



The biogeography of diet diversity of barn owls on Mediterranean islands

Franc Janžekovič | Tina Klenovšek 

Faculty of Natural Sciences and Mathematics, University of Maribor, Maribor, Slovenia

Correspondence

Tina Klenovšek, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, 2000 Maribor, Slovenia. Emails: tina.klenovsek@um.si

Funding information

Javna Agencija za Raziskovalno Dejavnost RS, Grant/Award Number: P1-0403

Handling Editor: Lisa Manne

Abstract

Aim: Following the classical MacArthur-Wilson island equilibrium model of species richness, we hypothesize that island size and isolation affect prey composition and diet diversity of predators on islands. We used the barn owl as a model predatory organism that is known for feeding and habitat flexibility and explored the patterns of its diet on Mediterranean islands in relation to the island biogeography and human population density.

Location: Mediterranean Islands.

Taxon: Barn owl (*Tyto alba*) and its prey.

Methods: Data on taxonomic composition of the barn owl diet were obtained from pellets (Adriatic island of Korčula) and from published studies performed on 18 Mediterranean islands. For each island, diet diversity indices were calculated and correlated with island area, linear distance from the mainland, human population size and density, and geospatial trends.

Results: Murinae mice and rats were the dominant prey. The proportion of birds and reptiles consumed was 5 and 18 times higher, respectively, than in Europe in general. Diet diversity correlated with island size, but not island isolation. Island size was also a good predictor of the proportions of the vertebrate prey. Human population density and longitude had no effect on diet diversity.

Main conclusions: Diet diversity of the barn owl on Mediterranean islands only partly followed the island biogeography theory. Diet diversity was greater on the larger Mediterranean islands. However, a more diverse diet did not mean a higher number of taxa, but a wider range of abundant and evenly represented taxa. The smaller the islands, the more birds and reptiles were consumed, compared to higher proportions of mammals on the larger islands. These findings support the idea of barn owls' feeding flexibility and opportunistic predator behaviour. Despite the barn owl being a synanthropic bird, urbanization had no influence on its diet diversity. Also island isolation had no significant effect.

KEYWORDS

birds, diet, island biogeography, MacArthur-Wilson equilibrium theory, pellets, prey, *Tyto alba*

1 | INTRODUCTION

The barn owl, *Tyto alba* (Scopoli, 1769) is an excellent model predatory organism for exploring patterns of dietary diversity, owing to its widespread distribution, habitat generalism and feeding flexibility, as well as methodologically, because of the ease of diet analysis from pellets. Its diet is well known, as numerous quantitative studies with primary data and some meta-analyses have been published on this topic (e.g. Bontzorlos, 2009; Jaksić, Seib, & Herrera, 1982; Milana, Lai, Maiorano, Luiselli, & Amori, 2016; Romano, Séchaud, & Roulin, 2020; Roulin, 2015, 2016a, 2016b; Roulin & Dubey, 2012 and literature mentioned therein). It is the most widely distributed species of owl found in a great variety of habitats, not surprisingly, also on continental and oceanic islands (Bruce, Christie, & Kirwan, 2014). Still, knowledge about the prey diversity of the barn owl on islands is inadequate and fragmentary. So far, only individual islands or archipelagos in the Mediterranean or elsewhere have been investigated (e.g. Amori, Rizzo Pinna, Sammur, & Luiselli, 2015; Guerra, García, & Alcover, 2014; Siverio, Siverio, Rodríguez, & Rodríguez, 2010).

The Mediterranean Basin, with more than 5,000 islands and islets, is a global biodiversity hotspot with high species richness and endemism (Vogiatzakis, Mannion, & Pungetti, 2008). Mediterranean islands vary considerably in size, shape, spatial arrangement, climate and distance from the mainland (Vogiatzakis & Griffiths, 2008). All these, together with geological age, temporal isolation from the mainland and human colonization, influence the islands' biotas (Vogiatzakis & Griffiths, 2008; Whittaker, 1998). Nevertheless, following the classic MacArthur-Wilson (1963, 1967) island equilibrium model of species richness, island area and isolation are two principal characteristics of island ecosystems (Lomolino, Brown, & Sax, 2010). Larger islands that are closer to the mainland are expected to support greater diversity of species compared to smaller and more distant islands. More specifically, the size of an island can be linked to habitat diversity, productivity and length of food chains (Holt, 1996; Schoener, 1989; Terborgh, 2009), which means that larger islands tend to have more distinct habitats, greater productivity, larger populations and longer food chains (Holt, 2009). Less isolated islands experience greater immigration from the mainland or neighbouring islands than more distant ones.

The barn owl is an opportunistic feeder that predaes mostly on small mammals and to a lesser extent on birds, lizards, amphibians, insects, etc. (Roulin, 2020; Taylor, 1994; Tores, Motro, Motro, & Yom-Tov, 2005). Prey selection on islands is limited by the presence of potential prey species and varies between individual islands. Although numerous factors can influence prey selection in owls (Comay & Dayan, 2018; Romano et al., 2020), we hypothesize that on islands the island's size, distance from the mainland and, as a proxy for urbanization, human population density also affect the pattern of the barn owl's prey composition. In this study, we present primary data on the diet of the barn owl on the Adriatic island of Korčula (Croatia) and include these results in a meta-analysis of available data on the

barn owl diet across Mediterranean islands. The pattern of the owl's diet variability on Mediterranean islands is additionally evaluated in the context of island biogeography and human population density.

2 | MATERIALS AND METHODS

2.1 | Island of Korčula

For the study of diet composition of the barn owl on the island of Korčula, pellets of the barn owl were collected by the first author in August of 2002, 2003, 2004 and 2013 (Table S1; data partly published in Janžekovič & Kryštufek, 2005). Collection sites were abandoned buildings at two locations near the town of Smokvica. In the years of collection, a large proportion of the area was covered with Mediterranean shrub. The rest was cultivated with vineyards and small fields with crops, which were harvested between February and July. Only whole pellets were used for the calculations and were dissected individually. The identity and number of small mammals was determined on the basis of skulls, mandibles and teeth (Kryštufek & Janžekovič, 1999; Niethammer & Krapp, 1990). Avian skulls and synsacrams were used to estimate the number and identity of the birds to the order level. Pellet content data were based on the minimum number of individuals (MNI). The relative importance of prey taxa in the owl's diet was expressed as a percentage of the number of individuals (or biomass) for each prey taxon versus the total number of individuals (or biomass) of all prey taxa. To calculate the biomass, the body mass of prey species reported in Kryštufek and Janžekovič (1999) was used. Differences in proportions of prey taxa among the collection years (except 2002) were tested with a Kruskal-Wallis H test. All material is deposited at the Faculty of Natural Sciences and Mathematics, University of Maribor.

2.2 | Mediterranean islands

For the meta-analysis of barn owl prey diversity on Mediterranean islands, we searched for the relevant literature entries in WoS, Scopus, ScienceDirect, Google Scholar and Google, using the following key words: Mediterranean islands, *Tyto alba*, Mammalia, Aves and Reptilia. We obtained data from 17 published studies of the barn owl diet performed on 18 Mediterranean islands (see Table S3 and references in Supporting Information). The research area extended from the Balearic Sea in the west to the Aegean Sea in the east (Figure 1). The islands varied in area size from the smallest, Espartar with 0.2 km², to the largest, Sardinia with 24,090 km² (Table 2). The linear distance of islands from the mainland ranged from 40 m (Euboea) to 250 km (Sardinia). Islands also varied extensively in human population size (Table 2). Population size was in high correlation ($r = 0.96$, $p < 0.0001$) with island area; therefore, average human population density (No. of inhabitants per km² of island area) was added. Data on island area size, distance and human population were tested for normality of distribution (Kolmogorov-Smirnov test for normality).

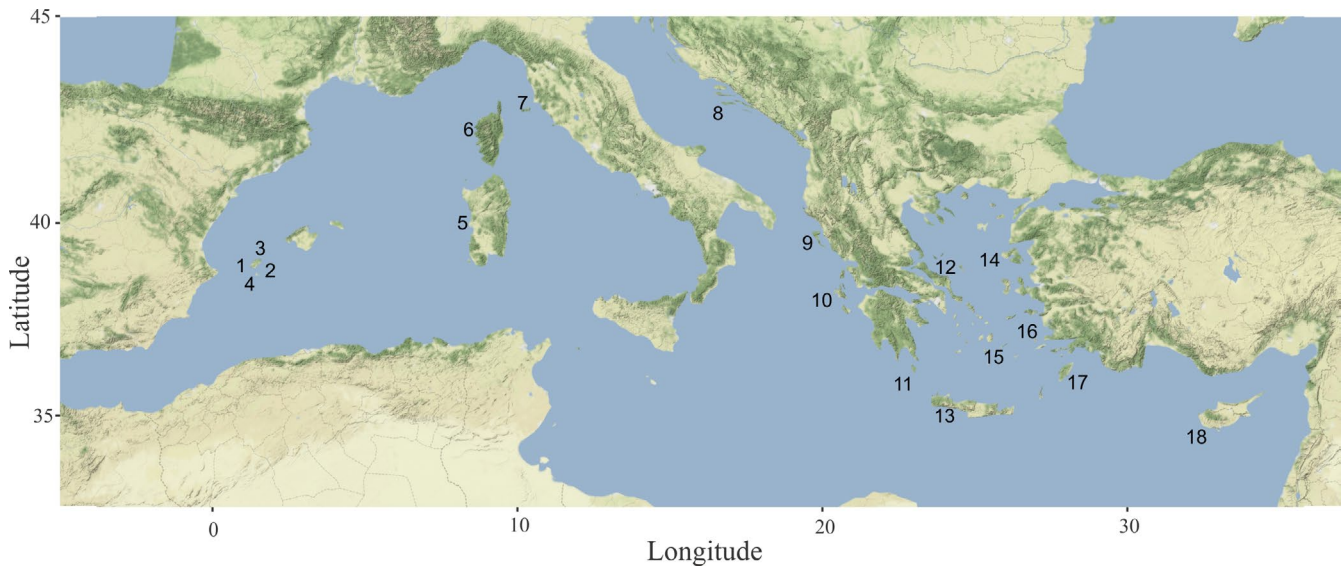


FIGURE 1 Map of the Mediterranean Sea. The islands' markings are in Table 2

TABLE 1 Results of the analysis of *Tyto alba* diet from the Adriatic Island of Korčula

Prey	Mean prey mass	Number		Biomass	
	g	n	%	g	%
<i>Crocodyra suaveolens</i>	5	108	16.2	540	3.9
<i>Pipistrelus pipistrelus</i>	9	1	0.1	9	0.1
<i>Apodemus sylvaticus</i>	19	127	19.0	2,413	17.5
<i>Mus musculus</i>	20	376	56.4	7,520	54.4
<i>Rattus rattus</i>	63	52	7.8	3,276	23.7
Aves	20	3	0.5	60	0.4
Total		667	100	13,818	100

To achieve normality, island area and human population data were log transformed (\log_{10}) and distance data square root transformed.

2.3 | Diet diversity

Data on the taxonomic dietary composition of barn owls on each island were used to calculate seven biodiversity or diet diversity indices (Legendre & Legendre, 2012): (1) species richness - S , the number of taxa; (2) number of specimens - n ; (3) Margalef diversity index - $R1$, where $R1 = S-1/\ln(n)$; (4) Menhinick diversity index - $R2$, where $R2 = S/\sqrt{n}$; (5) Evenness index - $E1$, where $E1 = H'/\ln(S)$; (6) Shannon-Weaver diversity index - H' and (7) Simpson's diversity index - λ . H' was calculated as $H' = -\sum_{i=1}^R p_i \ln(p_i)$, where p_i is the proportion of prey category (taxa) in the diet. Food Niche Breadth (FNB) was also calculated according to Levins (1968): $FNB = 1/(\sum p_i^2)$, which is the inverse value of the Simpson's index $1/\lambda$, where p_i is the proportion of prey taxon i in the owl's diet. The FNB range is from 1 to n (number of prey taxa), with larger values indicating a broader niche dimension. The Simpson's index ranges from 0 to 1; smaller values

indicate greater diversity. All indices were tested for normality. Only the number of specimens (n) was not normally distributed and was log-transformed.

2.4 | Statistical analyses

Relations among diet diversity indices as dependent variables and island area, linear distance from the mainland, human population size and human population density as independent variables were analysed using Pearson correlation analysis and simple linear regression. Polynomial regression was used to assess and illustrate possibly nonlinear relationships between proportions of mammals, birds or reptiles and island area. Diet diversity indices and proportions of vertebrate classes were checked for a spatial trend along longitude with the correlation analysis and for the presence of spatial autocorrelation with Moran I . Also the relationships between diet diversity indices were analysed with the Pearson correlation and tested for significance. The significance level for rejecting the null hypotheses was set at $p = 0.05$.

TABLE 2 Area, distance from the mainland, human population size, human population density, diversity indices and frequency of the major taxa in *Tyto alba* prey from the 18 Mediterranean islands

Island	Area [km ²]	Distance [km]	Human population size (N)	Human popul. density [N/km ²]	S	n	R1	R2	E1	H'	λ	FNB	Mammalia %	Aves %	Reptilia %	Insecta %	Others %
1-Espartar	0.2	87	10	50.0	4	32	0.87	0.71	0.68	0.94	0.49	2.05	25.0	65.6	9.4	0.0	0.0
2-Espalmdador	2	101	100	50.0	14	904	1.91	0.47	0.50	1.33	0.45	2.22	90.6	8.2	1.1	0.0	0.1
3-Ibiza	571	88	132,637	232.3	11	6,977	1.13	0.13	0.63	1.50	0.28	3.57	91.6	6.0	2.2	0.1	0.1
4-Formentera	82	98	11,545	140.8	10	292	1.59	0.59	0.70	1.61	0.24	4.14	59.3	39.7	0.7	0.3	0.0
5-Sardinia	24,090	250	1,663,000	69.0	7	208	1.12	0.49	0.73	1.42	0.29	3.48	98.5	1.4	0.0	0.0	0.0
6-Corsica	8,680	86	322,120	37.1	11	7,012	1.13	0.13	0.70	1.69	0.22	4.58	95.6	4.1	0.1	0.3	0.01
7-Elba	223	11	31,527	141.4	8	327	1.21	0.44	0.63	1.31	0.35	2.84	90.8	7.0	0.0	2.1	0.0
8-Korčula	276	24	16,182	58.6	6	667	0.77	0.23	0.65	1.17	0.39	2.59	99.5	0.4	0.0	0.0	0.0
9-Corfu	575	5	107,891	187.6	15	3,102	1.74	0.27	0.63	1.71	0.29	3.39	90.2	1.8	1.1	3.5	3.5
10-Cefalonia	786.6	37	35,800	45.5	7	84	1.35	0.76	0.78	1.52	0.29	3.39	91.6	5.9	0.0	2.38	0.0
11-Antikythera	20	59	70	3.5	8	106	1.50	0.78	0.65	1.36	0.34	2.95	73.6	16.0	10.4	0.0	0.0
12-Euboea	3,684	0	198,130	53.8	11	125	2.07	0.98	0.78	1.87	0.20	5.11	92.8	4.0	0.8	2.4	0.0
13-Crete	8,336	96	623,000	74.7	15	3,981	1.69	0.24	0.54	1.46	0.36	2.76	98.5	0.8	0.0	0.7	0.0
14-Lesbos	1632.8	16	86,436	52.9	12	870	1.63	0.41	0.77	1.92	0.19	5.12	95.5	4.1	0.0	0.3	0.0
15-Astypalaia	97	86	1,330	13.7	4	128	0.62	0.35	0.71	0.99	0.44	2.27	86.0	0.0	0.0	14.1	0.0
16-Kos	295	5	33,388	113.2	10	942	1.31	0.33	0.77	1.78	0.20	4.91	78.6	21.2	0.0	0.0	0.3
17-Tilos	65	58	780	12.0	7	166	1.17	0.54	0.84	1.64	0.21	4.66	88.6	7.8	0.6	3.0	0.0
18-Cyprus	9,251	79	788,500	85.2	6	3,312	0.62	0.10	0.52	0.93	0.19	5.26	96.1	2.96	0.0	0.9	0.0

3 | RESULTS

3.1 | Island of Korčula

132 whole pellets (and bones from pellet remains) were analysed. No significant differentiation was noted in the frequency of occurrence of prey taxa among collection years (Kruskal–Wallis test: $H = 1.63$, $df_1 = 2$, $df_2 = 18$, $p = 0.442$). Therefore, the material from different years was pooled. A total of 667 prey items were identified, with a mean of 3.1 prey items per pellet (Table 1 and Table S1). The main prey species were small mammals, accounting for 99.6% of the total number. Among these, murines (Muridae) were the most frequent, accounting for 83.2% of the total number and 95.6% of the total biomass. At the species level, the dominant prey was the house mouse (*Mus musculus*) and among non-murine species, the lesser white-toothed shrew (*Crocidura suaveolens*). Besides non-volant terrestrial small mammals, remnants of three Passeriformes birds and one bat were also found. The food niche breadth was relatively narrow (FNB = 2.59). From 7 potential non-volant terrestrial small mammal prey species on Korčula (Janžekovič & Kryštufek, 2005), 4 were detected (Table S2). The Shannon–Weaver diversity index was also relatively low ($H' = 1.17$), reflecting low diversity and evenness of prey species (Table 2).

3.2 | Mediterranean Islands

An overview of the barn owl diet on 18 Mediterranean islands is shown in Table 2 and Table S3. A total of 29,172 prey items were identified, with 4 to 15 taxa per island (on average, 9.2 taxa). Mammals and birds (on average, 85.7% and 10.9% of the total number of

taxa, respectively) were the most frequent prey and present in the owls' diet on all the islands investigated. In general, murine species (Muridae) were the most numerous (61.2%). On some islands, owls also preyed on reptiles (on average, 1.47% of total taxa), amphibians, insects (on average, 1.77% of total taxa) and even molluscs.

There were no significant correlations between diet diversity indices or vertebrate proportions and longitude ($R^2 < 0.23$, $p > 0.1$). Also spatial autocorrelation was not present (Moran $I < 0.3$, $p > 0.2$).

3.3 | Island size and isolation

Barn owl diet diversity for the 18 Mediterranean islands was statistically significantly correlated with island area (Table 3). With increasing island area, the Food Niche Breadth (FNB) increased (positive r and $z = 0.11$) and Simpson's diversity index (λ) decreased (negative r and $z = -0.047$), which means that larger islands obtained smaller λ and larger FNB values and that on larger islands, the owl's diet was more diverse (Figure 2a). Correlations among diversity indices and distances from the mainland showed the expected negative trend (Figure 2b), with lower diet diversity on more distant islands, but none were statistically significant (Table 3).

More specifically, the proportion of vertebrate classes in the barn owl diet also showed an important pattern of correlation with island area. The proportions of birds and reptiles were in relatively strong and significant negative correlation with island area (birds: $r = -0.68$, $p = 0.002$; reptiles: $r = -0.63$, $p = 0.005$). In contrast, a strong positive correlation was revealed between island area and the proportion of mammals ($r = 0.74$, $p < 0.001$). This means that on smaller islands, more birds and reptiles but fewer mammals were consumed by owls than in larger islands. The relations between the proportions of the

TABLE 3 Pearson correlation coefficients and probability (p) between diversity indices and environmental variables in *Tyto alba* prey on Mediterranean islands. Significant correlations ($p < 0.05$) are in bold

	Log Island Area	Sqr Distance from mainland	Log Human population size	Human population density
S	0.24	-0.22	0.33	0.39
	$p = 0.333$	$p = 0.382$	$p = 0.187$	$p = 0.107$
n	0.41	0.16	0.47	0.45
	$p = 0.088$	$p = 0.523$	$p = 0.049$	$p = 0.061$
R1	0.03	-0.34	0.06	0.12
	$p = 0.920$	$p = 0.168$	$p = 0.826$	$p = 0.651$
R2	-0.36	-0.19	-0.43	-0.40
	$p = 0.146$	$p = 0.441$	$p = 0.073$	$p = 0.103$
E1	0.08	-0.27	-0.01	-0.28
	$p = 0.753$	$p = 0.276$	$p = 0.969$	$p = 0.260$
H'	0.08	-0.06	0.11	0.29
	$p = 0.764$	$p = 0.824$	$p = 0.665$	$p = 0.242$
λ	-0.65	0.29	-0.62	-0.17
	$p = 0.004$	$p = 0.248$	$p = 0.006$	$p = 0.501$
FNB	0.55	-0.32	0.53	0.07
	$p = 0.017$	$p = 0.204$	$p = 0.025$	$p = 0.795$

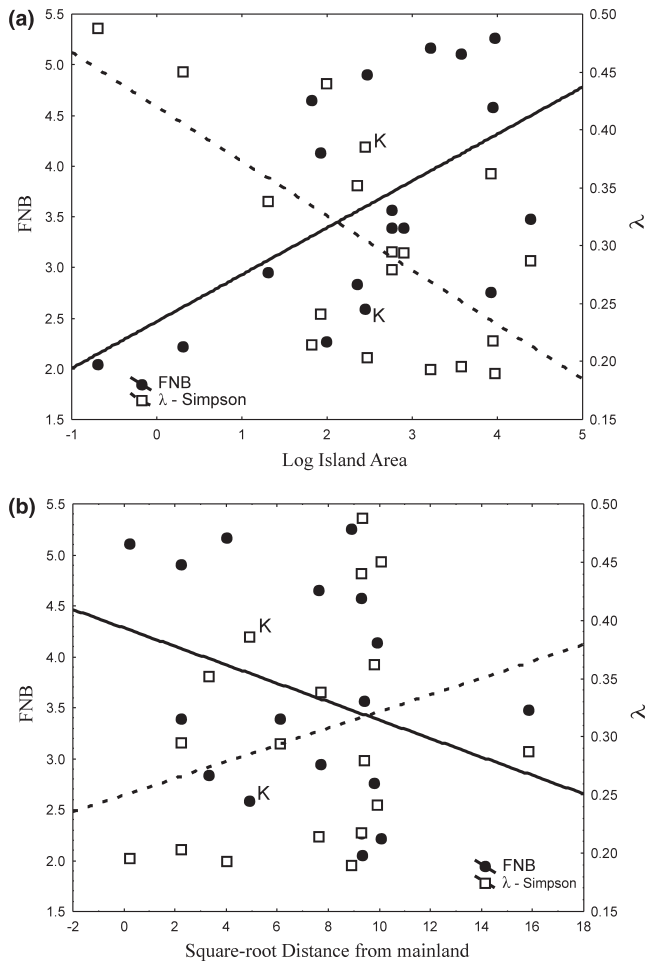


FIGURE 2 Effect of island area (a) and distance from the mainland (b) on the Food Niche Breadth (FNB) and Simpson diversity index (λ) in *Tyto alba* prey on the Mediterranean islands. The Island of Korčula is marked with the letter K

vertebrate classes and island area were best described by quadratic polynomial regressions (Figure 3a,b) (mammals: Multiple $R^2 = 0.64$, $F_{2,15} = 13.20$, $p = 0.0004$; birds: Multiple $R^2 = 0.58$, $F_{2,15} = 10.37$, $p = 0.0015$; reptiles: Multiple $R^2 = 0.48$, $F_{2,15} = 6.82$, $p = 0.0078$). There were no significant correlations between vertebrate proportions and the islands' distance from the mainland.

3.4 | Human population

Human population size on the Mediterranean Islands in the study was highly correlated with the owl's diet diversity (FNB and λ indices) and the number of prey specimens (n) (Table 3). This effect was not confirmed for human population density (Table 3).

3.5 | Correlations among indices

There was a very strong negative correlation between FNB and λ indices of diet diversity (Table 4). The number of taxa (S) was highly

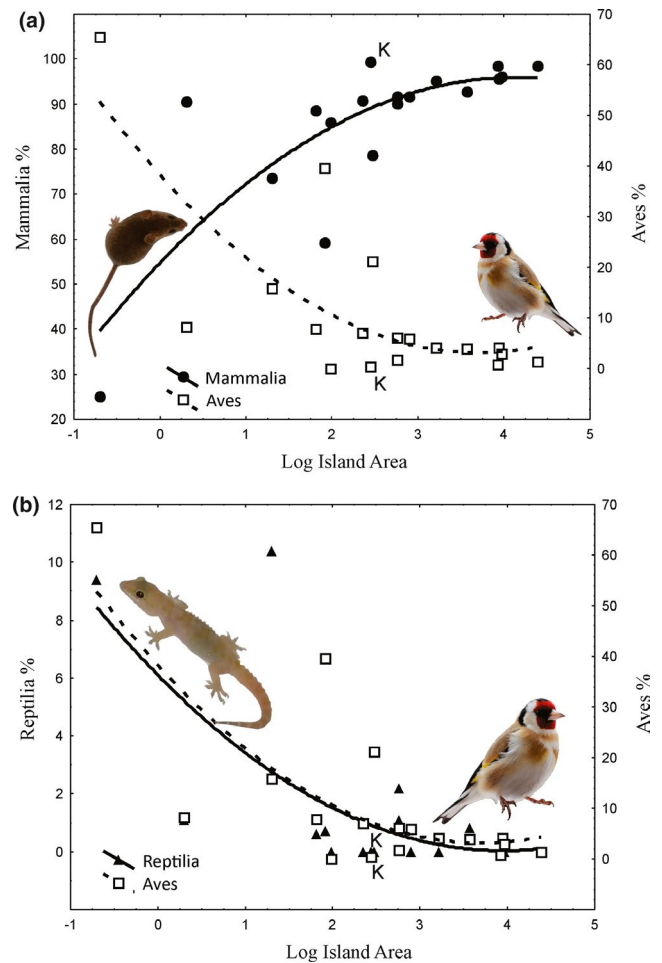


FIGURE 3 Effect of the island area on the proportion of birds and mammals (a), and on the proportion of birds and reptiles (b) in *Tyto alba* prey on the Mediterranean islands. The Island of Korčula is marked with the letter K

correlated with the Margalef diversity index ($R1$). The number of specimens (n), or sample size, was significantly correlated only with the Menhinick diversity index $R2$ (Table 4).

4 | DISCUSSION

Diet diversity of the barn owl on 18 Mediterranean islands partly followed the island biogeography theory. Diet diversity increased with increasing island area but was not influenced by the distance from the mainland. In general, diet diversity was greater on the larger Mediterranean islands. Island size was also a good predictor of the proportion of prey taxa. Small mammals were, in general, the main prey, but on smaller islands, consumption of birds and reptiles was higher. The Adriatic Island of Korčula, with its relatively small area and closeness to the mainland, fit well into these patterns of diet diversity of the barn owl on Mediterranean islands. Human population density on islands had no effect on the owl's diet diversity.

The barn owl is a selective opportunist predator (Tores et al., 2005) that preys mostly on non-volant small mammals. As

**TABLE 4** Pearson correlation coefficients and probability (p) among diversity indices of *Tyto alba* prey on Mediterranean islands. Significant correlations ($p < 0.05$) are in bold

	FNB	H'	λ	S	n	R1	R2
H'	0.12						
	$p = 0.643$						
λ	-0.97	-0.17					
	$p < 0.000$	$p = 0.491$					
S	0.16	0.34	-0.22				
	$p = 0.515$	$p = 0.172$	$p = 0.371$				
n	0.18	0.25	-0.24	0.44			
	$p = 0.464$	$p = 0.309$	$p = 0.341$	$p = 0.071$			
R1	0.15	0.27	-0.20	0.80	-0.0761		
	$p = 0.542$	$p = 0.279$	$p = 0.438$	$p < 0.001$	$p = 0.764$		
R2	-0.06	-0.07	0.08	-0.20	-0.7028	0.42	
	$p = 0.828$	$p = 0.799$	$p = 0.756$	$p = 0.431$	$p = 0.001$	$p = 0.080$	
E1	0.42	-0.04	-0.42	-0.29	-0.37	0.02	0.46
	$p = 0.084$	$p = 0.862$	$p = 0.081$	$p = 0.238$	$p = 0.126$	$p = 0.941$	$p = 0.058$

expected, on most Mediterranean islands, small mammals were the dominant prey. In contrast to the central European mainland, where Microtine voles are, together with mice, the most numerous prey (Taylor, 1994), on most Mediterranean islands, voles were absent and Murinae mice and rats prevailed significantly. Anthropogenic pressure on island fauna (Masseti, 2009) and dominance by generalist species (Janžekovič & Kryštufek, 2005) were reflected in high proportions of synanthropic house mice *Mus sp.*, house rats *Rattus rattus* as well as long-tailed field mice *Apodemus sylvaticus*. Nevertheless, rats are often the most widespread small mammals on the Mediterranean islands (Kryštufek & Vohralik, 2009). In Europe, shrews are often the second most frequently prey taken by barn owls (Taylor, 1994). On the islands in this study, *Sorex* shrew species were absent, but the importance of *Crocidura* species varied considerably, from non-existent to prevailing prey (e.g. Island of Crete). Meta-analyses by Roulin (2016a, 2016b) and Roulin and Christe (2013) showed that, in Europe, barn owls nowadays consume less invertebrates and insectivorous small mammals than they did in the past, with the exception of the anthropogenic *Crocidura* spp. Bats are rarely consumed, but more frequently on islands than on the mainland (0.3% on Mediterranean islands (this study) compared to 0.12% in Europe, in general (Roulin & Christe, 2013)). The proportions of prey birds and reptiles are usually larger on islands than on the mainland (Johnston & Hill, 1987; Roulin, 2015; Roulin & Dubey, 2012). Roulin (2015) reported that in Europe, barn owls consumed approximately twice as many birds on islands than on the mainland. In this study, the proportion of consumed birds was five times higher than in Europe, in general (2.4%; *ibid.*). The proportion of reptiles was 18 times higher (1.47% compared to 0.08% in Europe (Roulin & Dubey, 2012)). The importance of reptiles in the barn owl diet was, apart from the insularity effect, the result of the southern geographic position of the Mediterranean islands relative to the European continent and other European islands (*ibid.*). Furthermore, proportions of the three

mentioned vertebrate classes were in strong correlation with island size. The smaller the island, the more birds and reptiles were consumed, compared to higher proportions of mammals on the larger islands. Assuming that owls forage randomly and owl pellets are good estimators of prey abundance (Andrade, Saraiva de Menezes, & Monjeau, 2016), these results suggest that smaller Mediterranean islands support fewer small mammals, which are barn owls' primary prey, and confirm the barn owls' feeding flexibility and opportunistic predator behaviour. Isolation did not influence proportions among mammal, bird and reptile prey. A study of small mammals in the barn owl diet on the Tuscan Archipelago found no effect of island area or linear distance from the mainland on species richness (Amori et al., 2015). It has been noted that on archipelagos, and on very small islands, species richness and composition can vary independently of island area and isolation (MacArthur & Wilson, 1967; Lomolino et al., 2009). A small-island effect on the diet diversity of the barn owl was not tested because barn owls can, under conditions of prey shortage on small islets, extend their hunting range and potentially feed on neighbouring islands or islets (Guerra et al., 2014).

Moreover, factors other than island area and isolation can influence species communities on islands, for example, ecological requirements (e.g. food niche) and dispersion abilities of potential immigrant species, competition among the immigrant and resident species (Cadotte & Tucker, 2017; Ord, Emblen, Hagman, Shofner, & Unruh, 2017), and anthropogenic pressures like habitat destruction and introduction of alien species (Harris, 2009). Our study of barn owl diet diversity on Mediterranean islands only partly confirmed the classic MacArthur-Wilson theory that larger and less isolated islands have greater species richness than smaller and more isolated ones. The limitations of the study were considering only those species that are potential owl prey and the assumption that owls preyed randomly. Island size was in significant correlation with the FNB and λ indices, whereas isolation

was not correlated with any diversity index. The absence of correlation between simple species richness indices (S or R1) and island area showed that the relationship between diet diversity and island size is not as simple as saying that on larger islands owls eat more different prey taxa than on smaller islands. From more complex indices, the Simpson's diversity index (λ) gives more weight to evenness and dominant taxa compared with the Shannon-Weaver diversity index (H'), which is also strongly influenced by species richness (S) and was not correlated with island area. Therefore, the owl diet on larger islands was more diverse not because the owls ate more different taxa, but because there was a wider range of abundant taxa in its diet, which were also evenly represented. This supports the idea that the barn owl is a selective opportunist feeder (Tores et al., 2005): when it has the chance, it can specialize not only on one but on more species that are common in its habitat. Larger Mediterranean islands apparently support more small mammal species that are common and constitute the potential dominant prey for owls. Moreover, we found no effect of sample size (n) on the niche breadth (FNB) or Simpson's diversity index (λ) results. This is important, because in a study of geographical variability of the barn owl diet in Italy, Milana et al. (2016) found that sample sizes of prey from different sites significantly influenced the outcomes of the niche breadth results, which can mean serious problems in comparing results from different studies.

As mentioned, island isolation was not correlated with any diversity index. Besides the absence of an isolation effect, one reason could be that island isolation was measured as distance from the mainland, but smaller Mediterranean islands are often part of archipelagos; therefore, the degree of isolation is also geographically difficult to define. Helmus, Mahler, and Losos (2014) suggest the theory of island biogeography should also include the impact of economic isolation. They found that islands which were economically isolated, meaning they were not as well connected by shipping lines, had lower biodiversity. Moreover, the Mediterranean islands have been under anthropic pressure throughout history, and at least the majority of the insular, non-volant mammalian fauna has been influenced by man and is more or less similar to the present fauna of the rest of the Mediterranean region (Masseti, 2009). Interestingly, on the islands in this study, human population density did not influence owl diet diversity, despite the barn owl being a synanthropic bird (Taylor, 1994). On Mediterranean islands, human population size was highly correlated with island size, and accordingly with diet diversity; therefore, it was less appropriate as a proxy for human impact or urbanization than population density. This could be why Amori et al. (2015) found no effect of human population size on the Tuscan Archipelago on small mammal species richness.

ACKNOWLEDGEMENTS

Funding for this research was provided through the Slovenian Research Agency (Grant P1-0403).

DATA AVAILABILITY STATEMENT

All data to support the findings of this study are available in the manuscript and the Supporting Information of this manuscript and literature is cited in Table S3.

ORCID

Tina Klenovšek  <https://orcid.org/0000-0003-4656-834X>

REFERENCES

- Amori, G., Rizzo Pinna, V., Sammur, G., & Luiselli, L. (2015). Diversity of small mammal communities of the Tuscan Archipelago: Testing the effects of island size, distance from mainland and human density. *Folia Zoologica*, 64(2), 161–166. <https://doi.org/10.25225/fozo.v64.i2.a9.2015>
- Andrade, A., Saraiva de Menezes, J. F., & Monjeau, A. (2016). Are owl pellets good estimators of prey abundance? *Journal of King Saud University - Science*, 28, 239–244. <https://doi.org/10.1016/j.jksus.2015.10.007>
- Bontzorlos, V. A. (2009). *The trophic ecology of barn owl in the Agricultural ecosystems of central Greece: Its application in the distribution and abundance of its prey*. Tesis doctoral. Salamanca: Universidad de Salamanca.
- Bruce, M. D., Christie, D. A., & Kirwan, G. M. (2014). Common Barn-owl (*Tyto alba*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions.
- Cadotte, M. W., & Tucker, C. M. (2017). Should Environmental Filtering be Abandoned? *Trends in Ecology & Evolution*, 32(6), 429–437. <https://doi.org/10.1016/j.tree.2017.03.004>
- Comay, O., & Dayan, T. (2018). What determines prey selection in owls? Roles of prey traits, prey class, environmental variables, and taxonomic specialization. *Ecology and Evolution*, 8, 3382–3392. <https://doi.org/10.1002/ece3.3899>
- Guerra, C., García, D., & Alcover, A. (2014). Unusual foraging patterns of the barn owl, *Tyto alba* (Strigiformes: Tytonidae), on small islets from the Pityusic archipelago (Western Mediterranean Sea). *Folia Zoologica*, 63(3), 180–187. <https://doi.org/10.25225/fozo.v63.i3.a5.2014>
- Harris, D. B. (2009). Review of negative effects of introduced rodents on small mammals on islands. *Biological Invasions*, 11(7), 1611–1630. <https://doi.org/10.1007/s10530-008-9393-0>
- Helmus, M. R., Mahler, D. L., & Losos, J. B. (2014). Island biogeography of the Anthropocene. *Nature*, 513, 543–546. <https://doi.org/10.1038/nature13739>
- Holt, R. D. (1996). Food Webs in Space: An Island Biogeographic Perspective. In G. Polis, & K. Winemiller (Eds.), *Food Webs* (pp. 313–323). Boston: Springer. https://doi.org/10.1007/978-1-4615-7007-3_30
- Holt, R. D. (2009). Toward a Trophic Island Biogeography: Reflections on the Interface of Island Biogeography and Food Web Ecology. In J. B. Losos, & R. E. Ricklefs (Eds.), *The Theory of Island Biogeography Revisited*. Princeton: Princeton University Press.
- Jaksić, F. M., Seib, R. L., & Herrera, C. M. (1982). Predation by the Barn Owl (*Tyto alba*) in Mediterranean Habitats of Chile, Spain and California: A Comparative Approach. *The American Midland Naturalist*, 107(1), 151–162. Retrieved from <https://www.jstor.org/stable/2425196>. <https://doi.org/10.2307/2425196>
- Janžekovič, F., & Kryštufek, B. (2005). Non-volant terrestrial mammals (Mammalia) on the Adriatic island of Korčula. *Annales*, 15(1), 121–128.
- Johnston, D., & Hill, J. M. (1987). Prey selection of common barn-owls on Islands and mainland sites. *Journal of Raptor Research*, 21(1), 3–7.
- Kryštufek, B., & Janžekovič, F. (1999). *Ključ za določanje vretenčarjev Slovenije*. Ljubljana: DZS.



- Kryštufek, B., & Vohralik, V. (2009). *Mammals of Turkey and Cyprus Rodentia II: Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae, Castoridae*. Koper: ZRS Koper.
- Legendre, P., & Legendre, L. (2012). *Numerical Ecology*. Amsterdam: Elsevier.
- Levins, R. (1968). *Evolution in changing environments: Some theoretical explorations*. Princeton: Princeton University Press.
- Lomolino, M. V., Brown, J. H., & Sax, D. F. (2010). Island biogeography theory. Reticulations and reintegration of 'a biogeography of the species'. In J. B. Losos, & R. E. Ricklefs (Eds.), *The Theory of Island Biogeography Revisited* (pp. 13–51). Princeton: Princeton University Press.
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387. <https://doi.org/10.1111/j.1558-5646.1963.tb03295.x>
- MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography. Monographs in Population Biology*. Vol. 1. Princeton: Princeton University Press.
- Masetti, M. (2009). Mammals of the Mediterranean islands: Homogenisation and the loss of biodiversity. *Mammalia*, 73, 169–202. <https://doi.org/10.1515/MAMM.2009.029>
- Milana, G., Lai, M., Maiorano, L., Luiselli, L., & Amori, G. (2016). Geographic patterns of predator niche breadth and prey species richness. *Ecological Research*, 31, 111–115. <https://doi.org/10.1007/s11284-015-1319-6>
- Niethammer, J., & Krapp, F. (1990). *Handbuch der Säugetiere Europas. Band 3/1 Insektenfresser Herrentiere*. Wiesbaden: Aula - Verlag.
- Ord, T. J., Emblen, J., Hagman, M., Shofner, R., & Unruh, S. (2017). Manipulation of habitat isolation and area implicates deterministic factors and limited neutrality in community assembly. *Ecology and Evolution*, 7, 5845–5860. <https://doi.org/10.1002/ece3.3126>
- Romano, A., Séchaud, R., & Roulin, A. (2020). Global biogeographical patterns in the diet of a cosmopolitan avian predator. *Journal of Biogeography*, 47(7), 1467–1481. <https://doi.org/10.1111/jbi.13829>
- Roulin, A. (2015). Spatial variation in the decline of European birds as shown by the Barn Owl *Tyto alba* diet. *Bird Study*, 62, 271–275. <https://doi.org/10.1080/00063657.2015.1012043>
- Roulin, A. (2016a). Strong decline in the consumption of invertebrates by Barn Owls from 1860 to 2012 in Europe. *Bird Study*, 63, 146–147. <https://doi.org/10.1080/00063657.2015.1125440>
- Roulin, A. (2016b). Shrews and moles are less often captured by European Barn Owls *Tyto alba* nowadays than 150 years ago. *Bird Study*, 63, 559–563. <https://doi.org/10.1080/00063657.2016.1240149>
- Roulin, A. (2020). *Barn Owls: Evolution and Ecology*. Cambridge: Cambridge University Press.
- Roulin, A., & Christe, P. (2013). Geographic and temporal variation in the consumption of bats by European Barn Owls. *Bird Study*, 60, 561–569. <https://doi.org/10.1080/00063657.2013.847051>
- Roulin, A., & Dubey, S. (2012). The occurrence of reptiles in Barn Owl diet in Europe. *Bird Study*, 59, 504–508. <https://doi.org/10.1080/00063657.2012.731035>
- Schoener, T. W. (1989). Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture. *Ecology*, 70(6), 1559–1589. <https://doi.org/10.2307/1938088>
- Siverio, M., Siverio, F., Rodríguez, B., & Rodríguez, A. (2010). Long-term monitoring of an insular population of Barbary falcon *Falco peregrinus pelegrinoides*. *Ostrich*, 82, 225–230. <https://doi.org/10.2989/00306525.2011.629435>
- Taylor, I. R. (1994). *Barn Owls: Predator-Prey Relationships and Conservation*. Cambridge: Cambridge University Press.
- Terborgh, J. (2009). The Trophic Cascade on Islands. In J. B. Losos, & R. E. Ricklefs (Eds.), *The Theory of Island Biogeography Revisited*. Princeton: Princeton University Press.
- Tores, M., Motro, Y., Motro, U., & Yom-Tov, Y. (2005). The Barn Owl - A Selective Opportunist Predator. *Israel Journal of Zoology*, 51(4), 349–360. <https://doi.org/10.1560/7862-9E5G-RQJJ-15BE>
- Vogiatzakis, I. N., & Griffiths, G. H. (2008). Island Biogeography and Landscape Ecology. In I. N. Vogiatzakis, G. Pungetti, & A. M. Mannion (Eds), *Mediterranean Island Landscapes. Natural and Cultural Approaches* (pp. 61–81). Berlin: Springer.
- Vogiatzakis, I. N., Mannion, A. M., & Pungetti, G. (2008). Introduction to the Mediterranean Island Landscapes. In I. N. Vogiatzakis, G. Pungetti, & A. M. Mannion (Eds), *Mediterranean Island Landscapes. Natural and Cultural Approaches* (pp. 3–14). Berlin: Springer.
- Whittaker, R. J. (1998). *Island Biogeography: Ecology, Evolution and Conservation*. Oxford: Oxford University Press.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Janžekovič F, Klenovšek T. The biogeography of diet diversity of barn owls on Mediterranean islands. *J Biogeogr.* 2020;00:1–9. <https://doi.org/10.1111/jbi.13955>