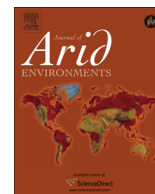


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# Relationship between diet and reproductive success in the Israeli barn owl

M. Charter<sup>a, b, \*</sup>, I. Izhaki<sup>a</sup>, Y. Leshem<sup>b</sup>, K. Meyrom<sup>c</sup>, A. Roulin<sup>d</sup><sup>a</sup> Department of Evolution and Environmental Biology, University of Haifa, 31905 Haifa, Israel<sup>b</sup> Department of Zoology, Tel-Aviv University, Ramat-Aviv, 69978, Israel<sup>c</sup> Kibbutz Nir David, Bet Shean Valley, Israel<sup>d</sup> Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland

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## ABSTRACT

The effect of diet on barn owl (*Tyto alba*) breeding biology has been well studied in the temperate regions but not in the more arid Middle East. In temperate regions, barn owls are darker colored and mainly prey upon Cricetidae rodents, whereas in arid regions, they are lighter colored and prey to a larger degree upon Muridae rodents. In this study we analyzed the diet and breeding success of 261 barn owl pairs nesting in Israel. The reproductive success of barn owls declined from March to August, and fledged more young when they consumed a larger proportion of social voles (*Microtus socialis guentheri*). Although the diet of the lighter colored barn owls in Israel comprises more Muridae than that of the darker morphs in temperate regions, in both regions the number of barn owl young increases with an increased proportion of voles in the diet.

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## 1. Introduction

Several authors have described barn owl (*Tyto alba*) reproductive biology in northern Africa and the Middle East (Wilson, 1970; Wilson et al., 1986; Meyrom et al., 2009). While the reproductive success of barn owls in Israel is affected by agricultural practices and density, location and placement of nest boxes (Meyrom et al., 2009; Charter et al., 2010, 2012a), it is unclear whether diet also affects breeding. Although studies in temperate regions of Europe and the USA have shown how the composition of voles in the diet of barn owls is associated with reproductive success (Klok and de Roos, 2007; Taylor, 1994), it is also important to study other geographic locations due to the latitudinal variations that exist in both diet (Herrera, 1974; Korpimäki and Marti, 1995) and breeding (Korpimäki and Norrdahl, 1991; Salamolard et al., 2000; Reif et al., 2004). Specifically, in some birds of prey, including owls, reproductive success is sometimes higher in the more northern latitudes

and they frequently specialize on specific prey (Herrera, 1974; Korpimäki and Norrdahl, 1991; Korpimäki and Marti, 1995; Salamolard et al., 2000; Reif et al., 2004).

The diet of barn owls mostly comprises species of the family Cricetidae (voles) in temperate regions, and various species of the family Muridae (e.g. mice, rats, jirds, gerbils) in Mediterranean and tropical regions (Taylor, 1994; Bonvicino and Bezerra, 2003; Pavey et al., 2008; Roulin, 2004a). Barn owls may not only select the prey that are most abundant in a specific region, but may also differ in their morphological adaptations to preying on Muridae. In the Middle East, barn owls are lighter colored than in temperate regions (Roulin et al., 2009), and Charter et al. (2012b) have shown in Israel that paler owls have shorter wings and tail and consume more Muridae, whereas darker-reddish owls have longer wings and tail and consume more Cricetidae. This may suggest that the abundance of Muridae rodents in the Middle East is reflected in selective processes favoring a lighter colored plumage in the barn owl, as already suggested for Europe (Roulin, 2004a).

Even though some regions of the Middle East possess among the largest known populations of barn owls in the world (Meyrom et al., 2009), it still remains unclear as to whether diet may affect the owls' reproductive success. One of the aims of the present study

\* Corresponding author. Department of Evolution and Environmental Biology, University of Haifa, 31905 Haifa, Israel.

E-mail address: [chartermotti@gmail.com](mailto:chartermotti@gmail.com) (M. Charter).

was therefore to test the hypothesis that in Israel, barn owl reproductive success is associated with the proportion of specific rodent species in the diet, as has been found in other countries in temperate regions of Europe and North America (De Bruijn, 1994; Taylor, 1994; Klok and de Roos, 2007; Bernard et al., 2010). Further, we discuss whether the proportion of Muridae in the barn owl diet may, at least in part, explain the evolution of a lighter-colored plumage in *T. alba erlangeri* than in its European counterpart *T. alba alba/guttata*. In this context, it is important to evaluate whether the proportion of Muridae and/or Cricetidae in the diet is associated with reproductive success, as this may indicate whether preying upon these species is a key determinant of selective processes (potentially color-specific) in the Middle East. In comparison to the darker barn owls in Europe, whose diet comprises mainly Cricetidae rodents, we tested whether the proportion of Muridae and/or of Cricetidae is correlated with breeding parameters in Israel, where barn owls are lighter colored.

## 2. Materials and methods

The reproductive success and diet of 261 barn owl broods located in nest boxes (50 cm wide × 75 cm long × 50 cm high; entrance 25 cm high × 15 cm, raised 2.5–3 m above the ground) were monitored during the 2008 to 2011 breeding seasons at six sites in Israel (Table 1). Four of the six sites were characterized by arid/semi-arid climates (annual rainfall less than 500 mm) while two sites had Mediterranean climates. Nest boxes were visited between two to five times annually and data on laying date (day first egg was laid) were determined by back-calculation, using wing length of nestlings to determine age, an incubation period of 32 d (Roulin, 2004b), and number of nestlings when the oldest individual was 40 days old. In some nests specific reproduction parameters were unknown and in such cases those nests were removed from some of the statistical analyses.

Barn owl pellets were collected when the oldest nestling was 40 days old, and we extracted mandibles, skulls, and femurs from the pellets to identify prey to species level. We identified, on average, 41 prey items per nest (range 7–141, SE = 1.3, N = 261) and even though the number of pellets analyzed varied between nests, as shown in an earlier study, diet analyzed from 11 or from 50 pellets gave similar results (Charter et al., 2012b).

Statistical analyses were performed with the software JMP 8.0. Tests are two-tailed and *P*-values < 0.05 are considered significant. Means are quoted ± SE. To analyze the relationship between reproductive success and diet, we performed a linear mixed model

with Year and Region as random factors to take into account annual and regional variation in reproductive success and diet. Number of fledglings was the dependent variable and diet the independent variable. Since the percentages of the three major prey species, house mice, social voles, and Tristram's jirds, were inter-correlated (Pearson's correlations,  $-0.19 < r < -0.66$ ,  $n = 261$ ,  $P < 0.0025$ ), we performed a principal components analysis with these three species. The first two components had eigenvalues larger than 1 (1st: 1.76, 58.8% of the variance explained; 2nd: 1.18, 39.4%).

## 3. Results

Including all pairs that laid at least one egg and pairs that failed to raise young, on average, barn owl pairs reared 4.6 (±0.15; standard error) nestlings per laying pair (range is 0 and 9;  $n = 223$  pairs). For those pairs that succeeded in raising at least one young, pairs reared an average of 4.9 nestlings ±0.13,  $n = 210$  pairs; Fig. 1. The mean laying date was March 17 (range January 26 and June 12, SE = 1.4 days,  $n = 238$  pairs) per laying pair (Fig. 2).

Overall, Muridae (Tristram's jirds *Meriones tristrami*, black rats *Rattus rattus*, house mice *Mus musculus*, *Gerbilla* sp., common spiny mice *Acomys cahirinus*) comprised 51%, and Cricetidae (social voles *Microtus socialis guentheri*) contributed 39.3% of the 10,811 prey specimens identified in barn owl pellets (Table 2). The three most abundant prey species were house mice, social voles, and Tristram's jirds, totaling 89.2% of the diet. The first principal component of diet was positively associated with the percentage of Tristram's jirds (eigenvector: 0.55) and house mice

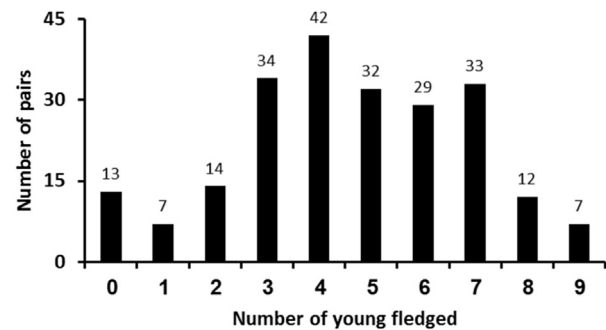


Fig. 1. Frequency distribution of the number of barn owl young fledged per laying pair in Israel from 2008 to 2011. Number above bars indicates the absolute number of broods.

Table 1

Number of nest boxes, mean elevation of the barn owl nests, mean rainfall and mean maximum daily temperature of the 6 study sites located in Israel.

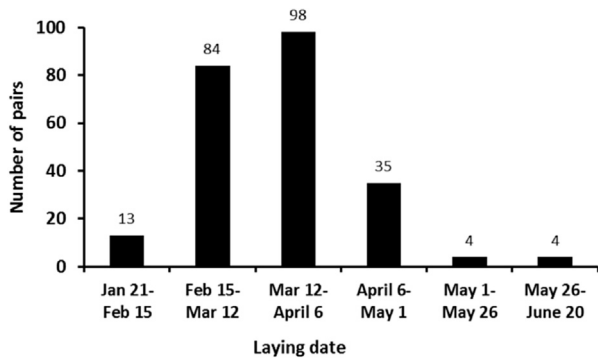
Study site	Coordinates	Mean elevation (m.a.s.l.)	Number of nest boxes <sup>a</sup>	Number of barn owl nests <sup>b</sup>	Mean rainfall (mm) <sup>c</sup>	Mean maximum daily temperature (C°) <sup>d</sup>
Hula Valley	33° 70'N, 35° 35'E	72.3	76	38	585	25.8
Jezreel Valley	32° 38'N, 35° 18'E	57.7	261	44	439	25.2
Beit-Shean Valley	32° 30'N, 35° 30'E	-221.1	270	87	253	28.2
Judea	31° 48'N, 34° 49'E	143.5	243	40	253	25.7
Golan Heights	32° 52'N, 35° 44'E	650.8	62	22	900	19.5
Northern Negev	31° 14'N, 34° 42'E	163.2	174	30	157	26.1

<sup>a</sup> Total number of nest boxes in the region.

<sup>b</sup> Number of active barn owl nests where we collected pellets.

<sup>c</sup> Data from 2008 to 2011 from the Kibbutz Sde Elyahu weather station of the Israel Meteorological Center (Tel Aviv).

<sup>d</sup> Mean maximum temperature from December 1 to July 31 2008 to 2011 from the Israel Meteorological Center idem.



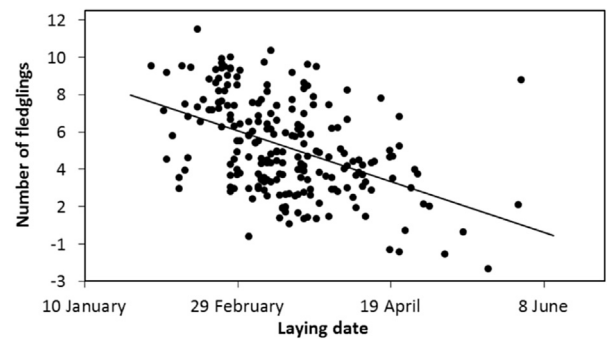
**Fig. 2.** Frequency distribution of the Julian laying dates of barn owl pairs in Israel from 2008 to 2011. Number above bars indicates the absolute number of studies. Number above bars indicates the absolute number of barn owl pairs.

(0.39), but negatively with social voles ( $-0.74$ ). In contrast, the second principal component of diet was negatively associated with Tristram's jirds ( $-0.62$ ), positively with house mice ( $0.78$ ), and not associated with social voles ( $-0.05$ ).

In linear mixed models, the random variable Year did not explain a significant variation in brood size at fledging, whereas the random variable Region accounted for 18.7% of the variation. The number of barn owl fledglings was negatively associated with the 1st principal component of diet ( $F_{1,170.2} = 11.47$ ,  $P = 0.0009$ ;  $-0.39 \pm 0.12$ ; estimate  $\pm$  SE) and date ( $F_{1,201.7} = 40.61$ ,  $P < 0.0001$ ; brood size decreased along the season:  $-0.04 \pm 0.006$ , Fig. 3), but not with the 2nd principal component of diet ( $F_{1,183.9} = 0.04$ ,  $P = 0.84$ ). Using a similar model as above, but with the principal components of diet replaced with the proportion of voles in the diet (Fig. 4a), mice (Fig. 4b) and jirds (Fig. 4c). From the loadings of the different prey species on these two principal components, we conclude that reproductive success increased with the proportion of voles in the diet, decreased with the proportion of mice (this relationship is significant because the proportions of voles and mice are negatively correlated,  $r = -0.40$ ,  $n = 261$ ,  $P < 0.0001$ ), but did not covary with the proportion of jirds in the diet.

#### 4. Discussion

Unlike some diurnal raptors in which breeding success decreases from higher to lower latitudes (Corbacho et al., 1997;



**Fig. 3.** Relationships between the laying date ( $F_{1,201.7} = 40.61$ ,  $P < 0.0001$ ) and the number of fledglings per successful barn owl pair in Israel. Predicted values from the linear mixed model presented in the results are reported.

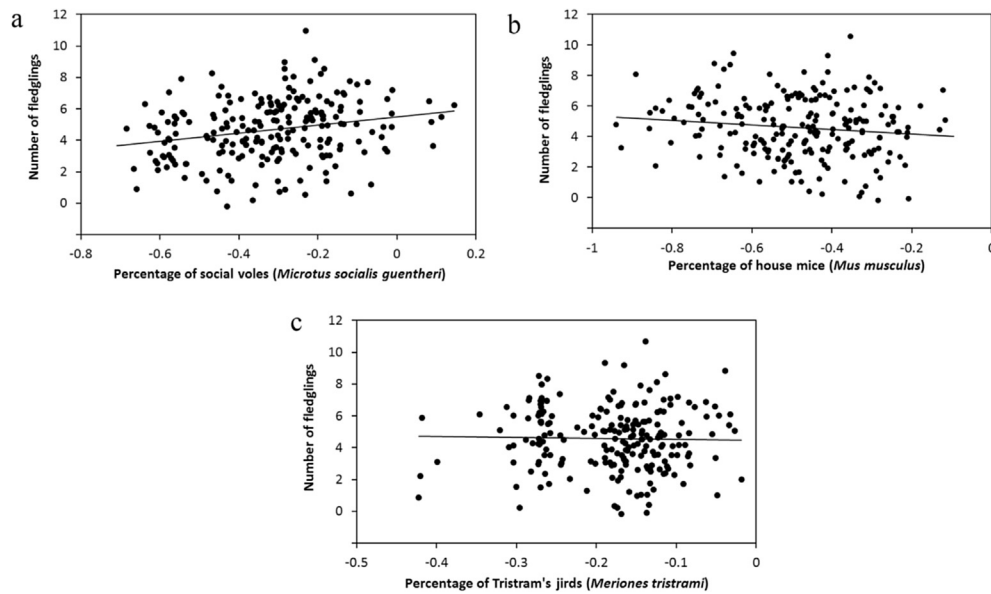
Carrillo and González-Dávila, 2009), the mean number of young barn owls fledged in Israel was high (4.9 nestlings per pair) compared with Europe (range 1.9–4.6 nestlings in Europe, see Taylor, 1994; Roulin, 2002a) despite the low latitude of our study site. Similar to studies in Europe (Taylor, 1994; Roulin, 2002b) the number of young that fledged decreased later in the breeding season in this study. Similar to temperate, tropical, and arid regions, small mammals comprised the majority of the diet of barn owls in Israel (review in Taylor, 1994). In comparison to Europe where barn owls rely mainly on Cricetidae (voles) (Roulin, 2004a), 51% of the diet of the barn owls in Israel consisted of rodents from the family Muridae (house mice and Tristram's jirds). This is similar to the findings from other studies from the Middle East, in which Muridae comprise up to 60% of the prey and voles only 15% (Rifai et al., 1998; Pokines and Peterhans, 1997; Tores and Yom-Tov, 2003; Baker et al., 2005; Shehab, 2005; Tores et al., 2005; Shehab and Charabi, 2006; Charter et al., 2007, 2009; Obuch and Benda, 2009).

Interestingly, in our study the reproductive success of barn owls increased with the proportion of voles in the diet, as found in Europe (Klok and de Roos, 2007), and was negatively associated with the proportion of mice (Muridae) but not jirds in the diet. Previously in the Middle East, the main prey were Muridae, which are more common in dry environments (Tores and Yom-Tov, 2003), whereas Cricetidae are found mainly in agricultural land (Tores et al., 2005; Charter et al., 2009). This was largely a result of over-grazing and irrigated crop fields were limited. Thus, Muridae rather than Cricetidae may have been more important during barn owl

**Table 2**

The diet of 261 barn owl pairs in Israel during the 2008 and 2011 breeding seasons. 51% of the diet of the barn owls in this study was comprised of Muridae rodents and 39.3% consisted of rodents from the family Cricetidae.

	Family	Prey species	Number of individuals	%	
Mammals	Vespertilionidae	<i>Pipistrellus</i> spp.	19	0.18%	
	Soricidae	<i>Crocodyra</i> spp.	557	5.15%	
	Cricetidae	<i>Microtus socialis guentheri</i>	4249	39.30%	
	Muridae	<i>Meriones tristrami tristrami</i>	1954	18.07%	
		<i>Rattus rattus rattus</i>	110	1.02%	
		<i>Mus musculus</i>	3444	31.86%	
		<i>Gerbilla</i> sp.	2	0.02%	
		<i>Acomys cahirinus</i>	3	0.03%	
		Spalacidae	<i>Spalax leucodon ehrenbergi</i>	66	0.61%
			Unidentified rodents	143	1.32%
	Aves		243	2.25%	
Reptilia	Sauria spp.	3	0.03%		
Insecta	Solifugae spp.	2	0.02%		
	Gyllotalipidae spp.	13	0.12%		
	Blattaria spp.	1	0.01%		
Gastropoda		2	0.02%		
Total			10,811		



**Fig. 4.** Relationships between the percentage of social voles ( $F_{1,198.5} = 13.60$ ,  $P = 0.0003$ ; a), house mice ( $F_{1,211.9} = 4.37$ ,  $P = 0.038$ ; b) and Tristram's jirds ( $F_{1,190} = 0.15$ ,  $P = 0.70$ ; c) in the diet and the number of fledglings per successful barn owl pair. Predicted values from the linear mixed model presented in the results are reported.

evolution in the Middle East, but this hypothesis would need to be tested. As found in the USA, barn owls were able to expand and exploit new regions once humans began to clear forested lands for agriculture (Colvin, 1985). Indeed, voles are abundant in agricultural fields. They have shorter legs, smaller eyes, and different mode of locomotion than Muridae (Edut and Eilam, 2004), possibly making them easier to capture, and potentially explaining why reproductive success is positively associated with voles and negatively with mice. Furthermore, by hunting mice and not voles, barn owls will need to catch three times the number of prey because mice weigh only one third of voles (14 g vs 45 g; Mendelsohn and Yom-Tov, 1999). In comparison to voles, jirds are faster and very large (79 g), with large eyes and large ears and hence probably beyond the optimal prey size.

Though barn owls in Europe are lighter colored at lower latitudes than those of the northern latitudes (Roulin, 2004a), variations of different color morphs coincide in Israel, varying from dark to white (Charter et al., 2012b). In both Israel and Switzerland (Charter et al., 2012b; Dreiss et al. 2012), the lighter colored morph has smaller wings and tail, which may assist in hunting the faster Muridae in rangeland. However, the dark morph has longer wings and tail, which are potentially more efficient when hunting the slower moving voles in crop fields using a slow gliding flight. If the lighter colored owls are better adapted to hunting Muridae, then why is the higher percentage of Muridae in these owls' diet not related to reproductive success?

It is possible that the increase in the number of fledglings when the owls consume more voles is due to the fact that the voles are found mainly in the agricultural areas close to the owls' nest boxes, are easier to capture, and their populations can be very large, allowing the owls to raise more young. In comparison, it is also possible that the lighter colored morph owls prey on more Muridae, which are located further away from the nest boxes, bordering rangeland, are more difficult to capture, and whose populations are smaller, therefore making it difficult for these owls to raise large broods. Future studies using GPS or other tags are needed to determine whether the different barn owl morphs hunt in different locations. Since vole populations fluctuate in Israel (Tores and Yom-Tov, 2003), darker colored barn owls may be able to raise large broods in years with large vole populations but may have reduced

reproductive abilities in years with low vole numbers; whereas light morphs are able to breed consistently by preying on the more stable Muridae populations in rangeland (Charter et al., 2012b). In regions where agricultural areas have increased, such as in Israel, darker barn owls may currently have a selective advantage over lighter colored owls, since voles are probably more abundant than they were thousands of years ago, because open fields have progressively replaced woodland and irrigation has reduced the surface occupied by dry habitats (Schiebel, 2013). The lighter colored barn owls may nonetheless still be able to coexist with the darker morph as long as the arid rangelands continues to exist around the agricultural areas and during years when voles are not abundant.

Further studies tracking the specific movements of barn owls with different color morphs are necessary in order to better understand not only why the different color morphs are not only morphologically different (wing and tail) and hunt different prey species (Charter et al., 2012b), but also to determine whether they hunt in different habitats and possibly also employ different hunting strategies (perch vs. active hunting).

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