta hiščnikov v pustynnyh rejonah Uzbekistana. Ekologia, *3:* 96—97.
17. Lockie J. D., 1961: The food of the pine marten *Martes martes* in West Ross-Shire, Scotland. Proc. zool. Soc. Lond., *136:* 187—195.
18. Lusk S. & Pokorny J., 1964: Zmeny vàhy a nekterýh rozmeru u ryb vlivem konservace ve 4% roztoku formaldehydu. Zool. Listy, *13*, 2: 135—142.
19. Marti C. D., 1969: Some comparison of the feeding ecology of four owls in North-Central Colorado. Southwest. Nat., *14:* 163—170.
20. Pearson O. P., 1971: Additional measurement of the impact of carnivores on California voles (*Microtus californicus*). J. Mammal., *52:* 41—49.
21. Pielowski Z., 1976: The role of foxes in the reduction of the European hare population. [In: »Ecology and management of European hare populations«. Eds. Pielowski Z. & Pucek Z.] Państw. Wyd. Roln. i Leśn.: 135—148. Warszawa.
22. Pimlott D. H., 1967: Wolf predation and ungulate populations. Amer. Zoologist, *7:* 267—278.
23. Pucek M., 1967: Changes in the weight of some internal organs of *Micromammalia* due to fixing. Acta theriol., *12*, 39: 545—553.
24. Raczyński J. & Ruprecht A., 1974: The effect of digestion on the osteological composition of owl pellets. Acta ornithol., *14*, 2: 25—38.
25. Rosenzweig M. L., 1966: Community structure in sympatric *Carnivora*. J. Mammal., *47*, 4: 602—612.
26. Ryszkowski L., 1971: Estimation of small rodent density with the aid of coloured bait. Ann. Zool. Fennici, *8:* 8—14.
27.. Ryszkowski L., Wagner C. K., Goszczyński J. & Truszkowski J., 1971: Operation of predators in a forest and cultivated fields. Ann. Zool. Fennici, *8*, 1: 160—168.
28. Ryszkowski L., Goszczyński J. & Truszkowski J., 1973: Trophic relationships of the common vole in cultivated fields. Acta theriol., *18*, 7: 125—165.
29. Rzebik-Kowalska B., 1972: Badania nad pokarmem ssaków drapieżnych w Polsce. Acta Zool. Cracov., *17*, 19: 415—506.
30. Schaller G. B., 1972: The endless race of life. Nat. History, *81:* 38—43.

31. Simpson G. G., Roe A. & Lewontin R. C., 1960: Quantitative zoology. Harcourt, Brace and Word: 1—440. New York.
32. Skoog P., 1970: The food of the Swedish badger, *Meles meles* L. Viltrevy, 7, 1: 1—120.
33. Smeenk C., 1972: Ökologische Vergleiche zwischen Waldkauz *Strix aluco* und Waldohreule *Asio otus*. Ardea, *60*: 1—71.
34. Southern H. N., 1954: Tawny owls and their prey. Ibis, *96*, 3: 384—410.
35. Ternovskij D. V., 1972: Ob otnošenijah hiščnika k žertvie. Teriologia, *1*: 395—400.
36. Truszkowski J., 1976: Role of the common buzzard (*Buteo buteo* L.) in agrocenoses of the Middle Wielkopolska. Pol. ecol. Stud., *2*, 1: 103—111.

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POWIĄZANIA MIĘDZY DRAPIEŻNYMI PTAKAMI I SSAKAMI A ICH OFIARAMI

Streszczenie

Czterolenie badania nad drapieżnymi ptakami i ssakami prowadzone przez okres pełnego cyklu zmian zagęszczenia nornika zwyczajnego w okolicach Turwi pozwoliły ocenić zmienność pokarmu, liczebności i penetracji terenu przez drapieżniki przy różnych liczebnościach nornika.

Spośród badanego zespołu drapieżników wyodrębniono grupę gatunków wyspecjalizowanych w wyłowie nornika. Zaliczono do niej: sowę uszatą, płomykówkę, myszołowy, łasicę, kota i lisa. Nornik stanowi dla tych gatunków podstawę pokarmu (Ryc. 2). Przy niskich zagęszczeniach nornika niektóre z wymienionych gatunków (np. lis) przestawiają się na pokarmy zastępcze. Możliwości zmiany pokarmu są, jak się wydaje, uwarunkowane między innymi wielkością drapieżnika (Tab. 5). Zmiany zagęszczenia nornika silnie wpływają na stan liczebny drapieżników. Masowy pojaw *M. arvalis* zwiększa np. ilość przelotnych myszołowów i liczebność kotów na polach (Tab. 7). Wzrost zagęszczenia nornika oddziałuje również na liczebność pozostałych gatunków z tej grupy stymulując ich rozrodczość. Stwierdzono, że drapieżniki te najczęściej penetrują uprawy o wysokich zagęszczeniach nornika, natomiast unikają orek i upraw roślin jarych, na których zagęszczenia tego gryzonia są praktycznie zerowe (Tab. 10, Ryc. 5).

Pozostałe gatunki, takie jak: puszczyk, kuny czy borsuk to drapieżniki-polifagi korzystające z nornika przede wszystkim przy wysokich jego zagęszczeniach. Nie stwierdzono, by niskie zagęszczenie nornika było dla tych gatunków czynnikiem ograniczającym ich liczebność (Tab. 7). Drapieżniki te dużą część swojego pokarmu zdobywają w lasach i zadrzewieniach (Tab. 8), a norniki chwytają na uprawach graniczących z terenami zadrzewionymi.

Oceniono wielkość presji drapieżników na populacje drobnych gryzoni. Mimo, że oceny mają charakter przybliżony wydaje się, że ogólną prawidłowością jest niski udział drapieżników w śmiertelności ogólnej i redukcji liczby obecnych gry-

zoni przy masowym pojawie nornika (Tab. 13). Natomiast przy niskich zagęszczeniach zarówno redukcja jak i udział w śmiertelności nornika przekraczają 50%. Rozmiary presji wskazują więc na fakt, że analizowane drapieżne ptaki i ssaki nie mogą zapobiec powstaniu masowego pojawu nornika ani też nie mogą likwidować tego pojawu.

Stwierdzono, że zmiany zagęszczenia nornika zwyczajnego wpływają pośrednio (poprzez zmiany wielkości presji drapieżników) na populacje innych gatunków ofiar (np. gryzoni leśnych i zajęcy) stanowiących uzupełniający pokarm drapieżników.