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DIET COMPARISON BETWEEN TWO SYMPATRIC OWLS—*TYTO ALBA* AND *ASIO OTUS*—IN THE NEGEV DESERT, ISRAEL

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ABSTRACT

We studied the diets of the barn owl *Tyto alba* and the long-eared owl *Asio otus* in an arid region in the northern and central Negev Desert, Israel. The diet of the two owl species consisted mainly of small mammals, but the long-eared owl consumed a significantly larger proportion of birds in all seasons than did the barn owl. Seasonal differences in the proportion of birds in the diet of the long-eared owl were mainly due to the consumption of migratory birds. Diet composition of each of the two species resembled more the diet of its conspecifics from other locations in that region and other seasons rather than that of the other species from the same location or season. This indicates that these two owl species do not consume prey in proportion to its availability, but prefer certain types of prey over others.

Keywords: barn owl, *Tyto alba*, long-eared owl, *Asio otus*, diet, Israel

INTRODUCTION

The barn owl (*Tyto alba*) and the long-eared owl (*Asio otus*) are nocturnal birds of prey whose distribution ranges overlap over large parts of the Holartic region. The enormous literature on their diet indicates that over most of their ranges they feed mainly on rodents and other small mammals, complemented by other animals, including birds and invertebrates (reviewed by Cramp and Simmons, 1985). Both species forage in the open, but the long-eared owl also hunts near and below trees (Cramp and Simmons, 1985), thus enabling it to feed on sleeping birds that roost in trees. Although body size of these species varies throughout their ranges, in the Western Paleartic they are rather similar in size. Wing length of adult barn owls ranges between 273 and 307 mm in both sexes, and of the long-eared owl is 252–312 mm in males and 269–319 mm in females. Since the two species are similar in size, diet, and time of activity, it may be presumed that they compete over the same resources, primarily over food, as predicted by Gause's principle (Begon et al., 1990).

As stated above, the diets of the two species have been studied extensively, mainly

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by examination of their pellets. Most studies were carried out in regions where the two species are allopatric, or dealt with the diet of one of the species in regions where they are sympatric. Several authors studied the diet of these two species in sympatry, and concluded that their diets are similar and feeding niches quite overlap (Marks and Marti, 1984; Capizzi et al., 1998). Some studies have shown that the barn owl has a broader diet than the long-eared owl (Marti, 1974; Amat and Soriguer, 1981; Veiga, 1981; Capizzi and Luiselli, 1996; Alivizatos and Goutner, 1999). Others (Marks and Marti, 1984; Janes and Barss, 1985) found that the barn owl feeds on significantly heavier prey than does the long-eared owl.

In Israel, the barn owl is a common resident, occurring mainly in the Mediterranean region, but also scattered in the desert where it occurs mainly (but not exclusively) in and near human settlements (Paz, 1986; Shirihai, 1996). Its diet has been studied in both Mediterranean (Dor, 1947; Tores et al., 2005) and drier areas (Yom-Tov and Wool, 1997; Pokines and Kerbis-Peterhans, 1998; Tores and Yom-Tov, 2003), and consists of mostly small rodents supplemented by a large variety of other animals, including reptiles, birds, and invertebrates. This species is an opportunistic predator, capable of switching the composition of its diet in accordance with prey availability (Tores et al., 2005). The long-eared owl is resident in Israel, occurring mostly in low-lying areas in the Mediterranean region, but during the last three decades it also inhabits agricultural settlements in the desert. Some of the long-eared owls seen in Israel are wintering or migrating birds (Paz, 1986; Shirihai, 1996). This species prefers semi-open areas such as agricultural settlements, plantations, and patches or lines of trees (Shirihai, 1996).

The aim of this study is to compare the diet of the barn and long-eared owls in the desert region of Israel, particularly in areas where both species live in sympatry.

METHODS

This study took place in the northern and central Negev, Israel. The region is relatively arid, and annual precipitation varies greatly from year to year, as well as spatially, ranging from 300 mm in the north to 100 mm in the south. Rain occurs only during winter (November–April). Mean monthly temperature ranges between 26 ºC in July and 11 ºC in January (Jaffe, 1988).

Long-eared owls roost in dense vegetation, which, in our study area, occurs only in settlements. We located communal winter roosts of long-eared owls, and nesting sites during the breeding season, in or near agricultural settlements. These were visited once or twice every month between May 2002 and December 2003, and data pertaining to the long eared owl diet were reported in Leader et al. (2008). We also located roosts and nests of barn owls in the same area, and locations where both species occur were regularly visited once or twice every month from December 2002 to December 2003. The data pertaining to both species' diets are presented and analyzed here. On each visit all pellets were collected and the area was cleaned of pellets and remains of prey, so that each collection was composed of "fresh" pellets accumulated since the last visit. Every pellet was kept in a separate bag and its date and location were recorded. All pellets were

allocated to one of four seasons: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). Pellets of long-eared owl were identified by their grey or light-black color and narrower width, while barn owl pellets are shiny, black, and wider. Pellets whose identification could not be determined were not used. In the laboratory every pellet was either separated to its components using pincers, or soaked in water and the remains and cranial and post-cranial elements were separated and dried. Species identification was done by comparison with identified specimens preserved in the collection of the Zoological Museum of Tel Aviv University and the collection of The Hebrew University of Jerusalem. We treated each single pellet as a unit containing the remains of the complete portion of food eaten. Under field conditions, bones of one prey item usually appear in one pellet and only rarely are they discarded in two or more pellets (Raczyński and Ruprecht, 1974). The main 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. All remains in the pellets were identified to the basic possible taxon, but since differences between species are often small, many of the remains were identified to genus level. A small proportion (2–11%) of post-cranial remains could not be identified to genus level, but since they belonged to either *Meriones* or *Gerbillus* (Gerbilidae), we divided those unidentified remains between the two genera by the relative amount that was actually found in the identifiable remains. The identified bird species were categorized according to their status in Israel (residents or migrants). However, some bird genera and even species have both resident and migratory populations in Israel. In such cases the remains were categorized according to the status of the most common species in the genus in the study area.

The nine settlements from which we collected pellets were divided into three categories according to the presence of owls (number of pellets collected in brackets):

a. Barn owls, with no long-eared owls. Magen 31°17′N 34°23′E (120 pellets); however, there was one long-eared owl pair there for one month in one year.
b. Long-eared owls, with no barn owls. Sde Boqer 30°52′N 34°48′E (280), Mashabei Sade 31°00′N 34°47′E (28), Tsohar settlements (a group of six settlements within a range of 1–2 kms from each other) 31°14′N 34°25′E (480), Omer 31°17′N 34°50′E (157).
c. Both owl species. Revivim 31°03′N 34°44′E (25 barn and 380 long-eared owl pellets), Gevulot 31°12′N 34°28′E (420 and 340), Tze'elim 31°12′N 34°32′E (110 and 97), Nirim 31°19′N 34°22′E (250 and 1300). Most of the comparisons between diet composition of the two owl species were done on data from these four settlements.

In all settlements there are ornamental trees, bushes, and grass lawns, and the surrounding area includes various field crops (potatoes, peanuts, carrots, etc.), as well as fruit trees (olives, avocado) and lined or scattered ornamental trees (palms, *Tamarisk* ssp., *Acacia* ssp.). The natural small mammalian fauna consists of several species of rodents and shrews, with a strong psammophilous element where the loess soil is mixed

with sand. Commensal rodents (rats and mice) are also present.

DATA ANALYSIS

Comparison of diet composition between barn and long eared owls was done by chi-square tests for independence (between owl species and prey species). Where the chi-square tests involved some rather small expected frequencies, so that the χ^2 distribution cannot be a reliable approximation there, the p values (i.e., the probabilities of rejecting the null hypothesis that prey frequencies are the same for both owl species) were estimated by computer simulations. For each location, 1000 simulated samples were drawn under the assumption of the null hypothesis. The proportion of samples which had a χ^2 statistic larger than (or equal to) the observed χ^2 was taken as an estimate of the real p value.

Shannon-Wiener's $H' = -\sum_k p_k \ln(p_k)$ and Simpson's $D = 1 - \sum_k p_k^2$ diversity indices (where p_k is the fraction of prey species k in the diet) were calculated for measuring diet diversity of the two owl species in the four locations where they occur sympatrically. Comparisons of the diversity indices between the two owl species in each of these locations were done by computer simulations. For each location, 1000 simulated samples were drawn under the assumption of the null hypothesis of similar diets. For each sample, the difference between the diversity indices of the two species was calculated. The proportion of samples in which the absolute value of the difference was larger than (or equal to) the observed absolute difference was taken as an estimate of the real p value.

Similarity between diet compositions of the two owl species was calculated using the modified Morisita's similarity index. This was done once for species × location combinations and again for species × season combinations. Thus, the similarity between two diets i and j is

$$MMSI_{ij} = \frac{2\sum_k x_{ik}x_{jk}}{\left[\sum_k (x_{ik}^2/N_i^2) + \sum_k (x_{jk}^2/N_j^2)\right]N_iN_j} \quad ,$$

where x_{ik} is the number of prey items of species k in diet i, and $N_i = \sum_k x_{ik}$ is the total number of prey items in diet i. Cluster analysis was used to generate dendrograms which demonstrate similarities between diets with respect to prey species composition. The UPGMA (Unweighted Pair-Group Method using arithmetic Averages) procedure was applied for creating the clusters.

We also compared the diversity indices of the diet of each owl species between locations where it occurred alone and locations where it occurred in sympatry with the other species. Thus, for the long-eared owl, its pooled diet over Sde Boqer, Mashabei Sade, Tsohar, and Omer was compared to its pooled diet over Revivim, Gevulot, Tze'elim, and Nirim; and for the barn owl, its diet in Magen was compared to its pooled diet over Revivim, Gevulot, Tze'elim, and Nirim.

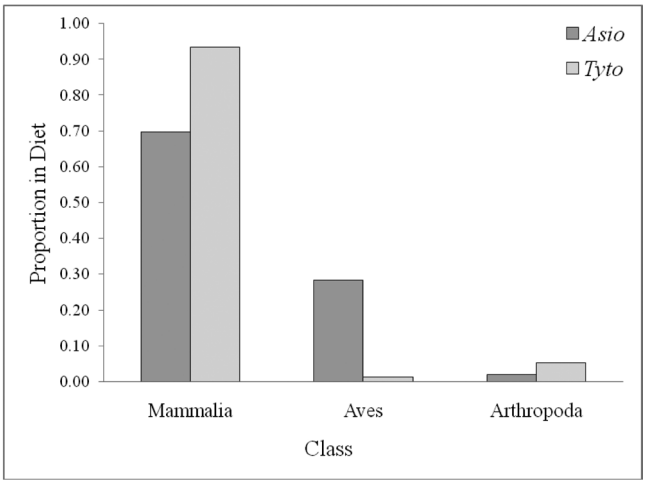

Fig. 1. Diet composition of the barn and long-eared owls sorted by classes of prey.

RESULTS

We collected 3062 and 925 pellets of long-eared and barn owls, respectively, yielding 6088 prey items. Figure 1 represents the percentage of mammals, birds and arthropods in the diet of the two species in the whole sample of pellets examined. While small mammals formed the great majority of the diet (69.7% and 93.3% for the long-eared and the barn owls, respectively), birds composed 28.3% of the diet of the long-eared owl, but only a negligible fraction (1.2%) of the barn owl's diet. The proportion of birds in the diet of the long-eared owl varied greatly between locations, and in Omer, Magen and Tze'elim it formed about 60% of the diet.

Comparing the diets of the two owl species in each of the locations where they occur simultaneously, indicated a highly significant difference in each of the four locations: $\chi^2_9 = 162.2$, $\chi^2_9 = 301.2$, $\chi^2_5 = 184.9$ and $\chi^2_9 = 353.7$ for Revivim, Gevulot, Tze'elim and Nirim, respectively; each $p < 0.001$.

Comparing the proportion of rodents within the diets of the two owls in each of the four locations where they occur simultaneously, gave an overall highly significant difference, indicating a larger proportion of rodents in the barn owl's diet. (The proportion was larger in each location—highly significant in three, but non-significant in Gevulot; the overall chi-square was $\chi^2_4 = 209.7$, with $p < 10^{-6}$).

Comparing the proportion of birds in the diets of the two owls in each of the four locations where they occur simultaneously, gave an overall highly significant difference, indicating a larger proportion of birds in the long-eared owl's diet. (The proportion was larger in a highly significant way in each location; the overall chi-square was $\chi^2_4 = 403.3$, with $p < 10^{-6}$).

Diversity of diet for each owl species in the four locations where they are in sympatry is presented in Table 1. Both the Shannon–Wiener's index and the Simpson's index show that diversity is similar in Revivim and Gevulot, is larger for the barn owl than for the long-eared owl in Tze'elim, and vice versa in Nirim.

Diversity of diet for each owl species in locations where it occurred alone and in locations where it occurred in sympatry with the other species is presented in Table 2. For each species, diversity is larger in sympatry than in allopatry (though not significantly regarding the Shannon–Wiener index for the *Asio*).

Figure 2 shows the changes in the proportion of birds in the diet over the seasons. Note the higher proportions of birds in the long-eared owl's diet during the migration seasons (autumn and spring).

Not all bird remains could be identified to the species level. Of the 922 birds found in long-eared owls pellets for which we could determine whether they belong to a resident or to a migratory species, 506 (54.9%) were found during the migration seasons (spring

Table 1

Diversity of diet (measured by Shannon-Wiener's and by Simpson's diversity indices) for each owl species in the four locations where they occur in sympatry. The *p* values indicate the significance of the difference between the indices of both species within the same location

Location	Revivim		Gevulot		Tze'elim		Nirim	
Owl Species	*Asio*	*Tyto*	*Asio*	*Tyto*	*Asio*	*Tyto*	*Asio*	*Tyto*
Shannon-Wiener's DI	1.421	1.305	1.323	1.284	1.128	1.257	1.509	1.316
	$p = 0.385$		$p = 0.486$		$p = 0.042$		$p < 0.001$	
Simpson's DI	0.694	0.665	0.612	0.626	0.593	0.647	0.745	0.662
	$p = 0.440$		$p = 0.429$		$p = 0.003$		$p < 0.001$	

Table 2

Diversity of diet (measured by Shannon-Wiener's and by Simpson's diversity indices) for each owl species in sympatry and in allopatry. The *p* values indicate the significance of the difference between the indices for each species in sympatry and allopatry

Owl Species	*Asio otus*		*Tyto alba*	
Locations	Sympatry	Allopatry	Sympatry	Allopatry
Shannon-Wiener's DI	1.708	1.676	1.499	0.925
	$p = 0.200$		$p < 0.001$	
Simpson's DI	0.790	0.780	0.712	0.509
	$p = 0.027$		$p < 0.001$	

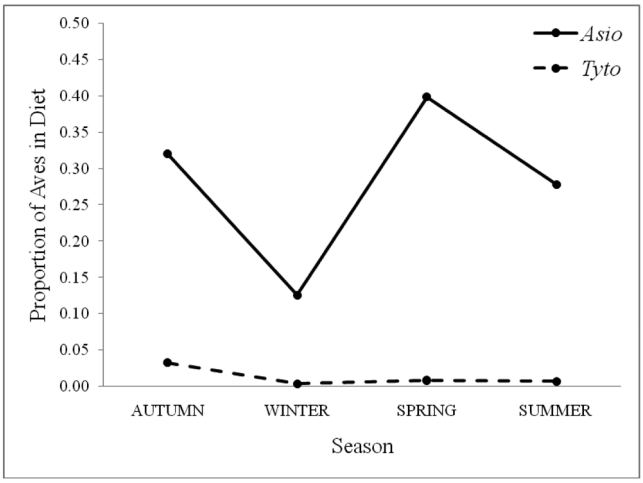

Fig. 2. Proportion of birds in the diet of the barn and the long-eared owls, sorted by season.

and autumn) and 416 (45.1%) during summer and winter. However, while the numbers of residents in the diet were almost the same during the migratory and non-migratory seasons (390 and 387, respectively), the number of migrants were 116 and 29 during these seasons, respectively. These findings indicate that the significant difference found in the proportion of bird remains in long-eared owl diet between the seasons is primarily due to the consumption of migrants (Fisher's exact test, $p = 10^{-11}$).

The variation between the diets of the two owl species is also demonstrated by cluster analysis. Figure 3a presents the clustering of eight owl × location combinations (the two owl species and the four locations where both species were present). The dendrogram shows that the eight combinations are clearly divided into two branches, one that is comprised of all barn owl combinations and the long-eared owls from Nirim, and the other that is comprised of the rest of long-eared owl combinations. This demonstrates that owl diet is more species-dependent than location-dependent. (There was one exception: The long-eared owls from Nirim had a high proportion of *Meriones* spp. and no *Gerbillus* spp. in their diet, similar to the diet of barn owls in all locations.)

Figure 3b presents the clustering of eight owl × season combinations (the two owl species and the four seasons). The dendrogram shows that these eight combinations are clearly divided into two branches, one that is comprised of all barn owl combinations and the long-eared owls in winter, and the other that is comprised of the other three long-eared owl combinations. This demonstrates that owl diet is more species-dependent than season-dependent. (Again, there was one exception, which probably reflects the scarcity of birds in the long-eared owl diet during the winter.)

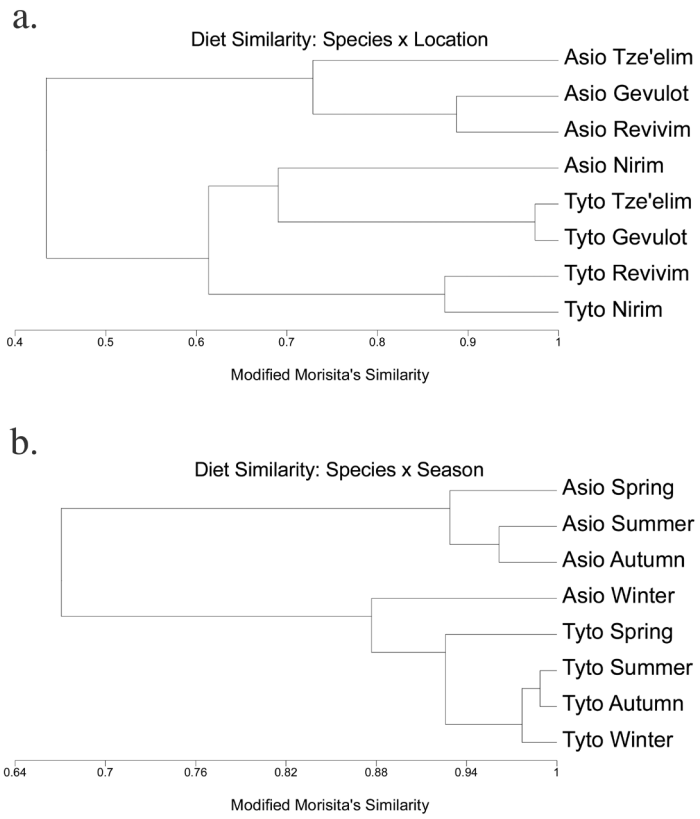

Fig. 3. Diet composition clustered according to (a) owl species and locations; (b) owl species and seasons.

DISCUSSION

We found that the diet of the two owl species consisted mainly of small mammals, but the long-eared owl consumes significantly larger proportion of birds in all seasons than does the barn owl. Similar findings were reported in many studies of the diet of these two species (reviewed by Cramp and Simmons, 1985). Cramp and Simmons reported that the diet of the long-eared owl, at least in northern and central Europe, consists largely of small voles (*Microtus agrestis* and *M. arvalis*), but in southern Iraq pellets collected between February and April contained 46.0% birds, 37.2% house mice *Mus musculus*, and 16.4% rats *Rattus* spp. (Cramp and Simmons, 1985). Further, Bertolino et al. (2001) found that the long-eared owl is an adaptable predator that expands its food niche in the presence of diversified prey. Yalden (1985) found that in the Peak District in England sympatric barn owl, short-eared owl and long-eared owl have very similar diets, but the

long-eared owl takes more birds than the other two, and avian prey are more important for it in the breeding season than in winter. The seasonal difference in the proportion of birds in the diet of the long-eared owl in our study was largely due to the consumption of migratory birds. Assuming that owl diet reflects the proportion of available prey species (Yom-Tov and Wool, 1997), it was reasonable to predict that the diet of both owl species from a certain location and season will resemble each other. We found that the opposite was true, and diet composition of each of the two species resembled more the diet of its conspecifics from other locations and seasons rather than that of the other species from the same location or season. In other words, each of the two owl species was consistent in the composition of its diet. This indicates that these two owl species do not consume prey in proportion to its availability, but prefer certain types of prey over others. Capizzi et al. (1998) found that in a woodland in Italy in the presence of the tawny owl *Strix aluco*, the diets of the barn and long-eared owls were similar, but the long-eared owl preyed upon voles and mice, while the barn owl preyed upon small rodents and shrews.

Several studies have shown that the barn owl has a broader diet than the long-eared owl (Marti, 1974; Amat and Soriguer, 1981; Veiga, 1981; Capizzi and Luiselli, 1996; Alivizatos and Goutner, 1999). We did not reach the same conclusions in our study—indeed, in one location (Tze'elim) the barn owl had a broader diet than the long-eared owl, but in another location (Nirim) the opposite was the case, while in two other locations (Revivim and Gevulot) no significant difference was observed.

The more diverse diet exhibited by each owl in sympatry might indicate a possible competition between the two owls—each species has to compromise in the presence of the other species, and resort to consuming also its less favorable prey. This speculation needs some further, more specifically planned experimental design.

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