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Variation in diet of Tawny Owl *Strix aluco* L. along an urbanization gradient

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The diet of Tawny Owl as a function of urbanization was studied in Central Poland in 1976-1984. The pellets were collected from 24 sites in habitats along an urbanization gradient ranging from the large, relatively undisturbed Kampinos Forest (1441 prey items), through small woodlots surrounding Warsaw (686) and into the city of Warsaw (2567). Diet varied due to urbanization: the proportions of mammals and amphibians were lowest in the city center (respectively 11.3% and 0%), but the proportion of birds, largely House Sparrow *Passer domesticus* increased from 2.9% in the forest to 88.7% in the city. Niche breadth and seasonal variation declined with urbanization. Relationships between diet composition and habitat structure of owl's hunting range in the city, as well as on the seasonal diet variation from owls hunting in forests, let to conclude that the owls were able to exploit locally abundant prey from a variety of habitats. Although the highest densities of Field Mouse *Apodemus agrarius* were noted in parks and cemeteries, our data suggest that Tawny Owls catch this species more effectively in small gardens and secondary growth areas. The predation on Field Mouse by a pair of owls breeding in an urban cemetery was low. Approximately 3.2% of the population were removed by the owl predation, considerably less than in a more rural population.

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INTRODUCTION

The diet of Tawny Owl has been the subject of numerous papers (e.g. Uttendörfer 1939, März 1954, Bogucki 1967, Ryszkowski *et al.* 1971, Smeenk 1972, Wendland 1972, 1984 and others), but data on variation in diet as a function of urbanization are scarce, especially for different habitats compared during the same time period (Schnurre 1961, Beven, 1964, Wendland 1980). In Warsaw and its surroundings, the diet of Tawny Owl has not been studied, but there have been numerous studies on mammals (Andrzejewski *et al.* 1978, Babińska-Werka *et al.* 1979, Goszczyński 1979) and birds (Luniak *et al.* 1964, Luniak 1981, 1982, Luniak *et al.* 1986). They showed that the city differs from not urbanized habitats in species composition and in densities of potential prey of Tawny Owl: there are fewer mammal species in the city but some of them, as well as passerine birds like House Sparrow, can attain high densities. This allows the study of a generalist predator response to spatial changes in potential prey densities and species composition.

According to foraging theory (Krebs *et al.* 1983) owls should restrict their hunting activity mainly to patches with locally high prey densities, abandoning other habitat patches in the city. Thus, we should expect narrowing of the diet spectrum with increasing urbanization.

We shall illustrate how quantitative differences in theriofauna and avifauna associated with urbanization influence the diet of a polyphagous predator, Tawny Owl. We present data on the diet of owls in locations with different levels of urbanization and in different seasons in and around Warsaw, Central Poland. We also analyse the influence of habitat structure on the diet and evaluate mortality of Field Mouse resulting from Tawny Owl predation at one location.

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STUDY AREA AND METHODS

We collected pellets at 24 sites from 1976-1984. Each site represented a different level of urbanization depending on its

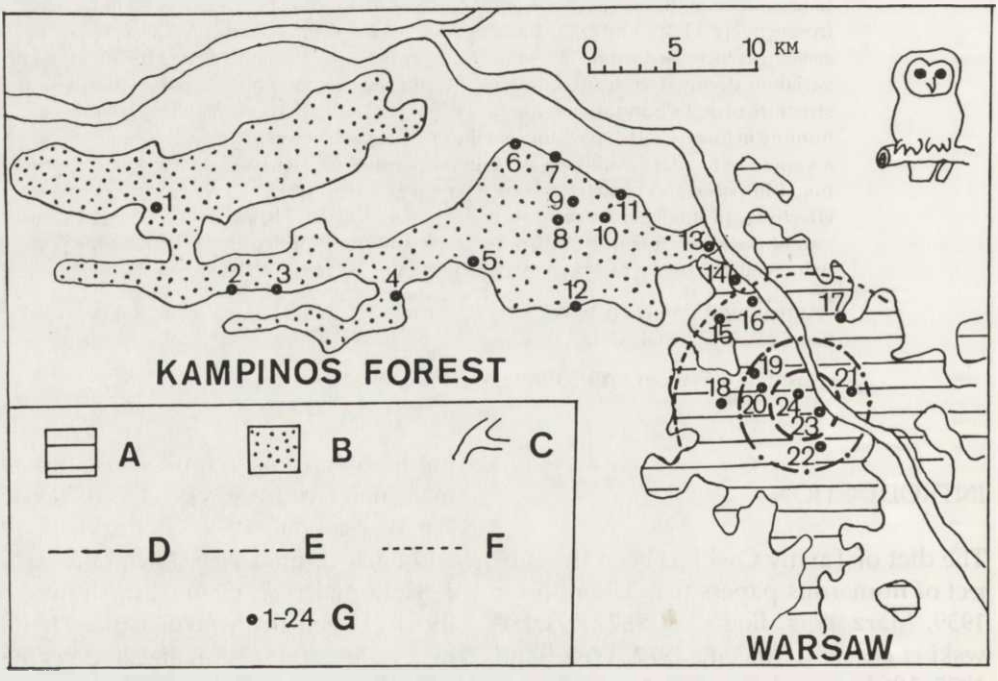

Fig. 1. Study area with marked sites of pellet collection. A – Built-up areas within the administrative borders of Warsaw, B – Forests, C – Vistula river, D – Borders of the central zone, E – Borders of the intermediate zone, F – Borders of the suburban zone, G – Sites of pellet collection: 1. Kobendza Oak, 2. Nart reserve, 3. Zamczysko reserve, 4. Debly reserve, 5. Zaborów Leśny reserve, 6. Kaliszki, 7. Palmiry, 8. Biały Grąd, 9. Młynisko, 10. Grabowy, 11. Dziekanów Leśny, 12. Lipków, 13. Młociny Park, 14. Bielany Park, 15. Wawrzyszew, 16. Kaskada Park, 17. Bródno Cemetery, 18. Orthodox Cemetery, 19. Powązki Cemetery, 20. Evangelical-Augsburg Cemetery, 21. Skaryszewski Park, 22. Łazienki Park, 23. Powiśle Park, 24. Saski Park.
Ryc. 1. Teren badań z zaznaczonymi miejscami zbioru wypluwek.

distance to the city center, from nonurbanized habitats through suburban areas into city of Warsaw (Fig. 1).The least disturbed was Kampinos National Park, a large forest area northwest of Warsaw where we collected pellets at 12 sites. These were located at the edge of the forest and in its interior. In the area of smaller woodlots surrounding the city, we collected pellets from two forest parks: in Młociny Forest (further from the city) and in Bielany Forest (closer to the city).

Within Warsaw we classified our collection sites into three progressively more urbanized zones: suburban, intermediate and central. Pellets were collected at 4 sites in the suburban zone, at 4 sites in the intermediate zone and at 2 sites in the center of the city (Fig. 1).

Prey items were identified from skull remains, teeth and other skeletal remains such as the *os ilium* of amphibians and *humerus* of *Talpa europaea*. In some cases, when bird skulls were so demaged that identification was impossible, only the size of prey was evaluated. We identified 1441 prey items from pellets collected in Kampinos Forest, 686 from forests surrounding Warsaw, and 2567 from Warsaw. Insect remains were detected in small numbers and ommitted from analyses. Results are presented as frequencies of occurrence of prey items.

We estimated the predation of Tawny Owl on Field Mouse based on data on population dynamics of the mouse in the Orthodox Cemetery (Wolska street) area. The owls' food from that cemetery was calculated as biomass percentages. This enabled the evaluation of number of mice eaten by Tawny Owl during one year and consequently the predatory impact on the prey population.

The Simpson index of food niche breadth was estimated by formula:

$$S = \frac{1}{\sum p_i^2}$$

where: p_i – proportion of each prey item in the diet.

Similarity of the diet composition between seasons was estimated with the Morisita index modified by Horn (1966):

$$C = \frac{2\sum_{1}^{n} x_i y_i}{\sum_{1}^{n} x_i^2 + \sum_{1}^{n} y_i^2}$$

where: x_i – percentage of i-th item in the diet in one season, and y_i – percentage of i-th item in the second season. The value of the index varies from 0 to 1, where 1 means that diet does not differ in seasons.

To examine the relationship between diet and habitat within an owl's hunting range, we assumed arbitrarily that Tawny Owl hunts within a circle with a radius of 500 m from the place where pellets were collected. If pellets were collected from several nearby points, the central point of this area was chosen as the center of the circle. We estimated the proportion of several habitat types within the circles at 11 sites in Warsaw. We distinguished the following habitat types: 1) built-up areas, including: 1a) residential areas, and 1b) industrial and commercial areas, 2) open areas, including: 2a) lawns and squares, some containing small woodlots, 2b) small gardens and secondary growth areas, and 3) parks and cemeteries.

We calculated a linear regression of the frequency of common prey species in the diet on the percentage of different habitats in the circular hunting range using the stepwise variable selection method. Thus, the final regression formula only included those habitats with regression coefficients that differed significantly from zero.

RESULTS

General description of the diet

Consumption of mammals and amphibians decreased and consumption of birds increased with increasing urbanization (Tab. 1). In the interior of Kampinos Forest 82% of prey was mammalian and 3% was avian, but in the center of the city the pattern was reversed: 11% mammals and 89% birds. Niche breadth also declined with urbanization (Tab. 1). As urbanization increased Tawny Owl preyed less on *Microtidae* and *Insectivora*, and more on *Muridae*. Among the *Muridae*, there was a strong increase in consumption of Field Mouse and two typical synanthropic species: *Mus*

Table 1. Changes in diet composition of Tawny Owl in urbanization gradient (1–8 as in Fig. 2). Frequencies of species in the total number of prey items. "+" – the remains found only once (frequency < 0.05).
Tabela 1. Zmiany składu pokarmu puszczyka w gradiencie urbanizacji (1–8 wzrastający stopień urbanizacji – patrz ryc. 2).

Prey type	Kampinos Forest			Woodlots surrounding city		The city of Warsaw		
	1	2	3	4	5	6	7	8
Chiroptera	0.1						0.1	
Talpa europaea	0.8	0.4	0.5	0.6	0.6	0.5	1.5	
Sorex araneus	17.1	14.4	2.1	1.7	0.6		+	
Sorex minutus	9.0	4.8	1.8					
Neomys fodiens	19.5		0.8	0.3				
Clethrionomys glareolus	11.9	25.5	35.4	14.6	8.0	0.9		
Pitymys subterraneus		1.1		12.0	6.0	0.9	4.5	
Microtus oeconomus	9.1	9.2	2.4	1.1		0.4		
Microtus arvalis	0.5	11.4	6.6	4.6	4.5	7.1	4.0	
Microtus agrestis	2.9	7.0	1.3					
Arvicola terrestris	1.5	0.4						
Micromys minutus	1.1		1.8	1.7			+	
Apodemus agrarius	0.6	0.4	3.9	15.1	26.8	13.3	7.9	4.9
Apodemus flavicollis	6.5	8.1	3.2	14.0	7.4	0.8		
Apodemus sylvaticus	0.3	3.7	8.9			0.9		
Mus musculus	0.2	1.8	2.1	0.6	2.1	4.4	10.2	3.8
Rattus norvegicus	0.4		0.3	0.3	0.6	1.3	2.5	2.6
Muscardinus avellanarius	0.5	0.4						
Sciurus vulgaris						+	+	
Passer domesticus			2.6	8.0	23.2	44.6	51.7	53.1
Passer montanus			0.5	2.0	3.9	3.6	3.1	1.3
Aves (other species and undetermined)	2.9	7.0	9.2	8.0	15.2	21.3	14.0	34.3
Anura	15.0	4.4	16.5	15.4	1.2		0.1	
Pisces							+	
Vertebrata (undetermined)							0.3	
Number of prey items (*Vertebrata*)	789	271	381	350	336	996	1493	78
The Simpson index of a niche breadth	7.89	7.71	5.59	8.48	5.94	3.69	3.24	2.47

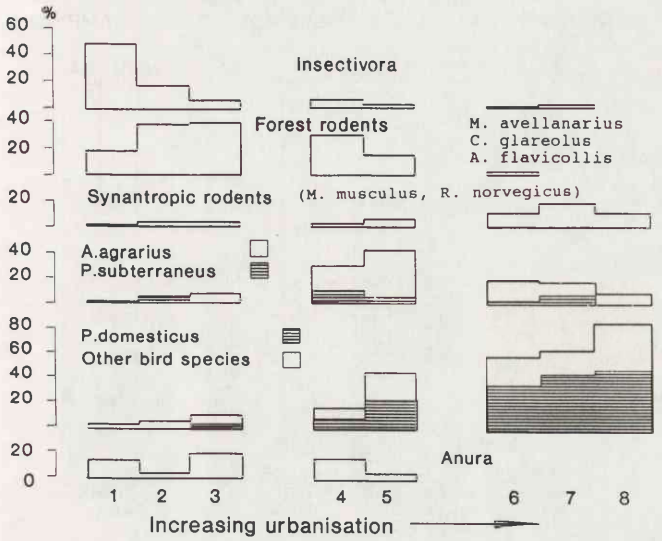

Fig. 2. Variation of prey frequencies along an urbanization gradient 1–8: 1 – Interior of the forest, 2 – Edge of the forest distant from city, 3 – Edge close to city, 4 – Suburban forest park Mlociny, 5 – Forest park Bielany, 6 – Outskirts of Warsaw, 7 – Intermediate zone, 8 – City center
Ryc. 2. Zmiany frekwencji zdobyczy w pokarmie puszczyka ze wzrostem stopnia urbanizacji (1–8).

musculus and *Rattus norvegicus*. Field Mouse was particularly frequent in pellets from forests bordering on Warsaw and from suburban areas. Typical forest species *Clethrionomys glareolus*, *Apodemus flavicollis*, *Muscardinus avellanarius* and species with preferences for wet habitats (*Soricidae*, *Microtus oeconomus*) were rarely found in pellets from urban areas. Almost no insectivores except *Talpa europaea* and single *Sorex araneus* were caught in urban habitats. Four species of rodents were registered in the center of Warsaw, 6 species in the intermediate zone, 9 in the suburbs, 7–9 in the forests bordering on Warsaw and 13 in the Kampinos Forest (Tab. 1).

Among avian prey, House Sparrow was the most frequently caught, and its consumption increased with increasing urbanization (Fig. 2). Other birds (*Passer montanus*, *Parus major*, *Sturnus vulgaris*, *Turdus merula*, *Turdus philomelos*, *Carduelis chloris*) were less frequently preyed upon (Tab. 1). *Columba domestica* comprised a suprisingly small part of the diet. Amphibians were a common diet item in forests but rarely found in the city (Fig. 2).

Seasonal variation of the diet

We analysed seasonal variation at four locations using data from 1976-1978 (Fig. 3). At the Mlociny Forest site and on other sites in Kampinos Forest (not shown) amphibian consumption was most variable, with a pronounced peak in the spring. In forests bordering on Warsaw the proportion of House Sparrow increased considerably in the winter, while in the city the proportion was high and steady all year. The frequency of insectivores in the diet varied regularly at most sites: it was the lowest in winter and the highest in summer + autumn. Other seasonal trends differed among sites.

For each of the 4 sites in Fig. 3 we calculated 3 values of the Morisita index of similarity: spring was compared with summer + autumn, summer + autumn with winter and winter with spring. The

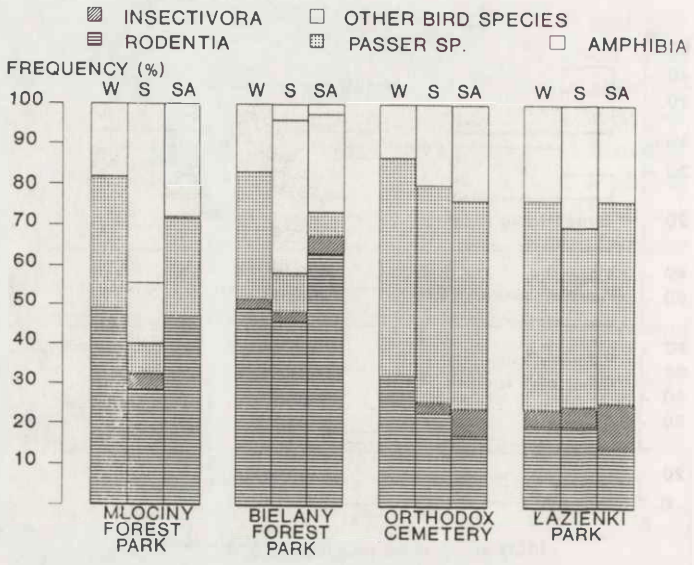

Fig. 3. Seasonal diet variation at chosen sites. W – Winter, S – Spring, SA – Summer and Autumn
Ryc. 3. Sezonowe zmiany pokarmu puszczyka na wybranych stanowiskach. W – zima, S – wiosna, SA – lato i jesień

mean for these three values was the lowest in Młociny Forest (C = 0.71), intermediate in Bielany Forest (C = 0.90) and the highest within the city (C = 0.97 at Orthodox Cemetery, C = 0.98 at Łazienki Park). Thus, seasonal differences decreased with increasing urbanization (Fig. 3).

We made similar comparisons for Kampinos Forest, woodlots surrounding Warsaw, and the city using data from the entire study period. Since we had no precisely dated pellets from the Kampinos Forest from summer + autumn, we only compared the winter diet with the spring one. Seasonal variation was most pronounced in Kampinos Forest (C = 0.78), where it resulted from great variation in proportions of rodents, insectivores, House Sparrow and amphibians. Seasonal variation in forests bordering on the city (C = 0.88) was mainly due to variation of amphibians and House Sparrow. Seasonal variation was the lowest in Warsaw (C = 0.98).

Habitat structure versus diet composition in Warsaw

The frequency of House Sparrow consumed increased with an increasing proportion of built-up areas in the hunting range (Fig. 4A). The frequencies of *Mus musculus* and *Rattus norvegicus* increased with increasing proportion of industrial and commercial areas (Fig. 4B). This relationship explained 42% of the variance in frequencies of both prey species.

There was a significant relationship between the frequency of Field Mouse in the diet and the percentage of open areas in the owl's territory: $y = 0.004 + 0.29x$, $R^2 = 0.67$, $p < 0.05$, $df = 10$. It was mainly caused by the positive relation of small gardens and secondary growth areas on the frequency of captured mice (Fig. 4C). This habitat type accounted for 59% of the variance.

Nearly 75% of the variance in frequency of *Microtus arvalis* was explained by the positive influence of open areas (Fig. 4D). As in the case of Field Mouse, this rela-

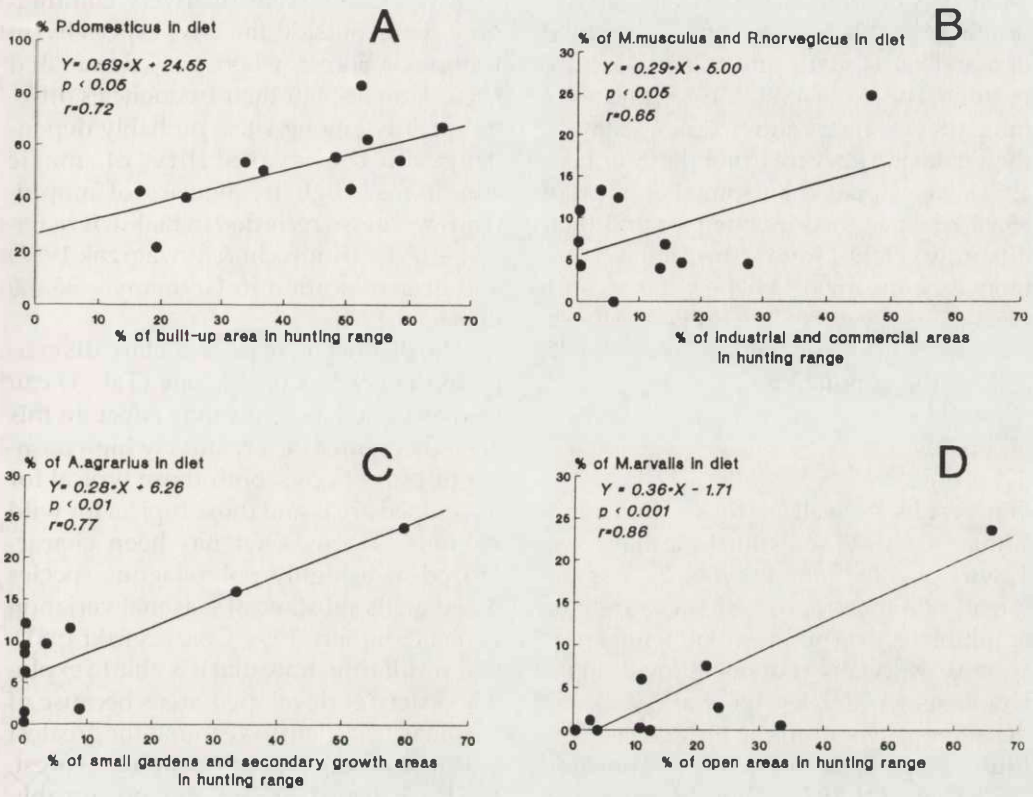

Fig. 4. Relationships between proportions of some prey species in diet and percentage of certain habitats in the hunting range of Tawny Owl in Warsaw.
A) *Passer domesticus* – built-up areas , B) *Mus musculus* and *Rattus norvegicus* – industrial and commercial areas, C) *Apodemus agrarius* – small gardens and secondary growth areas, D) *Microtus arvalis* – open areas
Ryc. 4. Relacje między frekwencją niektórych gatunków ofiar a procentowym udziałem różnych środowisk w obrębie arealów łowieckich puszczyka.

tionship could mainly be explained by the significant positive relationship with the percentage of small gardens and secondary growth areas: $y = 0.02 + 0.09x$, $R^2 = 0.64$, $p < 0.05$, $df = 10$.

Exploitation of Field Mouse by Tawny Owl

Succesive estimations of rodent density (Goszczyński 1979, Babińska-Werka *et al.* 1981) and owl pellet collections were made at the Orthodox Cemetery. Approximately 450 individuals of Field Mouse were born per 1 ha in one breeding season. After adding the adults present before the beginning of the season, we estimated a population of about 480 ind./ha. Thus the 12 ha cemetery had a total population of about 5760 individuals. The Orthodox Cemetery bordered on a park, industrial areas, extensive grasslands, and the narrow belt of small gardens. Since no Field Mouse was detected in these neighbouring habitats during trappings, we assume that all mice caught by Tawny Owl came from the cemetery. The cemetery was permanently in-

habited by one pair of owls, which had two nestlings in 1977. Based on a daily food demand of 54 g for adults and 46 g for nestling (Ryszkowski *et al.* 1973), and assuming that nestlings and fledglings stay on their natal territory for 6 months (Southern 1954), we estimated an annual biomass of 55.98 kg consumed by one pair and their offspring. Field Mouse constituted 8% of biomass consumed (4478 g). Based on a mean body weight of 24 g for Field Mouse, the owls consumed about 187 individuals, 3.2% of the population.

DISCUSSION

Our results as well as those from other similar studies (Tab. 2) illustrate that urban Tawny Owl fed mainly on birds, less frequently on mammals, and very rarely on amphibians. The number of potential prey species, especially rodents, is lower in urban areas (Andrzejewski *et al.* 1978), but densities of synanthropic prey can be very high – e.g. *Passer domesticus* (Tomiałojć 1970, Dyer *et al.* 1977). Thus the food niche of Tawny Owl is narrower in urban areas than in other habitats, which was our general expectation based on foraging theory (Krebs *et al.* 1983).

The diet of Tawny Owl in the center of Warsaw was very similar to that reported from London (Table 2). In both cities House Sparrow made up about 50% of the owl's diet, although a great proportion of House Sparrow (72.3%) was reported from the city of Poznań (Bogucki 1967). Other bird species also increased in the diet of urban owls in Berlin (Wendland 1980) and London (Beven 1964). Not surprisingly, the mammal species absent from the diet in Warsaw were those reported to be uncommon or absent within the city: *Sorex minutus*, *Microtus agrestis*, *Muscardinus avellanarius* (Andrzejewski *et al.* 1978).

Amphibians were relatively common prey items outside the city, especially in Kampinos Forest, where they dominated some samples, but their frequencies differed greatly among sites, probably depending on the availability of mesic conditions. High frequencies of amphibians were also recorded in Białowieża Forest – 37.9% (Ruprecht & Szwagrzak 1987) and at one location in Germany – 36.0% (Schaefer 1975).

The distinct increase in dietary diversity on the borders of Warsaw (Tab. 1) can be interpreted as an ecotone effect. In this zone there must be a relatively high number of prey species, both those typical for developed areas and those typical for wild habitats. Tawny Owl has been characterized as a highly polyphagous species based on its substancial seasonal variation in diet (Southern 1954, Goszczyński 1981). Our results illustrate that it is able to exploit a variety of developed areas because of its dietary plasticity. We found the greatest seasonal differences in Kampinos Forest, the least disturbed site. But presumably because of decreased seasonal diversity in prey as urbanization increased, interseasonal diet differences decreased (Fig. 3).

It appears that owls were able to exploit locally abundant prey (Goszczyński 1981). For example, *Microtus arvalis* (Fig. 4D) and *Talpa europaea* were caught mostly by owls foraging in open areas. The extent of urban development correlated with the frequency of House Sparrow in the owls diet (Fig. 4A), reflecting an increase in sparrow abundance in built-up areas (Tomiałojć 1970, Dyer *et al.* 1977), which may become especially attractive for hunting by owls because of large numbers of roosting sparrows (Górska 1975). Other birds were caught mainly in areas with greater tree cover, where their densities may be well over 100 pairs/10 ha (Luniak 1981). *Mus*

Table 2. Frequencies of mammals, birds and amphibians in all vertebrates in the diet of Tawny Owl in Warsaw, its environs and in different places in Europe. References: A and E – Schnurre 1961, B – Southern 1954, C – Serafiński 1954, D and H – this paper, F – Beven 1964, G – Bogucki 1967
Tabela 2. Porównanie udziału ssaków, ptaków i płazów w pokarmie puszczyka na terenach miejskich i pozamiejskich.

Nonurban areas:	Berlin A	Oxford B	Western Poland C	Warsaw D
Mammals	73.1	94.9	92.5	82.0
Birds	10.0	5.1	5.1	2.9
Amphibians	14.5	0	2.3	15.0
Centers of towns:	Berlin E	London F	Poznań G	Warsaw H
Mammals	13.1	9.0	8.4	11.3
Birds	82.0	91.0	90.1	88.7
Amphibians	4.9	0	1.5	0

musculus and *Rattus norvegicus*, typical urban pests, were caught most frequently in areas where nonresidential buildings (Fig. 4B) dominated.

Although the highest densities of Field Mouse were noted in parks and cemeteries (Babińska-Werka *et al.* 1979) Goszczyński 1979, our data suggest that owls catch this species more effectively in small gardens and secondary growth areas (Fig. 4C). The ground there is often covered by low vegetation, probably increasing the hunting efficiency of owls (Southern & Lowe 1968).

Data from sampling of Field Mouse population in the Orthodox Cemetery suggest that Tawny Owl predation was very low (3.2% of total biomass in season). In agricultural habitats in western Poland Tawny Owl reduced this species by 33% (Ryszkowski *et al.* 1973). Since the density of Field Mouse was much lower in western Poland, these results suggest that owl predation is not a numerical response to prey density. In spite of relatively high densities of mice on Orthodox Cemetery the remaining prey species (mainly House Sparrow) are so numerous that they may dominate the prey base and hence diet of the owls, or habitat structure at the cemetery makes rodents more difficult to capture. Unfortunately, direct verification of the first hypothesis is imposible, but higher frequency of Field Mouse in the diet of owls at Bielany and Młociny, where this rodent is less common, provide indirect support for the first hypothesis. Babińska-Werka *et al.* (1981) also support the first hypothesis, since they found no differences in abundance of shelters for rodents between sites in forests and in cemetery.

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STRESZCZENIE

[Zmienność składu pokarmu puszczyka w gradiencie urbanizacji]

Badania nad zmiennością składu pokarmu puszczyka prowadzono w Warszawie i jej okolicach. Miejsca zbioru wypluwek dobrano tak, aby poszczególne stanowiska reprezentowały wzrastający stopień urbanizacji, od stosunkowo mało zmienionych terenów Puszczy Kampinoskiej, przez podmiejskie lasy Warszawy, różne strefy miejskie, aż do centrum (ryc. 1).

Stwierdzono spadek konsumpcji płazów i ssaków oraz wzrost konsumpcji ptaków przez puszczyki w miarę wzrostu stopnia urbanizacji (tab. 1, ryc. 2). W Puszczy Kampinoskiej udział ssaków wynosił 82%, a ptaków ok. 3%, natomiast w centrum miasta te proporcje były odwrotne: ptaki stanowiły 89% wszystkich zjadanych ofiar, a ssaki zaledwie 11%. Szerokość niszy pokarmowej puszczyka zmniejszała się w kierunku centrum miasta (tab. 1). Wśród ssaków malało spożycie *Microtidae* i *Insectivora*, a zwiększał się

udział *Muridae*: myszy polnej i 2 synantropijnych gatunków – myszy domowej i szczura wędrownego. Wśród zjadanych ptaków gwałtownie wzrastało spożycie wróbla domowego (ryc. 2).

Wzrost urbanizacji zmniejszał różnice sezonowe w składzie pokarmu i sprzyjał ujednoliceniu pożywienia w skali roku (ryc. 3). Analizy związków między strukturą terytoriów zajmowanych przez puszczyki a składem pokarmu poszczególnych par wykazały, że: a) ze wzrostem powierzchni zajętej przez zabudowę wzrasta spożycie wróbla domowego (ryc. 4A), b) udział zabudowy przemysłowej i usługowej w obrębie terytorium wpływa na frekwencję myszy domowej i szczura wędrownego w pokarmie puszczyka (ryc. 4B), c) istnieje istotny związek między frekwencją myszy polnej i nornika zwyczajnego w pokarmie sowy a udziałem powierzchniowym działek i zieleńców oraz terenów otwartych w areale łowieckim puszczyka (ryc. 4C i 4D).

W przypadku jednego stanowiska (Cmentarz Prawosławny) oceniono redukcję populacji myszy polnej przez sowy. Z przeprowadzonych wyliczeń wynika, że puszczyki usuwały zaledwie ok. 3% wszystkich osobników tego gatunku, co jest presją bardzo małą w porównaniu z redukcją na innych pozamiejskich terenach.

Wyniki pracy potwierdzają wykazywany przez innych autorów oportunizm pokarmowy puszczyka (tab. 2).