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Barn owls as biological control agents: potential risks to non-target rare and endangered species

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Abstract

Rodent agricultural pests cause significant food loss every year. Attempts at mitigation via chemical pest control may cause secondary poisoning and harm non-target species. Biological pest control by bolstering barn owl *Tyto alba* populations through the provision of artificial nest boxes is in use in several countries. The national biological pest control project of Israel began in the early 1980s in the Mediterranean zone and was subsequently expanded to the northwestern Negev desert, including areas adjacent to nature reserves and natural sand dunes, a threatened habitat in Israel. We analyzed prey of barn owls in the northwestern Negev to determine whether owls preyed on non-target endemic, threatened rodents. A total of 14 632 prey items were collected from 95 nesting boxes between 2013 and 2016. We found that barn owls feed on protected and locally endangered species such as *Gerbillus andersoni allenbyi* (vulnerable – VU), *Gerbillus pyramidum* (VU), the endemic *Meriones sacramenti* (endangered) and *Gerbillus gerbillus* (critically endangered). These species constitute a significant proportion of barn owl diets (sometimes more than half of the prey items in a single nest box), especially in areas under 5 km from sand dunes, suggesting that bolstering the barn owl population may threaten locally endangered species. It could be hypothesized that agricultural crops serve as a resource for endangered species, allowing their numbers to increase, in which case their conservation status should be reassessed. However, extensive rodent trappings in agricultural fields in the region revealed <1% *Gerbillus* individuals, while in nearby dunes only gerbils were trapped. Insufficient data are available to assess whether or not *M. sacramenti* could have become a local pest. Our study highlights the risks that may be associated with the use of barn owls as rodent control agents in areas where natural open landscapes and nature reserves are interspersed with agricultural landscapes.

Introduction

Rodents are significant agricultural pests (e.g., Stenseth *et al.*, 2003); rodent agricultural damage includes a high abundance of nesting burrows in fields, gnawing on produce and banding of tree barks. Furthermore, rodents also harm and destroy agricultural equipment, such as water pipes (Poché *et al.*, 1982; Tobin & Fall, 2004). Studies have found that the extent of damage from rodents varies with the type of agricultural crop, habitat and region. Anticipated annual chronic crop damage of 5–15% can increase in years of rodent irruption up to 80% of yields. Therefore, control of rodents in agricultural landscapes is an important economic goal (Singleton *et al.*, 1999; Stenseth *et al.*, 2003; Hodara & Poggio, 2016).

Farmers commonly use pesticides to control rodent populations. The major drawback to this practice is that it may result in secondary poisoning of non-target organisms such as red fox *Vulpes vulpes* and raptors feeding on the poisoned rodents (Burns & Connolly, 1995; Hosea, Finlayson & Littrell, 2001; Eason, Ross & Miller, 2013; Geduhn *et al.*, 2015; Hindmarch & Elliott, 2018). There is currently a global effort to develop and implement holistic approaches to sustainable and environmentally friendly agriculture that involve, among others, the reduction in the use of toxic chemicals in agriculture (Hosking, Sullivan & Welsby, 1994; Kremen & Merelender, 2018). Smith (1919) defined classical biological control as controlling the population of pests with the help of their natural specific enemies. The development of biodiversity friendly agricultural practices includes the increased use of biological control agents which involve the control of a pest population by means of their natural predators or parasites, thus minimizing the toxic pesticide damage to the environment (Seastedt, 2015). It is now widely recognized that in order to minimize the risk of damage to the recipient ecosystem, biological control agents should be specific to the pest species (Mazzeo *et al.*, 2019).

The study of barn owl *Tyto alba* (Fig. 1) diet and notions of its contribution to controlling rodent pests date to the 19th century (Fisher, 1896): the first attempted introduction of barn owls to control invasive rats dates to 1899 and the second to 1922–1950, to New Zealand and to Lord Howe Island (Tasman Sea), respectively (Long, 1981). Both introductions failed, but were followed with successful ones to the Seychelles Islands in 1951–1952 to control the black rat *Rattus rattus* (Lever, 2010) and to Hawaii in the late 1950s and early 1960s to control rats in sugarcane plantations (VanderWerf *et al.*, 2007; Shiels *et al.*, 2014; Raine *et al.*, 2017). The barn owl is a generalist predator that feeds on a wide range of prey species, which makes it an unusual choice for biological control by modern standards. Indeed, the use of barn owls as biological control agents in the Seychelles and Hawaii was an unsuccessful venture that also has conservation repercussions due to barn owl consumption of non-target organisms (Henri, Milne & Shah, 2004; Samways *et al.*, 2010; Raine *et al.*, 2017).

The barn owl is a nocturnal predator with an almost cosmopolitan distribution (Bruce, 1999). Barn owl populations have declined in their native range in many parts of the world for a variety of possible reasons including agricultural intensification, use of chemical biocides and loss of nest sites associated with renovation of old buildings (e.g., Taylor, 1994; Askew, Searle & Moore, 2007; de Jong, 2009). Barn owls nest in cavities, in ruins and in old water wells, and as these habitats become increasingly rare, availability of nesting places becomes the limiting factor to their populations (de Jong, 2009). Therefore, beginning in the 1970s, provisioning of nest boxes was used as a means to increase barn owl populations for their conservation in the United States (Utah; Marti, Wagner & Denne, 1979), Switzerland (Altwegg *et al.*, 2003), Scotland (Klein *et al.*, 2007) and the Netherlands (de Jong, 2009). Concurrently, in search of an alternative to the use of pesticide, farmers in various parts of the world began examining the possibility of biological control by bolstering the population of native barn owls using the same technique. While barn owl prey includes arthropods, birds, reptiles, bats, amphibians and fishes (Glue, 1974; Herrera & Jaksić, 1980; Taylor, 1994; Carmona & Rivadeneira, 2006; Woolley, 2010; Hodara & Poggio, 2016), the barn owl has a distinct preference for rodents and shrews (Mikkola, 1983; Taylor, 1994; Shehab, 2005; Obuch & Benda, 2009; Comay & Dayan, 2018). A viable barn owl population could contribute to depressing pest populations directly by removal of individuals from the population and indirectly by affecting activity and foraging of their prey that, in turn, carry fitness costs (Richard, 2003). Barn owls are now being used for biological control in the United States (Hawaii, California, New Jersey, Florida, Oregon), Malaysia, Chile, Spain and Israel (Hegdal & Blaskieioi, 1984; Hafidzi, Zulkifli & Kamarudin, 1999; Wood & Fee, 2003; Gervais & Young, 2007; Meyrom *et al.*, 2009; Martin *et al.*, 2010; Motro, 2011; Muñoz-Pedreros *et al.*, 2010; Paz *et al*., 2011; Puan *et al*., 2011).

The rodent biological control project in Israel began in 1983 in Beit She'an Valley, in the northern Mediterranean region of Israel (Meyrom *et al.*, 2009). Bolstering the native barn owl population by placing nesting boxes increased predation pressure on rodents, and regular monitoring revealed that most of the rodent prey taken were indeed agriculture pests (Kahila, 1992; Aram, 1999; Charter *et al.*, 2009; Motro, 2011; Zaitzove - Raz, 2015). The barn owl project in the north of Israel was considered a success and became the first national level barn owl project globally. Subsequently, the project's geographical scope was expanded to other parts of the country (Motro, 2017).

In 2004, the barn owl biocontrol project reached the agricultural areas in the southern coastal plain and northwestern

Figure 1 A fledgling barn owl *Tyto alba* above a nesting box near Kibbutz Ruhama, August 16, 2016. Photographed by Michal Zaitzove - Raz.

Negev Desert (NWN) of Israel. However, the rodent fauna of this region includes not only pest species but also protected and endangered psammophiles (whose main habitat is sand dunes), including the endemic Buxton's jird *Meriones sacramenti* and Anderson's gerbil *Gerbillus andersoni allenbyi*; the former is an endemic species in Israel and the Sinai Peninsula while the latter is an endemic subspecies in Israel alone (Dolev & Pervolotzky, 2002). The sand dunes of the coastal plain and NWN are a unique ecological habitat that is being rapidly lost to urbanization, quarrying sand for construction, development and agricultural expansion (Dolev & Pervolotzky, 2002; Ahiron-Frumkin *et al.*, 2003; Perlberg *et al.*, 2006). Moreover, the spread of agriculture into the Negev desert enabled Mediterranean species to penetrate and establish populations in this area, sometimes displacing native and endemic species (Cohen, Shacham & Rothschild, 2011). Enhancing the sparse local barn owl population by providing nesting boxes involves the increase in predation pressure by a generalist predator and may contribute to the risk of threatened and endemic rodent populations.

The presence of agricultural areas close to the dunes could mean that the introduction of the barn owl for biological pest control will affect the sandy habitats as well as the agricultural fields. The combination of habitat loss and increased predation could then affect the populations of EN rodents where the dwindling sand dune habitat is in close proximity to agriculture and an enhanced barn owl population.

We studied the diet of barn owls in the southern coastal plain and NWN at varying distances from intact dunes, to ask to what extent barn owls prey upon psammophilic species and estimate how many of them are taken by barn owls in the entire study region.

Materials and methods

Research area

The study was carried out in Israel's southern coastal plain and NWN (Fig. 2). The region is a characterized by a sharp latitudinal precipitation gradient, from 514.5 (Negba, 31.66°N) to 204.1 (Beer Sheba, 31.25°N) mm rain per annum (Israel Meteorological Service, 2019) – a 60% decrease in precipitation over 48 km. Much of the land is cultivated and irrigated, with a few nature reserves and sand dunes; the latter are concentrated in the south and north–west of the study area. During the years 2013–2016, we mapped all barn owl nesting boxes in the region using GPS. We then studied the contents of 3–5 actively occupied nesting boxes per agricultural farm. Several different models of barn owl nesting boxes are used in the research area, and are usually installed about 4 m above the ground.

Pellet collection

Overall, 115 barn owl prey assemblages were collected between 2013 and 2016 from 95 active nesting boxes (the units of replication) in agricultural fields or near them. Barn owl nesting boxes were randomly selected in the first research year, and revisited in the following years, pending their occupation. In cases where the nest previously sampled was not occupied, a nearby occupied nest was chosen. Only 10 boxes were active consecutively between 2013 and 2016. Therefore, for each unoccupied nesting box, we sampled an adjacent one. The collected material included whole pellets as well as broken down pellet mass. The nesting boxes were cleaned during each visit (May–August), after the breeding season, to ensure that prey remains collected in the following visit were no older than the interval between visits (usually 1 year).

Material processing

Whole and fragmented owl pellets were first dry-sorted and then soaked in tap water to loosen them and minimize the loss of delicate and small prey remains such as arthropods and lizards. Vertebrate taxonomic identification and counts were based on skulls and mandibles, while for arthropods they were based on heads, chelicerae and limbs. We relied on morphology for taxonomic identification, using both the literature (Shalmon, Kofyan & Hadad, 1993; Qumsiyeh, 1996; Mendelssohn & Yom Tov, 1999) and two comparative collections: (1) that of the Steinhardt Museum of Natural History (Tel Aviv University); (2) a collection of intact dead individuals found in barn owl nests or animals that died at the I. Meier Segals Zoological Research Garden, Tel Aviv University. Prey was identified to the lowest taxonomic level possible, usually to the species level. Exceptions were *Meriones* sp. specimens that lacked tympanic bullae in areas of *M. sacramenti* and *M. tristrami* sympatry, and arthropods (n = 370, Tables 1 and 2).

Prey counts in each nest box were based on the minimal number of individuals (MNI) method: MNI is the highest number of conspecific elements. For instance, if one left and one right *Microtus guentheri* mandibles are found in the assemblage, one prey individual will be recorded because they may have originated from the same individual. However, if two right *M. guentheri* mandibles are found, two prey individuals will be recorded because they cannot originate from a single individual. Prey items that were not ingested by barn owls (such as decapitated individuals left to rot) were not counted to avoid counting the same individual twice (e.g., once as a skull and once as a decapitated corpse).

Pest and psammophilic rodents

The following rodents are considered pests under the Israeli law (Wildlife Protection Act, 1955 and its regulations): *Microtus guentheri*, *Meriones tristrami*, *Rattus rattus, Rattus norvegicus*, *Mus musculus* and *Spalax ehrenbergi* (superspecies, including four chromosomal species in Israel; Mendelssohn & Yom Tov, 1999). The following local rodent species were defined as psammophiles according to their descriptions and distributions (as in Mendelssohn & Yom Tov, 1999) and their local threat category was based on Dolev & Pervolotzky (2002): *Gerbillus pyramidum*

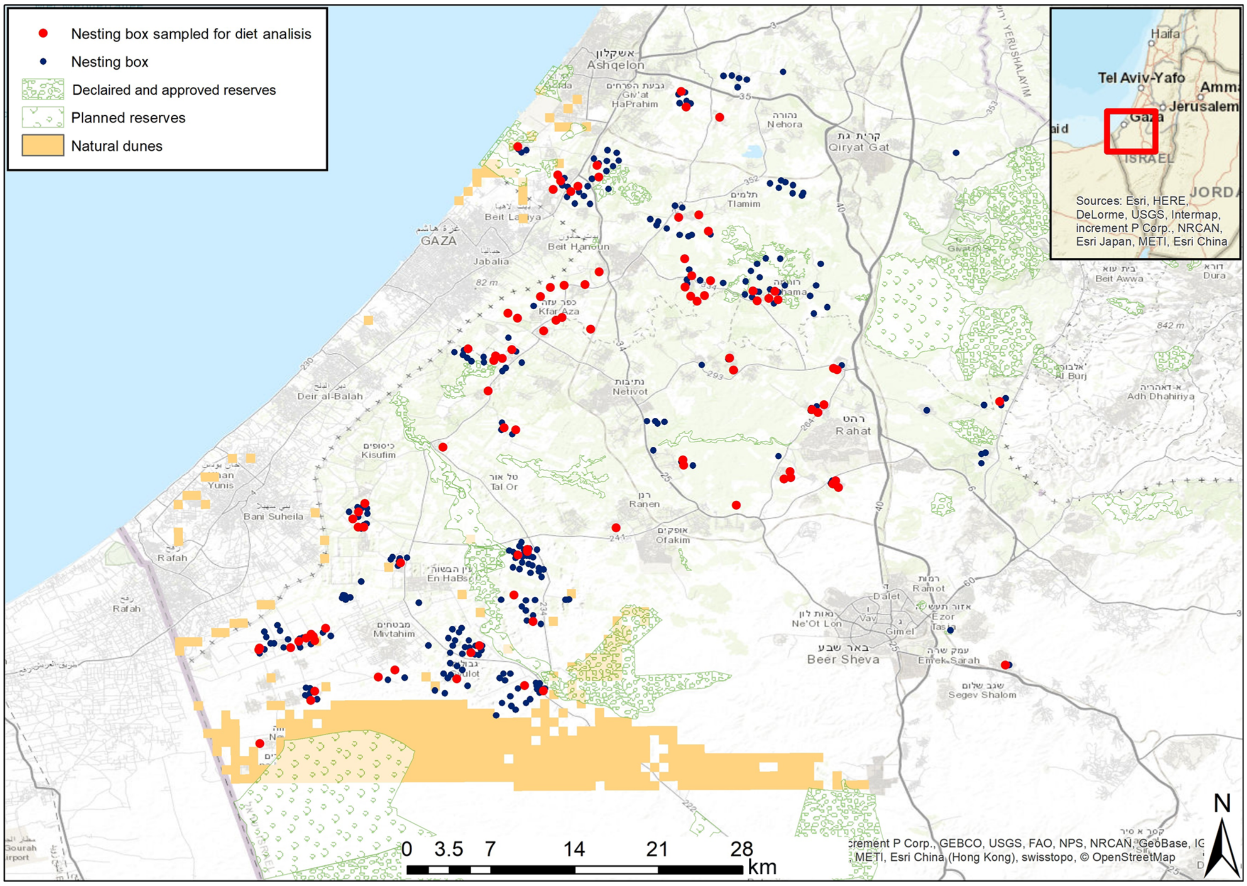

Figure 2 Nesting boxes in the northwestern Negev. In the entire study area, 324 nesting boxes were mapped) blue dots), out of which 95 nesting boxes were randomly selected for dietary analysis in 2013–2016 (red dots).

(Vulnerable – VU), *G. andersoni allenbyi* (VU), *G. gerbillus* (Critically Endangered – CR), *Meriones sacramenti* (EN), *Meriones crassus* (least concern – LC) and *Jaculus* spp. (either *J. vocator* or *J. schlueteri*; their threat category was assessed together as subspecies of *J. jaculus* as VU). The local threat criteria used by Dolev & Pervolotzky (2002) follow those used by the International Union for the Conservation of Nature and Natural Resources (Baillie & Groombridge, 1996).

Data analysis

Prey count data were summed from all the years studied per site (nest boxes) in a table in which the rows stood for the different nesting boxes and the columns stood for the prey taxa. We focused our analysis on mammal prey taxa (97% of prey MNI – 14 203 out of 14 632 prey specimens; Tables 1 and 2). We calculated the percentage of each mammal prey taxon MNI out of the total mammal MNI of every nesting box. Browning *et al.* (2016) found that individual barn owls in California hunt on average 152 rodents per chick and 165 rodents per adult per annum; multiplied with mass data for the prey species in their study (Vaughan, 1967; Verts & Carraway, 1998) and their relative abundance in Browning *et al.*'s (2016) study that amounts to annual intakes of 17 866 g per adult and 16 458 g per chick. Hence, in a nest with two adults and four chicks (the mean barn owl brood size in our study area; Peleg, 2018), a total of (2 × 17 866 + 4 × 16 458) 101 564 g biomass would be consumed every year. However, as barn owls in California weigh considerably more than those in the Negev (470 vs. 280 g; Paz, 1986; Haresign & Moiseff, 1988), we adjusted the expected biomass consumed according to the equations predicting the fresh food intake in carnivorous birds according to their body mass (equation 64 in Nagy, 2001). According to this calculation, birds of prey weighing 280 g would take 29% less food than birds of prey weighing 470 g, and thus we estimated the annual intake of a nest with two adults and four chicks as (101 564 × 0.71) 71 971 g. We calculated the expected number of prey individuals that would be taken from each taxon if four chicks were raised in each nesting box per annum, based on these estimates of annual biomass consumption intakes and using each taxon's mass (Mendelssohn & Yom Tov, 1999) and percentage of all mammalian prey items. This was done because we could not resample the same nesting boxes

Table 1 Mammalian prey taxa found in 95 nesting boxes in the northwestern Negev, sorted by descending raw abundance. *Meriones* spp. are either *M. tristrami* or *M. sacramenti*, whose threat category and legal status are different and thus were not summed for the purpose of estimating number of individuals taken per annum

Prey taxon	MNI	No. of nest boxes it occurs in	Mean relative abundance per nesting box[a]	Local threat category	Legal status	Individuals taken per annum, assuming 100% occupancy		Individuals taken per annum, assuming 31% occupancy	
						Min.	Max.	Min.	Max.
Microtus guenteri	4294	51	30.9% ± 41.4%	LC	Pest	78 933	167 417	24 469	51 899
Mus spp.	4077	94	34.7% ± 31.4%	LC	Pest	67 190	246 704	20 829	76 478
Meriones tristrami	3576	94	33.3% ± 25.2%	LC	Pest	91 489	168 074	28 362	52 103
Rattus rattus	586	50	5.2% ± 16.9%	LC	Pest	4863	15 103	1508	4682
Meriones sacramenti[b]	538	24	6.2% ± 13.8%	EN	Protected	23 795	38 466	7376	11 924
Crocidura spp.	393	75	3.3% ± 3.5%	VU	Protected	4415	26 781	1369	8302
Gerbillus andersoni allenbyi[b]	262	21	3.0% ± 7.5%	VU	Protected	8798	24 566	2727	7615
Gerbillus pyramidum	205	24	2.1% ± 5.2%	VU	Protected	6462	18 233	2003	5652
Meriones spp.	105	16	1.1% ± 2.7%	–	Varies	1096	10 347	340	3208
Spalax judaicus	67	32	0.4% ± 0.7%	LC	Pest	844	4216	262	1307
G. pyramidum/ G. andersoni allenbyi	52	9	0.4% ± 1.5%	VU	Protected	1214	4619	376	1432
Suncus etruscus	34	16	0.3% ± 0.8%	VU	Protected	483	4161	150	1290
Meriones crassus	11	1	0.1% ± 1.0%	LC	Protected	112	430	35	133
Gerbillus gerbillus	2	2	0.0% ± 0.1%	CR	Protected	45	166	14	51
Jaculus sp.	1	1	0.0% ± 0.1%	VU	Protected	31	125	10	39
Total	14 203	95				289 770	729 408	89 830	226 115

Legal status is according to the Israeli Wildlife Protection Act (1955) and its regulations (1976). See text for the method used to calculate the number of individuals taken per annum.

MNI, minimum number of individuals; abbreviations of local threat categories (Dolev & Pervolotzky, 2002): LC, least concern; VU, vulnerable; EN, endangered and CR, critically endangered.

[a]Expressed as the mean (±SD) percent of prey individuals out of the total mammalian prey individuals. The sampling units were the nesting boxes (total prey individuals were summed over several visits when necessary).

[b]Endemic to Israel alone (*G. andersoni allenbyi*) or to Israel and Sinai Peninsula (*Meriones sacramenti*; Mendelssohn & Yom Tov, 1999).

(because they were often not occupied) in subsequent years to directly calculate how many prey individuals are taken per annum. For instance, if a prey assemblage comprised a hundred identified mammals, 10 of which were *Meriones sacramenti* (weighing 120 g on average, and thus 1200 g overall), and the other 90 are all *Mus* sp. (weighing 16 g on average, and thus 1440 g overall), then *M. sacramenti* comprise 1200/(1200 + 1440) = 45.5% of the biomass consumed. Multiplying this percentage by the total annual intake of 71 971 g would lead us to an estimate of 32 747 g *M. sacramenti* taken per annum, which are equivalent to (32 747/120) = 273 *M. sacramenti* individuals taken by barn owls in this nesting box per annum. For these calculations, we used the mean weight of all congeneric species if the prey was only identified to the genus level (i.e., *Gerbillus andersoni allenbyi*/*G. pyramidum*).

After calculating the mean number of individuals taken per taxon per annum for the 95 nesting boxes sampled, we used automatic ordinary Kriging using the R package automap (Hiemstra *et al.*, 2009) to create a raster layer (cell size: 620.5 × 620.5 m) of the expected number of prey individuals taken per taxon per annum, as well as to interpolate the expected values for all nesting boxes that were mapped in the study region, including those that were not sampled for prey analysis. The raster layers were then summed to calculate two summary raster layers: one for all pest species and one for all psammophilic species (see above). In other words, this calculation answers the question: 'how many individuals of species X would have been taken from this point, if there was a nesting box here'? We did not account for potential impacts of competition (e.g., assuming that barn owl living in near-by nests would specialize on different prey species to avoid competition) or any environmental effects on species occurrence because testing such models was outside the scope of this study. Afterwards, we used the predicted and standard deviation values from the Kriging output to estimate the minimum (prediction minus standard

Table 2 Non-mammalian prey taxa found in barn owl pellets in the northwestern Negev, sorted by descending raw abundance

Prey taxon	MNI
Arthropods	265
Birds	133
Passer domesticus	14
Gryllotalpa gryllotalpa	12
Lizards	3
Galeodes sp.	2
Total MNI	429

MNI, minimum number of individuals.

deviation) and maximum (prediction plus standard deviation) number of prey individuals that would be taken under the assumption of four chicks per nesting box. Minimal estimates were only allowed non-negative values (i.e., when the prediction was lower than the standard deviation, the minimal number of prey individuals taken were assumed to be zero rather than a negative number). Finally, we summed the minimal and maximal estimates of the number of non-target organisms from all the nesting boxes in the region, to obtain a range estimate.

Data were analyzed using R version 3.5.3 (R Core Team, 2019) with RStudio version 1.1.453 (RStudio Team, 2015) and its packages raster (Hijmans, 2019; spatial analysis) and data.table (Dowle & Srinivasan, 2019); ArcGIS desktop version 10.4 (ESRI, 2016) and QGIS 3.6 (QGIS Development Team, 2019) were used to create maps. The R script used to analyze the data is given in Appendix S1.

We used a geographic information system (GIS) layer of soil types (Israeli Ministry of Agriculture & Rural Development, 2015) to infer the locations of sandy soils, and a GIS layer of land cover (HaMaarag, 2017) for a subset of only non-vegetated dunes or those covered with low, natural vegetation (grasslands or shrublands but not planted forests). Once the locations of intact dunes were determined, we calculated the distance of each nesting box sampled for diet analysis to the nearest intact dune. Next, we computed the correlation between the distance to the nearest intact dune and the percentage of psammophilic individuals found in each nesting box using a permutation correlation test through the R package RVAideMemoire (Hervé, 2019). Afterwards, we randomly sampled without replacement of 324 (the number of nesting boxes found) points from the study area, calculated their distances to the nearest dune and compared these distances with those of the nesting boxes from the nearest dune using a permutation *t*-test with 999 permutations, to examine whether the nesting boxes were located nearer or farther away from dunes than expected by chance. We repeated this process over a hundred iterations, resulting in 100 sets of 324 random points in the study area, and calculated the minimum, maximum, mean and standard deviation of the mean distance of these sets of random points to the nearest dunes.

Results

A total of 324 nesting boxes were mapped in the studied region (Fig. 2), and 95 of them were sampled for dietary

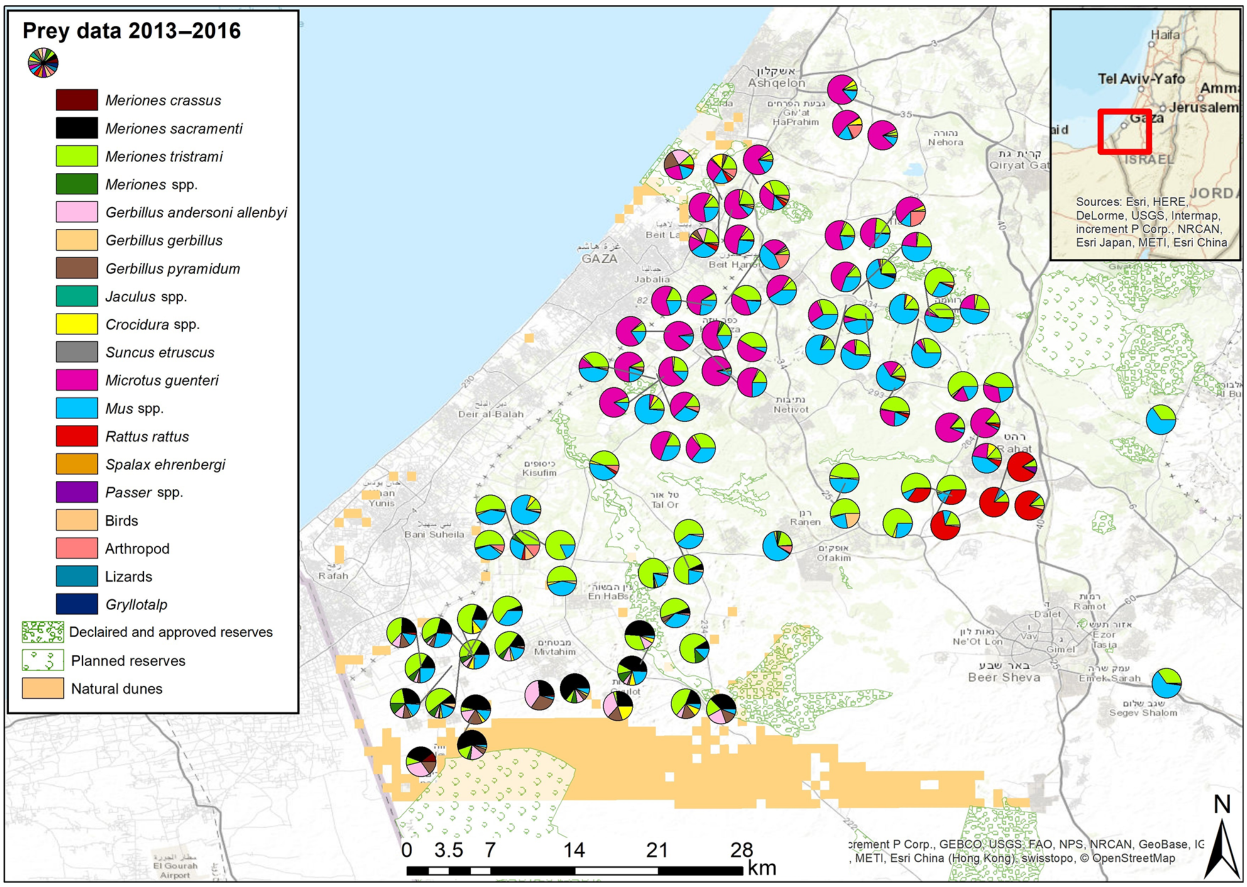

Figure 3 Barn owl prey data 2013–2016. Pie charts depicting the proportion of each prey species in barn owl diets from nesting boxes in NW Negev.

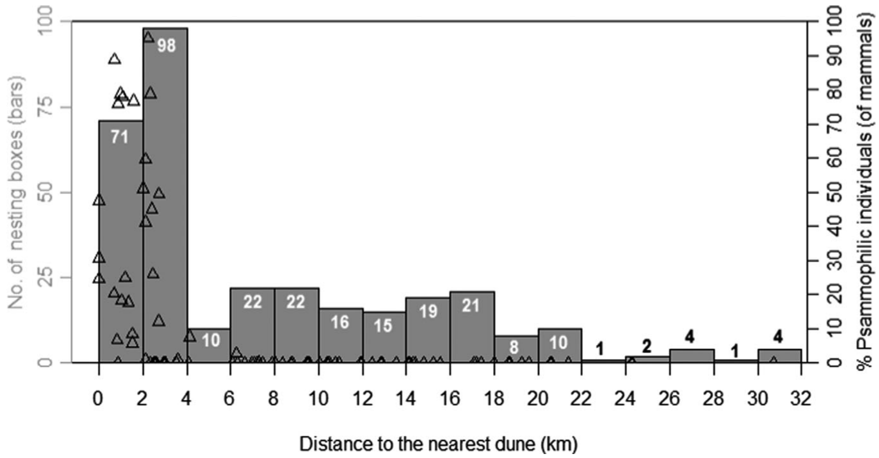

Figure 4 Bars: histogram of distance of the 324 nesting boxes mapped in the study area to the nearest natural dune. Of these, 95 nesting boxes were sampled for diet analysis. Triangles: percent of psammophilic prey individuals in barn owl *Tyto alba* diets out of all mammalian prey by distance to the nearest dune. See Materials and methods for definitions.

Table 3 Mean distance to the nearest dune – actual nesting boxes locations (total 324) compared to 100 sets of 324 random points in the study area

Variable	Nesting boxes	100 sets of random points
Minimum mean distance	–	8.4
Mean distance ± SD	7.6	9.7 ± 0.5
Maximum mean distance	–	11.3
Mean *P* value ± SD	0.011 ± 0.026	

All distances are in kilometers. Minimum, maximum and standard deviation of the mean relate only to the 100 sets of random points. *P* values are those of permutation *t*-tests with 999 permutations each.

analysis (Appendix S2; the geographical coordinates of the nesting boxes are not included because barn owls are a protected species in Israel; these are available from the corresponding author). Barn owls in our study exhibited a generalist diet that included not only mammals but also arthropods, birds and reptiles. Not a single mandible, maxilla or skull was left unidentified, at least to a coarse level (Tables 1 and 2). The majority of prey items and the focus of our study were rodents (13 776 of 14 632 MNI), followed by shrews (427 MNI; Table 1). All non-mammalian prey taxa combined numbered 429 MNI (Table 2). Of the rodents, pest species such as the Levant vole *Microtus guentheri* and house or Macedonian mice *Mus musculus/M. macedonicu*) were most common (Table 1), especially in the north and east of the study area (Fig. 3). However, psammophilic species such as *Gerbillus andersoni allenbyi* (VU), *Gerbillus pyramidum* (VU), the endemic *Meriones sacramenti* (EN) and *Gerbillus gerbillus* were also taken, especially near the dunes in the southwestern part of our study area (Fig. 3), and constitute up to 95% (58 out of 61) of the all mammalian prey MNI taken in a single nesting box. Figure 4 shows that over half (169) of the nesting boxes are located within 4 km from a natural sand dune. The mean distance between the nesting boxes and the nearest dune (7.6 km) was significantly lower (over 2 km nearer) than those of the 100 sets of 324 random points (Table 3).

In addition, the distributions of the psammophilic taxa as reflected in the barn owl diets (Fig. 5 and Fig. 1S in Appendix S3) are considerably more limited than those reported in the literature (Mendelssohn & Yom Tov, 1988; Dolev & Pervolotzky, 2002). Figure 5 depicts the possible range fragmentation for *G. pyramidium*, *G. andersoni allenbyi* and *M. sacrementi*, whereas Fig. 1S in Appendix S3 shows that no individuals of *G. gerbillus*, *M. crassus* and *Jaculus vocator/J. schluteri* were taken near the dunes of the southern Coastal Plain, but only near the dunes of the northwestern Negev and even there they were extremely rare.

Figure 6 depicts the spatial pattern of the pest (Fig. 6a) and psammophilic (Fig. 6b) prey taxa taken. The correlation between the percentage of psammophilic prey MNI and the distance to the nearest natural sand dune (Fig. 4) was highly significant (permutation Pearson correlation test with 9999 permutations: $r = -0.49$, $P < 10^{-4}$). An average of 29% of the prey MNI comprised psammophilic taxa in the analyzed 38 nesting boxes that were located fewer than 5 km away from the nearest natural sand dune; this figure is 41% for the analyzed nine nesting boxes that were located <1 km away from the nearest dune.

Table 1 summarizes the estimates of the minimum and maximum number of individuals removed from each species' populations, using the locations of the 324 mapped nesting boxes and assuming a predation rate of 71 971 g prey mass per annum. The minimum estimate of psammophilic rodent individuals preyed upon in the entire study region is 40 457 per annum assuming all 324 nesting boxes are occupied, or 12 541 if only 31% of them are occupied, as found by nesting box occupation surveys in the region during 2013–2016 (Peleg, 2018). Corresponding maximum estimates are 86 605 and 26 846 individuals per annum, respectively.

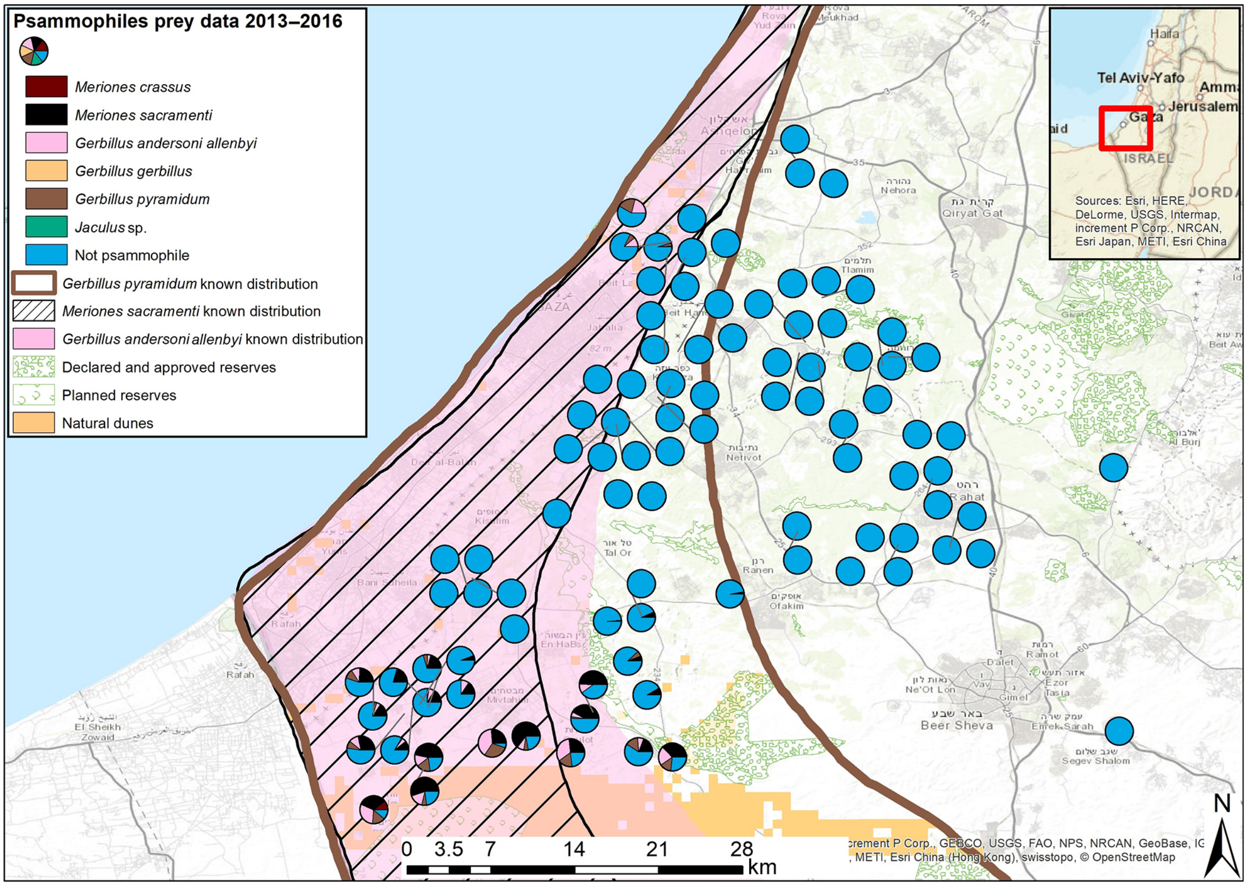

Figure 5 Distributions of the psammophilic rodents *Gerbillus pyramidium* (brown), *Meriones sacramenti* (black diagonal strips) and *G. andersoni allenbyi* (pink) from the literature (polygons; Mendelssohn & Yom Tov, 1988; Dolev & Pervolotzky, 2002), overlaid by barn owl prey data (pie charts). The distributions of these species in the literature are considerably wider than what found in the owl pellets, suggesting possible range fragmentation.

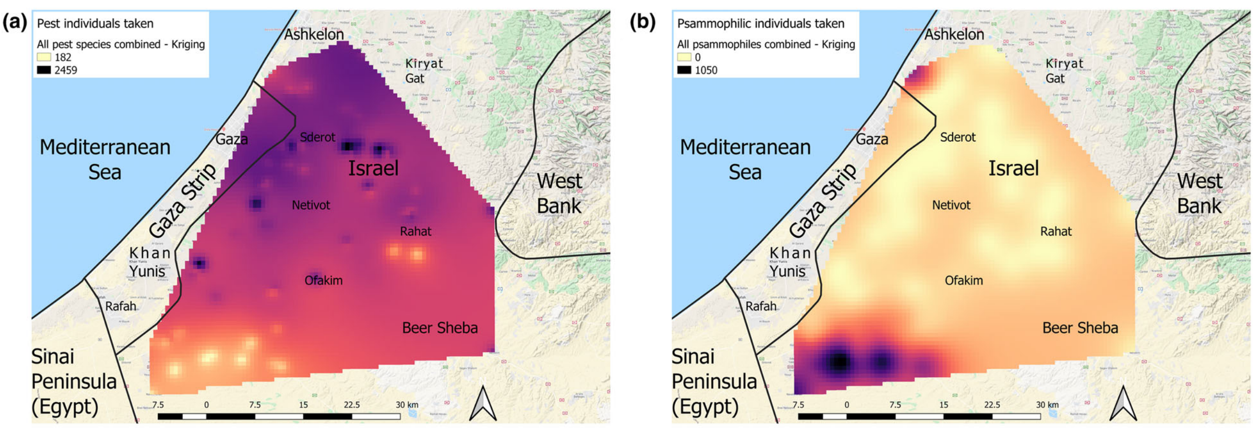

Figure 6 Total expected number of (a) pest and (b) psammophilic rodents taken by nesting barn owls *Tyto alba* per annum by the location of the nesting box, calculated using ordinary Kriging from 95 nesting boxes, without considering interactions among barn owls (e.g., competition) and ecological effects on prey taxa (e.g., predator avoidance behavior). See text for full details.

Discussion

Barn owl diet in the northwestern Negev (Tables 1 and 2) is very similar to studies conducted elsewhere in the world, where it was found that small mammals (rodents and shrews) comprised at least half of the prey items (and often up to 80–90% and even more), depending on the environment and the composition of the fauna (Taylor, 1994; Bruce, 1999; Obuch & Benda, 2009; Comay & Dayan, 2018). We found that barn owls, in the southwestern part of the research area, prey to a significant degree on non-target rodent species. Lovari Renzoni & Fondi (1976) reviewed articles about barn owl flight distances and found that barn owls may fly in a range of 800 m to 5 km. Marks *et al.* (2016) reviewed studies that revealed foraging flight distances of 1.6–5.6 km; both these estimates are in line with our results. Our results suggest that as barn owl populations increase, predation pressure on already threatened desert rodents may increase and could play a role in their possible decline or local extinction. Our results demonstrate that all of the psammophilic rodents preyed by barn owls in our study were found in nesting boxes fewer than 8 km away from the nearest dune and the overriding majority in distances of under 5 km (Fig. 4). Thus, we recommend that barn owl nesting boxes be placed no closer than 5 km from the nearest dune, thus reducing predation risk dramatically.

Enhancing barn owl populations by adding nesting boxes to control for rodent pests is a method used increasingly in various parts of the world. Agricultural areas harbor large populations of rodent pests which allow for the development of a robust barn owl population where nesting sites are not limiting. Barn owls, small mammal specialist, can switch their diet between the more common rodents and thus adapt to inter-annual differences in rodent pest abundances, a distinct advantage for pest control (Tores *et al.*, 2005; Obuch & Khaleghizadeh, 2011). However, the flexibility in diet implies that barn owls may prey on non-target prey from fairly diverse taxa (Bunn, Warburton & Wilson, 1982; Hodara & Poggio, 2016).

In most regions where barn owls are used to control rodent pest populations, agriculture occupies large tracts of the landscape and usually (apart from Israel), the farms that place nesting boxes to enhance barn owl populations comprise a small fraction of the general agricultural landscapes. In these areas, barn owl diets generally comprised almost entirely agricultural pests (Charter *et al.*, 2009; Meyrom *et al.*, 2009; Kross, Bourbour & Martinico, 2016). Labuschagne *et al.* (2016) carried out a literature review to assess the effectiveness of biological control by raptors for rodent pest management in agriculture, and found that most of the literature focused on barn owls but also that there are too few studies, and of those the minority showed scientific rigor. Many studies reported the food habits of barn owls in agricultural landscapes (e.g., Charter *et al.*, 2009; Kross *et al.*, 2016) but few reported actual impact on pest populations, crop damage and economic implications (but see Motro, 2011; Kan *et al.*, 2013; Browning *et al.*, 2016). Kan *et al.* (2013) found that in Beit-She’an Valley, a semi-arid agricultural environment in the north of Israel, alfalfa yields could increase from 13.03 (if no nesting boxes were in place) to 17.07 tons per hectare if the existing 58 barn owl nesting boxes would be placed optimally (compared to 14.38 tons per hectare under the current locations of the nesting boxes).

In areas where the barn owl’s efficiency as biological control agent was studied, the cosmopolitan barn owl is a native species (Paz *et al*., 2013). On the other hand, barn owls imported to Seychelles and Hawaii became problematic invasives. The barn owl was introduced to Mahe’ Island of the Seychelles and from there it spread and became abundant, posing a high-risk factor for sea bird chicks (Lever, 2010). Barn owls introduced to Hawaii Island, Moloka‘i, O‘ahu and Kaua‘in established and became common on all the main Hawaiian Islands; they have also been seen in the Northwest Hawaiian Islands and are implicated in contributing to the elimination of six endemic sea bird species (Funasaki *et al.*, 1988). While in the Seychelles and Hawaii, the barn owl is invasive and attempts are being made to eradicate it, it would be appropriate to remember that it is an effective generalist predator which can have an appreciable impact on its prey populations even where it is a native species (Sergio *et al*., 2008; Labuschagne *et al*., 2016).

A key challenge faced in Israel is balancing between the advantages and risks of rodenticide use and that of rodent biological control; it appears that both methods carry the risk of harming non-target organisms. Rodenticides could harm various predators by secondary poisoning, and barn owls can hunt non-target prey species. Local farmers report rodent damage to crops even in areas where no pest species (as defined by Israeli law: *Mictorus guentherti*, *Mus musculus*, *Meriones tristrami*, *Rattus rattus* and *Spalax ehrenbergi*) except for mice *M. musculus* are found. Thus, it could be hypothesized that the local psammophilic species may have become agricultural pests in this region, and this, in turn, could contribute to their population increase. Nevertheless, rodent trappings conducted by the Israeli Ministry of Agriculture and Rural Development in agricultural fields in our study area (Motro, 2008, 2009; Motro & Gendler, 2010; Motro, Goldin & Rimon, 2011; Motro, Rimon & Goldin, 2012; Motro *et al.*, 2013; Motro, Gendler & Muller, 2014; Motro *et al.*, 2015, 2016, 2017, 2018, 2019) in the years 2008–2019 found that only one individual of 304 was a psammophile (*G. andersoni allenbyi*), while a study in dunes in the northwestern part of our study area found 19 out of 19 trapped individuals were *G. andersoni allenbyi* or *G. pyramidum* (HaMa’arag, unpubl. data). Thus, there is no evidence of the local psammophilic species exploiting the agricultural lands. As *Meriones sacramenti* is rarely trapped, it is difficult to ascertain whether or not it may have become a pest species.

Moreover, our study reveals a significant spatial gap for *G. andersoni allenbyi*, *G. pyramidum* and *M. sacramenti* between their populations in the southern coastal plain and those in the NWN (Fig. 5). In addition, *G. gerbillus*, *M. crassus* and *Jaculus* sp. were not found in nesting boxes located in the northern part of their known distributions

(Mendelssohn & Yom Tov, 1988; Dolev & Pervolotzky, 2002); for *Jaculus* sp., this includes all nesting boxes found in the coastal plain – a significant part of its known distribution (Fig. 1S in the Appendix S3). This suggests that most of the agricultural matrix in this region is not habitable for the psammophiles. In this case, it is unlikely that agriculture is bolstering the populations of threatened and EN species; it is entirely possible that the conservation status of these species may be even more dire due to their fragmented or more limited range.

Results of our study show that endemic and EN psammophilic species comprise a significant percentage of barn owl diets adjacent to natural sand dunes, and that the sum total of individuals removed from their populations is high. Moreover, our results suggest that these populations may be declining due to habitat transformation into agriculture in this area. This study calls for comprehensive research on the population ecology of the native VU and EN species in agricultural and natural landscapes in this region that is crucial to determine the status of these species and for proof that barn owl predation is indeed a major risk factor. Until such a study is conducted, we advocate caution in the use of barn owls for biological control in agricultural areas adjacent to the habitat of the species at risk. This approach should be taken also in other parts of the world where endemic, EN or protected rodent species may be harmed by increased predation risk from barn owls used for biological control.

The scientific literature, where available, focuses on the effectiveness of barn owls in biological control (e.g., Van Vuren, Moore & Ingels, 1998); it does not address the possible harmful effect of a growing barn owl population on non-target organisms. To our knowledge, our study is the first attempt to gain insight into this issue. The research results suggest that enhancing the barn owl population in the north-western Negev may further endanger the already threatened populations of native gerbillids. Our study highlights the risks that may be associated with the use of barn owls as rodent control agents in areas where natural open landscapes and nature reserves are interspersed with agricultural landscapes.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. R script: estimating how many psammophilic individuals are taken per annum.
Appendix S2. Total prey individuals per species per nesting box.
Appendix S3. Figure 1S: Distributions of *Gerbillus gerbillus*, *Jaculus jaculus* and *Meriones crassus*.