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THE BARN OWL—A SELECTIVE OPPORTUNIST PREDATOR

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ABSTRACT

There are differing views in the literature regarding the feeding strategy of the barn owl (*Tyto alba*, Strigiformes). Whereas some authors conclude that the barn owl is a selective predator, selecting to prey on certain species, others maintain that it is an opportunist. We studied the diet composition of barn owls from agricultural fields in northern Israel, using pellet analysis. Over 4,000 prey items were identified, comprising a total of at least 27 species. We found that during 1997–2001 there was a significant change in the barn owl's diet: it switched its main prey species from the Levant vole (*Microtus guentheri*) to two other Myomorpha species, the house mouse (*Mus musculus*) and Tristram's jird (*Meriones tristrami*), probably as a result of changes in the field abundance of the main prey items. Hence, although our barn owls select one prey species at a certain period of time, they exhibit an opportunistic feature in their ability to easily switch between prey items in their diet.

INTRODUCTION

Owl pellet analysis is a common, easy, and inexpensive way to study diet and behavior. It can also be a way to learn about the prey community that provides the predator diet, so long as the data are correctly interpreted. One possible bias can be caused by the different feeding strategies of the predator (either opportunistic or selective behavior).

An opportunistic predator hunts a variety of prey species, in relation to their relative abundance in the field. A selector, by contrast, focuses on one or a few prey species, and has a restricted ability to switch between prey species (Murdoch, 1969; Andersson and Erlinge, 1977).

If a predator hunts its prey opportunistically in relation to the field density of the prey, it is reasonable to assume that its diet will reflect the community structure of the prey species. In such a case, using pellet analysis to study community structure is much easier and cheaper than using traps. By contrast, if it hunts selectively, we can expect a bias towards the more favorable prey species relative to their actual densities in the field, and thus the diet composition cannot indicate the field density of the prey community.

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The barn owl (*Tyto alba*, Strigiformes) diet has been well studied during the past century, and its preference for small mammals is well known (Bunn et al., 1982; Mikkola, 1983; Taylor, 1994). However, its hunting tactics remain controversial. Most researchers have claimed that the barn owl hunts its prey opportunistically (Herrera, 1974; Bunn et al., 1982; Mikkola, 1983), and thus its diet may represent the true relative abundance of prey in the field (Hanney, 1962; Herrera, 1974). This claim has usually been based on the wide range of prey species found in the barn owl's diet, including small mammals, birds, reptiles, amphibians, and invertebrates (Bunn et al., 1982). Other researchers (Perrin, 1982; Derting and Cranford, 1989; Muñoz and Murua, 1990; Yom-Tov and Wool, 1997) have claimed that the barn owl is a selective predator, hunting its prey by preference; thus its diet would not represent the true abundance of prey species in the field. This latter claim was based on laboratory and field studies, either by showing preference for hunting one or more prey species or by comparing trapping data with pellet analysis. It is reasonable to assume that the above contrasting claims are influenced by the length of time that a study took place. Prey availability may change over time, and pellets collected during a long-term study may reflect such a change, while pellets collected duing a short-term study may show the opposite. Hence, the above debate may reflect not the true hunting strategy of a predator, but the availability of a certain food item at one point in time.

Some rodents, i.e., the Levant vole and Tristram's jird, have marked changes in their adundance in Israel (Mendelssohn and Yom-Tov, 1999), being very common in one year and much rarer a year or two later. Thus, a study that lasts more than 5 years may include a peak and a trough in abundance of such rodents, and this may be reflected in the composition of owl pellets deposited over that time period. A selective predator is expected to consume a narrow range of prey species regardless of their abundance, while an opportunist will take its prey in proportion to its abundance at any point of time.

The aim of the present study was to try to examine whether the contents of barn owl pellets change over time. This may contribute to the debate of whether the barn owl hunts its prey opportunistically or selectively, and consequently, whether one can use its pellets to learn about the prey community in the field. This study may have important implications for further ecological, paleontological, and applied studies. The study of fossil pellets, for example, may reveal the composition of past prey communities. Moreover, the barn owl could be used as a biocontrol agent to eliminate pests in agriculture fields if its hunting tactics are found to be opportunistic, because of its ability to stabilize its prey density at a low level.

METHODS

SPECIES

The barn owl is a common resident in central and northern Israel (Shirihai, 1996). Its breeding season lasts 6 months (February–July) and it usually rears only one brood per season (Kahila, 1992). It generally prefers hunting small mammals, especially rodents, which make up more than 70% of its diet (Herrera, 1974; Marti, 1974; Bunn et al., 1982; Mikkola, 1983; Taylor, 1994). Previous research in our study area (Kahila, 1992) has shown that mammals make up more than 95% of total prey taken, with one common species, the Levant vole (*Microtus guentheri*), contributing more than 50% of total mammals taken.

STUDY AREA AND MATERIALS

The study was conducted in the agricultural fields of Kibbutz Sde Eliyahu, Bet She'an Valley (32º26′N, 35º37′E), northern Israel. The climate in this region is characterized by two seasons: a relatively cold wet winter, and a dry and hot summer. Average annual rainfall is about 270 mm per year, concentrated mainly between November and March. Average annual temperature is 22 °C, and average annual relative humidity is 55%, and these two elements create a medium-to-high heat load (Jaffe, 1988). Most of the area is cultivated with varied perennial and annual crops such as palm groves, vineyards, citrus orchards, alfalfa, wheat, corn, and vegetable fields.

During the past twenty years, a wild barn owl population has been established in the area through erecting nest boxes, and this is now being used as a means of biological pest control as part of the kibbutz's organic farming. Rodenticides are not used.

PROCEDURE

Before the breeding season begins, all nesting boxes are checked and cleaned. At the end of the breeding season (July–August) the contents of the nesting boxes are collected and brought to the laboratory for further study. Thus each nesting box represents the diet of the occupants of this nest box for one breeding season.

Five different nesting boxes from different agricultural areas in the kibbutz were selected for this study, and their contents were analyzed for two separate breeding seasons: 1997 and 2001. The pellets of two of these nesting boxes were additionally analyzed for six successive seasons (1997–2002).

The contents of a nesting box were mostly comprised of densely packed material composed of pellets and dung trampled together ("aggregates"), as well as a small number (a few dozen or less) of complete pellets. The pellets and compacted material were soaked in water for at least 24 h, and cranial and post-cranial elements were separated and dried in a warm room (35 °C) for an additional period of at least 24 h. Species identification was done by comparison with specimens preserved in the collection of the Zoological Museum of Tel Aviv University and the collection of The Hebrew University of Jerusalem. The most commonly identified elements were crania, mandibles, and femura for mammals; skulls and humeri for birds; mandibles for reptiles; and exoskeleton pieces for invertebrates. Minimum number of individuals (MNI) was calculated from the most common element for every species. For body weights of (male) prey species, we used Mendelssohn and Yom-Tov (1999).

RESULTS

We found that the barn owls' diet was composed of at least 27 species, representing six different classes (Table 1). There were eight species of mammals, comprising almost 94% of the diet. Three mammal species made up more than 87% of total prey taken: the house mouse *Mus musculus* (37.5%), the Levant vole *Microtus guentheri* (30.2%), and Tristram's jird *Meriones tristrami* (19.6%). The second common class was birds,

Table 1
The diet composition of the barn owl (*Tyto alba*) in Kibbutz Sde Eliyahu

Prey Taxon	Total MNI	MNI (%)	Mean Ind. Mass (g)	Total Biomass (g)
Microtus	1,215	30.25	51.0	61,965
Mus	1,507	37.52	14.0	21,098
Meriones	786	19.57	77.0	60,522
Crocidura	199	4.96	7.0	1,393
Suncus	15	0.37	1.4	21
Rattus	38	0.95	141.0	5,358
Spalax	8	0.20	195.0	1,560
Rousettus	2	0.05	130.0	260
Total Mammals	**3,770**	**93.87**		**152,147**
Streptopelia	65	1.62	101.0	6,565
Passer	54	1.34	27.7	1,496
Coturnix	19	0.47	96.5	1,834
Alauda	8	0.20	40.0	320
Carduelis	3	0.07	15.6	47
Turdus	3	0.07	113.0	339
Galerida	6	0.15	40.5	243
Columba	1	0.02	354.5	355
Coracias	1	0.02	146.0	146
Sturnus	2	0.05	82.3	165
Sylvia	5	0.12	25.0	125
Anthus	1	0.02	18.4	19
Upopa	1	0.02	61.4	61
Motacilla	1	0.07	21.0	21
Pycnonotus	3	0.07	44.0	132
Unknown	5	0.12		
Total Aves	**178**	**4.43**		**~12,000**
Gryllotalpa	51	1.27		
Solifugae	8	0.20		
Total invertebrates	**59**	**1.47**		
Gekkonidae	8	0.20		
Anura	1	0.02		

comprising 4.4% of total prey taken, with two main genera, turtledoves (*Streptopelia* spp.) and sparrows (*Passer* spp.). Four other classes, Insecta, Arachnida, Reptilia, and Amphibia, were scarce (1.3%, 0.2%, 0.2%, and 0.02%, respectively).

The remains found in each of the five different nesting boxes were examined for the years 1997 and 2001. We compared diet composition of the ten different nesting events (nests by breeding seasons) by cluster analysis (using Ward's method of squared Euclidean distances and minimum variance amalgamation). As shown in Fig. 1, two main clusters are formed: one for 1997 and the other for 2001. This result suggests that the diet of the barn owls showed greater similarity between the different boxes for the same year than for the same nesting box in different years.

We also compared the difference in diet composition between the nesting boxes with their actual spatial distances from each other (Fig. 2). No significant correlation was found between these factors (Mantel test, for 1997: $r = -0.45$, $p = 0.19$; for 2001: $r = 0.44$, $p = 0.22$).

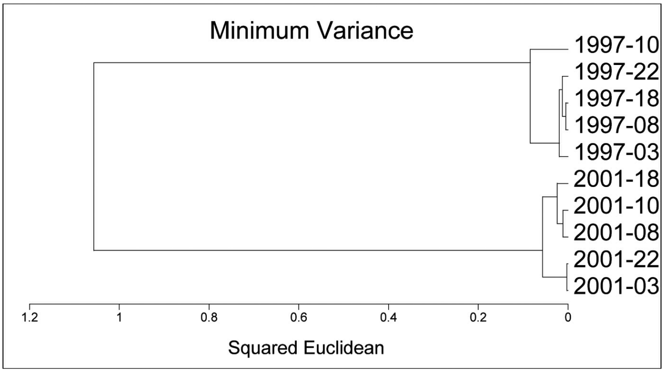

Fig. 1. Similarity in the owls' diet among ten different nesting events for the years 1997 and 2001. Clustering was done by Ward's method.

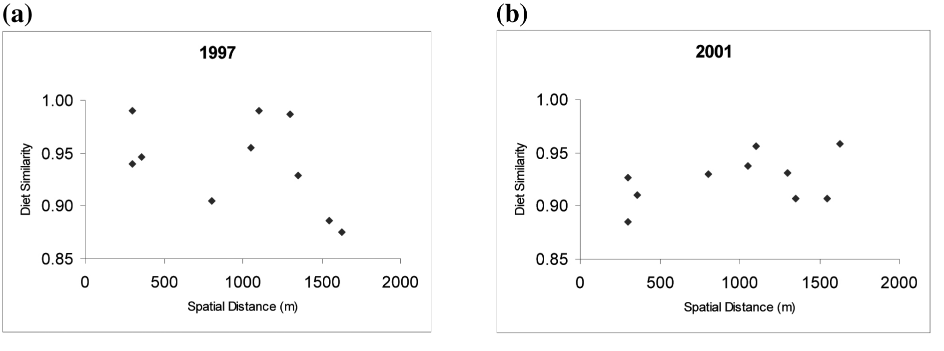

Fig. 2. The degree of diet similarity as a function of the distance between the nesting boxes. The data refer to five different nesting boxes (hence, 10 distances) in two different years: (a) 1997 and (b) 2001. The Y-axis represents the degree of similarity (calculated by Pearson's product moment correlation coefficient). The X-axis represents the distance measured using a 1:10,000 map.

In the five boxes that were analyzed in 1997 and 2001, the difference between the years appears to derive from changes in the proportion of the main prey species in the diet (Fig. 3a). For 1997, our results were similar to previous Israeli studies (Dor, 1947; Hoter, 1983; Kahila, 1992): the main prey species was the Levant vole (comprising almost 60% of all prey items), followed by the house mouse (18%). However, in 2001 the proportions were reversed: the house mouse became the main prey species (60%), and the Levant vole proportion decreased to 10%. These differences are statistically significant for both species (two-tailed paired *t*-test, Levant vole: $t_4 = 6.9$, $p < 0.01$; house mouse: $t_4 = -9.0$, $p < 0.01$). There were no significant differences in the proportions of other prey species.

We also compared the biomass of the different species collected from the same five boxes in the years 1997 and 2001. The results were similar: a switch in the total weight of the main prey species between the years 1997 and 2001 (Fig. 3b). The total

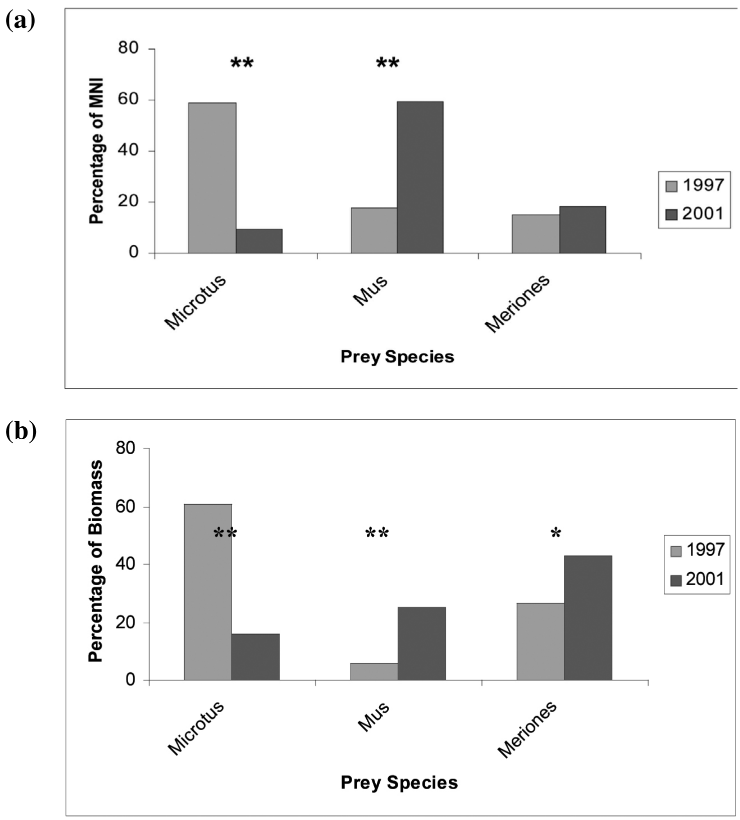

Fig. 3. Comparing the three main prey species in the diet composition of the barn owls between 1997 and 2001. (a) Presented as MNI (Minimum Number of Individuals), and (b) presented as biomass. (*$p < 0.05$, **$p < 0.01$.)

biomasses taken in 1997 and 2001 were similar (47 kg and 52 kg, respectively), but the proportion of each of the main species had changed (in 1997: Levant vole—61%, house mouse—6%, Tristram's jird—26%; in 2001: 16%, 25%, and 43%, respectively). The results significantly differed for all three prey species (two-tailed paired *t*-test, Levant vole: $t_4 = 5.6$, $p < 0.01$; house mouse: $t_4 = -6.4$, $p < 0.01$; Tristram's jird: $t_4 = -3.9$, $p = 0.02$). There were no significant differences in the proportions of other prey species.

The contents of two nesting boxes were examined for six successive seasons (1997–2002). The two nesting boxes were selected due to continuous nesting during the six years, and the relatively great distance (1,300 m) between them. Figure 4 shows the alternation in the diet composition during the years 1997–2002. Whereas during the first three years (1997–1999) the Levant vole was the dominant prey species, in the follow-

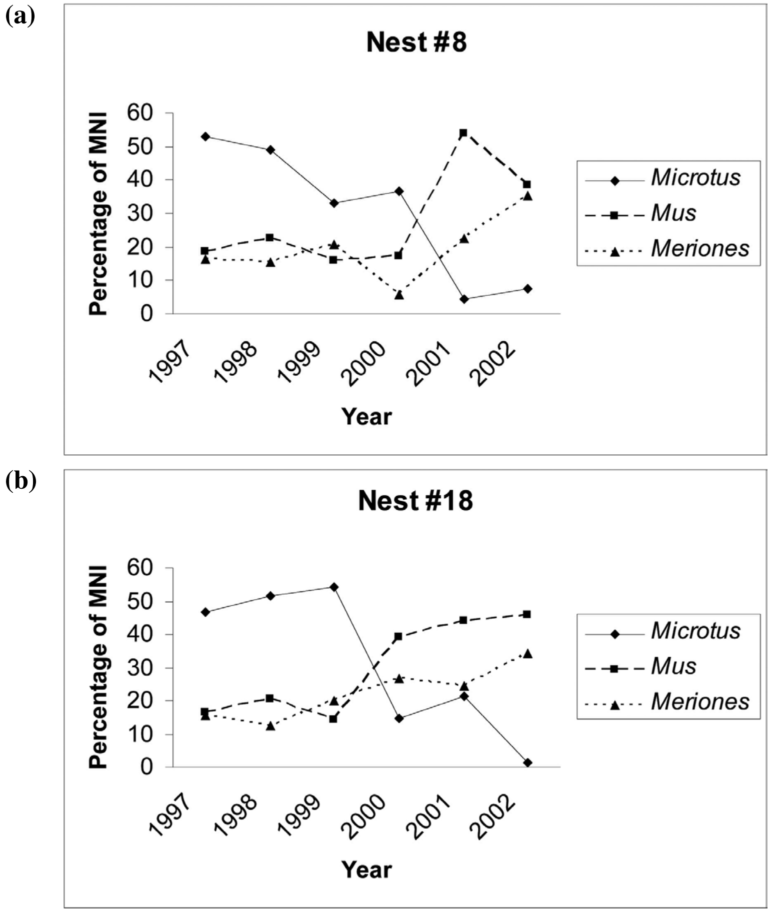

Fig. 4. Diet composition (in MNI) of the barn owls in six successive breeding seasons: (a) Nest #8, (b) Nest #18.

ing years there was a major decrease in its frequency. Corresponding to this decrease, an increase in the frequencies of both the house mouse and Tristram's jird is evident. The changes occurred concurrently in both nesting boxes—the correlation coefficients over the years are positive for the Levant vole, the house mouse, and Tristram's jird ($r = 0.72$ and $p = 0.05$; $r = 0.72$ and $p = 0.05$; $r = 0.51$ and $p = 0.15$, respectively).

DISCUSSION

The barn owl's hunting tactics are a source of controversy. Most researchers claim that the barn owl hunts its prey opportunistically. For example, Bunn et al. (1982) contend that the barn owl has no prey preference and it will hunt whatever it comes across, as long as this lies within the right range of size and ease of capture. Mikkola (1983), too, claims that the barn owl hunts its prey opportunistically according to its abundance in the field. Herrera (1974) found significant differences between diet compositions of barn owls from several countries in Europe, and concluded that the barn owl is an opportunistic predator that changes its diet according to the abundance of prey where it hunts. Thus, Herrera (1974) concluded that "small mammal diversity as calculated from the food analysis, may be used as a rough estimate of the population diversity in the area".

In contrast to the opportunistic argument, other studies have claimed that the barn owl's feeding strategy is selective, and the prey composition revealed from pellet analysis does not represent the true abundance of the prey community. Smith and Cole (1989) argued that barn owls probably prey selectively on individual species, making the composition of their pellets a poor indicator of their relative abundance within small mammal communities. Muñoz and Murua (1990) and Marti (1974) noted that some species are actively selected as prey, while Perrin (1982) showed differences between the composition of the local small mammal community as observed from trapping, and that obtained from pellet analysis. Yom-Tov and Wool (1997) suggested that contents of pellets might be biased towards the larger prey species. Furthermore, experiments performed in captivity also supported the selective point of view, showing that barn owls preferred one prey species over two others (Derting and Cranford, 1989).

The above arguments represent two extremes of a continuum of behavioral strategies; thus categorizing the barn owl as either an absolute opportunist or an absolute selector might be over-simplistic and not necessarily correct.

According to earlier studies (Dor, 1947; Hoter, 1983; Kahila, 1992; Aram, 1999), the Levant vole was shown to be the main prey species in the barn owl's diet in central and northern Israel. While this conclusion is valid for the time period during which these studies were conducted, our present results are somewhat different. In 1997, the most common prey species was indeed the Levant vole, comprising about 60% of the total prey taken, while the house mouse and Tristram's jird composed together less then 30%. In 2001, however, the Levant vole comprised only 18% of the total diet, while the house mouse and Tristram's jird together comprised more than 70%. This change in the diet occurred gradually and simultaneously in the three main prey species. The proportions of the other prey groups did not change significantly.

A change in the occurrence of a particular prey species in the diet of the barn owl may reflect a change in its abundance or in its availability to the barn owls, as a possible result of habitat modification (Love et al., 2000). Since there was no significant habitat management modification in our study area during the study period that might have led to this kind of a change, we conclude that the change was driven by a change in the prey species abundance. The Levant vole is known to have multi-annual population oscillations in Israel (Bodenheimer, 1949), as do other voles (Krebs and Myers, 1974; Hansson and Nilsson, 1975). The last known vole outbreak in our study area occurred during winter 1996–spring 1997, and since then the vole population density has remained very low. Local farmers reported progressively decreasing crop damage caused by the Levant vole since the last outbreak, and a corresponding decrease in the number of its burrows in the fields (Shaul Aviel, personal communication). This decrease has changed Levant vole availability to the barn owl. Other studies, too, have shown a diet change caused by seasonal or multi-annual population oscillations (Marti, 1974; Campbell et al., 1987; Catalisano and Massa, 1987; Bose and Guidali, 2001).

Changes in prey availability may result in the barn owl searching for a better habitat, may prevent breeding (selective feeding strategy), or enhance a switch to other prey species (opportunistic feeding strategy). Heywood and Pavey (2002) found that barn owls are capable of switching to other prey when rodent populations decline, while Morton and Martin (1979) found that the barn owl became uncommon (due to dispersal or starvation) after a drop in abundance of their main prey species, and that they did not switch to an alternative prey.

Our present results show that the barn owl had switched its main prey species to alternatives (the house mouse and Tristram's jird), which in the past have been only secondary in importance. This switch indicates that the barn owl has an opportunistic feeding strategy that allows it to remain and even breed in the area despite the declining population of its main prey species. In our study area, the percentage of occupied nesting boxes was extremely high during the breeding seasons of 1997 and 1998 (66% and 57%, respectively), after which it dropped to a lower level of 19–25% in the following years (1999–2002). One reasonable explanation for this high occupation of nesting boxes is the Levant vole outbreak that took place during the winter of 1996–1997. A year later, the Levant vole density was still high enough to sustain the breeding barn owls. These data imply that during a massive increase in the availability of their main prey, the barn owls bred prolifically; but during the crash phase, they switched to an alternative prey species and also reduced their breeding rate. This functional response may act to control the rodent population at a low density (Murdoch, 1969; Andersson and Erlinge, 1977; Erlinge et al., 1983; Hanski et al., 1991; Korpimaki and Krebs, 1996). Consequently, the barn owl may offer an efficient means of bio-control of rodent pests (Murua and Rodriguez, 1989; Muñoz and Murua, 1990; Kahila, 1992; Aram, 1999).

Our study supports the claim that the barn owls' feeding strategy is opportunistic, based on their ability to switch between prey species according to their abundance in the field. It is no coincidence that those authors who summarized data from wide areas or over a considerable length of time support the claim that the barn owl is an opportunistic feeder (Bunn et al., 1982; Mikkola, 1983; Taylor, 1994). However, being an opportunist does not mean that the barn owl hunts its prey randomly. Yom-Tov and Wool (1997) have shown that while it takes a wide range of prey items, it prefers larger species over smaller ones, apparently due to high return on investment in hunting effort. This observation may explain the differences shown in several studies between data collected from trapping and these from pellet analysis (Marti, 1974; Morton and Martin, 1979; Perrin, 1982; Smith and Cole, 1989).

Thus, we suggest that the barn owl can be defined neither as a pure opportunist nor as a pure selective hunter. Even positioning this species somewhere on the linear continuum between opportunism and selectivity will be rather simplistic. While it prefers a certain type of prey, which has the most suitable characteristics (crepuscular or nocturnal, having high density, in the right size range, easy to capture, etc.)—and usually it is the local vole (*Microtus*) species that meets these requirements (see also Campbell et al., 1987)—the barn owl will readily switch to a different prey species once *Microtus* numbers decline below a certain level. In other words, the barn owl prefers voles, and will favor them over other species as long as they are sufficiently abundant, but it can switch its diet in vole-limited years or areas to alternative prey species. This flexible hunting strategy of the barn owl makes it a very successful predator, and explains why the distribution range of this species is cosmopolitan, and far greater than those of most other bird species.

Our results also suggest that pellet analysis cannot represent the exact density of the small mammal community in an area, but it can be used as a complementary tool to assess temporal as well as spatial changes in relative density of the main prey groups.

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