

FEEDING ECOLOGY OF THE LONG-LEGGED BUZZARD AND DIET OVERLAP WITH SYMPATRIC BONELLI'S EAGLE ON CYPRUS

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ABSTRACT.—Interspecific competition occurs when two sympatric species utilize the same limited supply of a basic resource, such as food; the degree of diet overlap is an essential metric for examining potential competition between the species. The Long-legged Buzzard (*Buteo rufinus*) is a relative newcomer to the island of Cyprus, where it is sympatric with the larger Bonelli's Eagle (*Aquila fasciata*), a potential competitor for both food and space (nesting territories). We studied the diet of the Long-legged Buzzard in the 2005, 2006, and 2018 nesting seasons through analysis of pellets and prey remains collected at 38 sites. The most abundant prey class was mammals (68.8% frequency, 58.9% biomass), followed by reptiles (16.8% frequency, 36.3% biomass), and birds (4.3% frequency, 4.6% biomass). The most numerous prey species were black rats (*Rattus rattus*), starred agamas (*Stellagama stelio*), house mice (*Mus musculus*), and large whip snakes (*Dolichophis jugularis*), but in terms of biomass, the most important prey items were black rats, large whip snakes, long-eared hedgehogs (*Hemiechinus auritus dorotheae*), and starred agamas. We compared the diet of the Long-legged Buzzard to that of the Bonelli's Eagle, whose diet was dominated by birds (62.1% frequency, 76.1% biomass) and to a lesser degree by mammals (29.5% frequency, 21.9% biomass). The mean prey biomass for the Long-legged Buzzard was estimated as 167 g, compared to 350 g for the Bonelli's Eagle; this difference reflected the almost two-fold difference in mass between females of the two species. Diet overlap measured with Pianka's index was <0.5 , suggesting an intermediate niche overlap mainly due to utilization of an abundant prey resource, such as the black rat. Niche breadth for the Long-legged Buzzard measured using Levins' index ranged from 0.485 in 2005 to 0.081 in 2018. This decrease in niche breadth over time in a generalist species can occur when there is a superabundance of a particular prey. The mean Levins' index for the Bonelli's Eagle was also low, 0.271 (1999–2001). Based on the diet comparison, we concluded that there was no evidence for interspecific competition in terms of food.

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KEY WORDS: *Long-legged Buzzard*; *Buteo rufinus*; *Bonelli's Eagle*; *Aquila fasciata*; *avian*; *breadth*; *competition*; *diet*; *interspecific*; *niche*; *raptor*.

ECOLOGÍA TRÓFICA DE *BUTEO RUFINUS* Y SOLAPAMIENTO DE DIETA CON *AQUILA FASCIATA*, UNA ESPECIE SIMPÁTRICA, EN CHIPRE

RESUMEN.—La competencia interespecífica ocurre cuando dos especies simpátricas utilizan el mismo suministro limitado de un recurso básico, como por ejemplo la comida; el grado de solapamiento de la dieta es una métrica esencial para examinar la competencia potencial entre las especies. *Buteo rufinus* es una especie relativamente nueva en la isla de Chipre, donde se presenta en simpatria con *Aquila fasciata*, de mayor tamaño, un competidor potencial tanto por comida como por espacio (territorios de nidificación). Estudiamos la dieta de *B. rufinus* en las temporadas de cría de 2005, 2006 y 2018 mediante el análisis de egagrópilas y restos de presas recolectados en 38 sitios. Las presas más abundantes fueron los mamíferos (68,8% de frecuencia, 58,9% de biomasa), seguido de los reptiles (16,8% de frecuencia, 36,3% de biomasa) y las aves (4,3% de frecuencia, 4,6% de biomasa). Las especies de presa más numerosas fueron *Rattus rattus*, *Stellagama stelio*, *Mus musculus* y *Dolichophis jugularis*, si bien en términos de biomasa las presas más importantes fueron *R. rattus*, *D. jugularis*, *Hemiechinus awritus dorotheae* y *S. stelio*. Comparamos la dieta de *B. rufinus* con la de *A. fasciata*, cuya dieta estaba dominada por aves (62,1% de frecuencia, 76,1% de biomasa) y en menor medida por mamíferos (29,5% de frecuencia, 21,9% de biomasa). La biomasa de la presa promedio para *B. rufinus* se estimó en 167 g, en comparación con 350 g para *A. fasciata*; esta disparidad reflejó la diferencia de masa de casi el doble entre las hembras de las dos especies. El solapamiento de dieta medido con el índice de Pianka fue $<0,5$, lo que sugiere un solapamiento de nicho intermedio debido principalmente a la utilización de un recurso de presa abundante como *R. rattus*. La amplitud de nicho para *B. rufinus*, medido con el índice de Levins, fluctuó entre 0,485 en 2005 y 0,081 en 2018. Esta disminución en la amplitud de nicho a lo largo del tiempo en una especie generalista puede ocurrir cuando hay una sobreabundancia de una presa en particular. El índice de Levins medio para *A. fasciata* también fue bajo, 0,271 (1999–2001). Basados en la comparación de la dieta, concluimos que no hubo evidencia de competencia interespecífica en términos de alimentación.

[Traducción del equipo editorial]

INTRODUCTION

Interspecific competition occurs when two sympatric species utilize the same resources that are in limited supply, with nesting sites and food resources being the most basic ecological components that two species of birds of prey might compete for (Newton 1979). The degree of diet overlap is essential for examining potential competition (Friedemann et al. 2016), even though the food resource utilized must be in limited supply (Gerstell and Bednarz 1999). Korpimäki (1987) stated that “competition theory predicts that diet overlap should be lower during prey shortage and that diet similarity should be especially reduced in neighboring pairs.” This overlap may be reduced through prey partitioning (type and size) and segregation of feeding areas, whereas predator size is a factor that could influence interspecific trophic relationships (García and Arroyo 2005).

The Long-legged Buzzard (*Buteo rufinus*) is a medium to large raptor with a mean female body mass of 1.350 kg (Newton 1979). This bird nests in

the southern Palearctic and is one of the least studied buteos (Friedemann et al. 2011). Due to its extremely large range, its conservation status has been evaluated as of least concern (BirdLife International 2015). In Europe the species breeds in the southeastern dry steppes and its population is increasing, forming approximately 17% of its global range (BirdLife International 2015). During the last three decades, the Long-legged Buzzard has expanded across most of Eastern and Central Europe, colonizing areas of Eastern Romania and Hungary (Danko 2012, Lawicki et al. 2013, Baltag et al. 2014). This has been attributed to climate change and food availability (Mrlik and Landsfeld 2002). Evidence emerging from the Iberian Peninsula suggests that the recent colonization by the African subspecies, (Atlas Long-legged Buzzard; *B. r. cirtensis*), may be attributed to the northward expansion of Mediterranean biomes, as winters become warmer (Chamorro et al. 2017), and researchers have predicted its future distribution (Chamorro et al. 2020).

The Long-legged Buzzard is a newcomer to the island of Cyprus, regarded as a scarce and irregular winter visitor, and scarce passage migrant until the early 1990s (Flint and Stewart 1992). The first confirmed nest was found in 1992 (Kourtellarides 1998, Whaley and Dawes 2003) but the species was probably overlooked. In 2005, 34 pairs were counted, 80% of which were in the southwestern part of the island (Kassinis 2009). The species shows an increasing population trend (Kassinis and Mammidis 2016), expanding eastward and to the central mountainous parts of the island, from 63 nesting pairs in 2012 (BirdLife International 2015) to 80 pairs in 2017 (Flint 2019).

The Long-legged Buzzard is sympatric to the Bonelli's Eagle (*Aquila fasciata*), a relatively large eagle species with a mean female body mass of 2.450 kg (Cyprus Game and Fauna Service unpubl. data), resident on Cyprus and a flagship species of the Mediterranean ecosystem. Its population is currently estimated at 37–40 active territories in areas under the effective control of the Republic of Cyprus with another 10-plus pairs estimated to have territories in the areas not under the effective control of the Republic of Cyprus (Beton et al. 2013). The two species have a good conservation status in Cyprus and a wide distribution, living in relative proximity to each other in many areas. After the demise of the scarce Eastern Imperial Eagle (*Aquila heliaca*) in the early 1980s (Kourtellarides 1998), the severe decline of the Griffon Vulture (*Gyps fulvus*) since the 1990s, and the near extirpation of the Common Raven (*Corvus corax*), the Long-legged Buzzard and Bonelli's Eagle are potentially the main competitors for food and space (nesting territories) on the island, along with the forest-dwelling Northern Goshawk (*Accipiter gentilis*) and the smaller Peregrine Falcon (*Falco peregrinus*).

Even though the Bonelli's Eagle is mostly a tree-nester on Cyprus (Kassinis 2010) and the Long-legged Buzzard a predominant cliff-nester (Kassinis 2009), they both share some common areas for nesting and foraging. In Israel an analogy exists between the Long-legged Buzzard and the Short-toed Snake-Eagle (*Circaetus gallicus*); the two species are sympatric in many areas, and breed in proximity to each other (the snake-eagle nesting mostly in trees and the Long-legged Buzzard mostly on cliffs; Friedemann et al. 2016). The few studies on the Long-legged Buzzard's diet across its range report that it feeds mostly on small mammals, mainly European ground squirrels (*Spermophilus citellus*;

aka European sousliks) but also on voles, rats, lizards, snakes, birds, and occasionally insects (Alivizatos and Goutner 1997, Khaleghizadeh et al. 2005, Wu et al. 2008, Kassinis 2009, Milchev 2009, Bakaloudis et al. 2012, Friedemann et al. 2016). In Cyprus, it feeds mainly on small mammals, such as black rats (*Rattus rattus*), reptiles (mostly starred agama [*Stellagama stellio*]), and snakes (primarily the large whip snake [*Dolichophis jugularis*]; Kassinis 2009, Bakaloudis et al. 2012). These prey species, to a lesser degree, are also utilized by the Bonelli's Eagle, a species that is mostly an avian predator and less a mammalian predator (Iezekiel et al. 2004, Kassinis 2010). The Bonelli's Eagle may take larger mammals such as European hares (*Lepus europaeus*), lambs, fox pups, and cats; in fact, it was found to prey on Cyprus mouflon lambs (*Ovis gmelini ophion*) for the first time in 2009 (Kassinis 2010).

Given the limited research to date, the main aim of this study was to evaluate changes or shifts in the Long-legged Buzzard's diet during a 13-yr period and identify any possible competition with the Bonelli's Eagle. The specific objectives of the present study were to (1) analyze the most updated, and complete information on the Long-legged Buzzard's diet from 38 sites and a larger area (island-wide) than previous studies, and (2) examine whether there is evidence of interspecific competition between the Long-legged Buzzard and the Bonelli's Eagle by examining their dietary overlap.

METHODS

Study Area and Sites. Cyprus is the third largest Mediterranean island (after Sicily and Sardinia), covering an area of 9251 km² (Vogiatazakis et al. 2020). The island is dominated by two mountain ranges, the central Troodos Mountains and the smaller Pentadaktulos Range with the large, flat central plain of Mesaoria in between. Cyprus has a Mediterranean climate with dry, hot summers and rainy, mild winters with relatively short autumn and spring seasons. Cyprus high forests, mainly of Calabrian pine (*Pinus brutia*), cover 17% of its surface. The endemic golden oak (*Quercus alnifolia*) exists in either pure stands or under conifers in altitudes over 700 masl across the Troodos Range. Dominant shrubs typical of Mediterranean landscapes occur as scrubland (aka *maquis* of *Olea*, *Ceratonia*, and *Pistacia* species) with low thorny cover, and shrubland (aka *matorral*; *Juniperus phoenicea*) characteristic of the coastal areas (Tsintides et al. 2007). The island's proximity to the Middle East

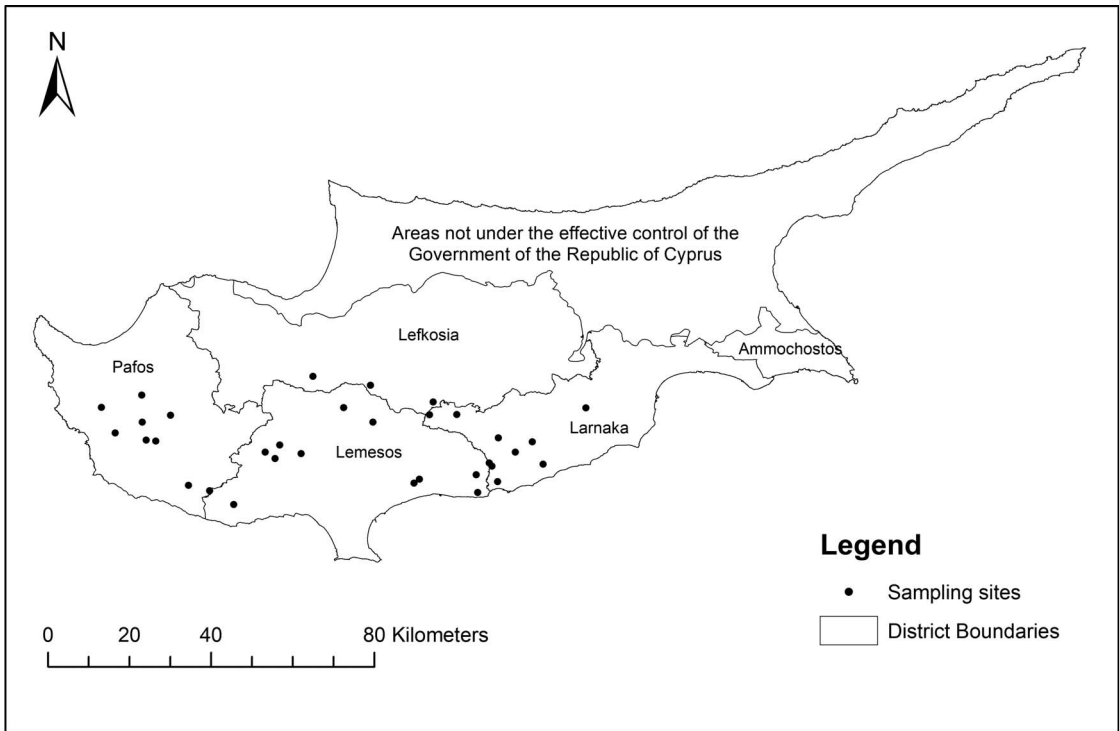


Figure 1. The distribution of Long-legged Buzzard sampling sites on Cyprus.

makes it one of the hottest parts of the Mediterranean. The mean annual temperature has increased by approximately 1°C during the last century, with a more rapid increase of 0.015°C per annum since the 1970s (Flint 2019). During the last century the climate has become increasingly arid, with droughts and water shortages becoming a frequent phenomenon (Tsiourtis 2002). During the 20th century, the average annual precipitation was 559 mm in its first 30 yr and 462 mm in its last 30 yr, a decrease of 17% (Flint 2019), whereas in the first 19 yr of this century (2001–2019), the annual average precipitation was 491 mm (calculated from data provided by the Department of Meteorology 2020).

A total of 38 sites (35 nests and 3 roosting perches) were surveyed (Fig. 1) during 2005, 2006, and 2018. For the purposes of this study, only areas under the effective control of the Republic of Cyprus were surveyed.

Collection and Analysis of Prey Items. For the Long-legged Buzzard, we examined whether there were changes or shifts in diet between the two decades (2005 and 2006 vs. 2018) through the collection of pellets and prey remains. The first

decade was during the species' rapid expansion and the second during the species' almost 30 yr of presence and wider establishment on the island.

The combined analysis of pellets and prey remains is regarded as a widely accepted method for investigating raptor diets (Redpath et al. 2001, Ontiveros et al. 2005, Friedemann et al. 2016). Therefore, regurgitated pellets and prey remains were collected from fairly accessible, and active nesting and roosting sites of Long-legged Buzzards. In our case we used pellets/prey remains collected under nesting/roosting trees/cliffs where accessible, which ensured comparability with the Bonelli's Eagle study (sampling done 1999–2001) that involved mostly pellets and prey remains data. Even though trail cameras have been used over the years in nest site monitoring, they were not considered on a large scale for this study due to possible disturbance when placed and checked regularly (Harrison et al. 2019). Trail cameras would also have been very labor-intensive and expensive (Francksen et al. 2016).

To minimize disturbance, all material was collected during the middle of the nestling period in May and

after nestlings had fledged in June. Overall, 487 pellets and prey remains were collected from the 38 sites.

The 35 nesting sites belonged to 29 territorial pairs (four nesting sites were sampled twice in 2005 and 2006 and two were sampled twice in 2005 and 2018; Kassinis 2009). The same nesting sites were not sampled every year due to difficulties in reaching a site when the pair nested in a less accessible alternative cliff/tree. Prey remains were obtained from and under the nesting cliffs or trees, and feeding and roosting perches.

The nesting sites surveyed were located in the southern part of the island and varied from low-elevation steep earth banks, mid-elevation rocky canyons, tree nests on steep slopes, and high-elevation stone cliffs (up to 1200 masl).

Identification of Samples. Both pellets and prey remains were used for the Long-legged Buzzard's diet analysis and were identified to the lowest possible taxonomic level (at least to order), with the aid of reference and personal collections, using skeletal remains, skulls, feathers or scales. Prey items were classified in five categories: insects, amphibians, reptiles, birds, and mammals. Pellets were put in an 8% solution of sodium hydroxide for 8 hr to dissolve fur. Skulls and jawbones of each species were summed separately for each nest site, and the number of each prey species was determined by the number of skulls or pairs of jawbones, whichever was larger. Invertebrates were identified and counted using mandibles, femurs, wings, or parts of exoskeletons (Ganey 1992). The estimated weights of different prey species (body mass) were obtained from the literature (Steenhof 1983) and from local specimen records after consulting relevant experts.

Data analysis. *Long-legged Buzzard prey composition.* To present the range of the prey items that constitute the entire diet composition of the Long-legged Buzzard in Cyprus during the nesting season, we summed all prey items from all sites, divided by the prey categories as referred above and individual species where this was appropriate. We calculated the percent frequency of occurrence (% FO; the proportion of a particular species in the total number of prey items found $\times 100$) and percent biomass (% B; the [estimated biomass of each eaten prey category/total estimated biomass] $\times 100$; Table 1, Supplemental Material Table S1).

We also calculated the percentages of prey items, prey richness, and prey categories found at each site. To prevent the bias of using dietary data from the same site sampled twice in 2005 and 2006 (four nests),

and 2005 and 2018 (two nests), we used generalized linear models (GLM) to assess the effect of year on prey items at these nests. Repeated sampling sites were removed based on the number of prey items (the nests with the highest number of prey items were kept for analysis) and were excluded from the year effect analyses and diet overlap tests (below).

Effect of year on Long-legged Buzzard diet. The diet composition (prey species) was described between the nesting sites in a multidimensional context through a detrended correspondence analysis (DCA). This procedure allows sites with greater similarity of prey species to be closer to one another in ordination space and also closer to the species most represented in the Long-legged Buzzard's diet (McGarigal et al. 2000). Sampling sites were then grouped based on the three sampling years (2005, 2006, 2018).

GLMs with Poisson and negative binomial error distributions were constructed to analyze whether prey items, prey categories, and prey species richness changed between years. Each model performance was checked graphically using diagnostic plots (Zuur et al. 2010) and the normality of residuals was checked by Kolmogorov-Smirnov tests. We also calculated the percentage of deviance explained (D^2) as a measure of the explanatory power of the models.

We tested whether prey items differed significantly between years: (1) 2005 and 2006, (2) 2005 and 2018, and (3) 2006 and 2018. We performed *t*-tests when the condition of a normal distribution was satisfied (Shapiro-Wilk test) or the nonparametric alternative (Mann-Whitney *U*-test), using the number of prey items at each site. In addition, we performed analysis of similarities (ANOSIM) to detect whether there was a significant difference in prey composition between the years (Clarke 1993).

Diet overlap/comparison of Long-legged Buzzard and Bonelli's Eagle. The diet of the Long-legged Buzzard (this study) was compared to the diet of the Bonelli's Eagle from a previous study (Iezekiel et al. 2004) to calculate any degree of overlap that might indicate interspecific competition. Limitations of this comparison were (1) the fact that the Bonelli's Eagle diet sampling took place in 1999–2001, earlier than our study, and (2) the Bonelli's Eagles sampling sites were not included in the Bonelli's Eagle study; therefore no spatial comparison with neighboring pairs of Long-legged Buzzards was possible.

We used Bonelli's Eagle diet data (Iezekiel et al. 2004) and pooled pellet and prey remains analysis into a common prey items category, and we calculated the % FO and % B to compare with our

Table 1. Diet composition for Long-legged Buzzard (excluding repeated sites). Note: % FO = percent frequency of occurrence; % B = percent biomass.

TAXONOMIC CATEGORY	PREY RICHNESS	ABBREVIATION	PREY TAXA	% FO	% B
Insects		Ortho	Unidentified Orthoptera	0.27	0
		Coleo	Unidentified Coleoptera	9.26	0.05
Total insects	2			9.5	0.05
Amphibians		<i>Bviri</i>	Green toad (<i>Bufo viridis</i>)	0.27	0.06
Total amphibians	1			0.27	0.06
Reptiles					
Lizards		<i>Eschn</i>	Schneider's skink (<i>Eumeces schneideri</i>)	0.54	0.24
		<i>Llaeo</i>	Smooth lizard (<i>Lacerta laevis troodica</i>)	0.27	0.08
		<i>Sstel</i>	Starred agama (<i>Stellagama stellio</i>)	10.35	4.64
Snakes		<i>Djugu</i>	Large whip snake (<i>Dolichophis jugularis</i>)	5.18	29.03
		<i>Minsi</i>	Montpellier snake (<i>Malpolon insignitus</i>)	0.27	1.37
		<i>Mlebe</i>	Blunt-nosed viper (<i>Macrovipera lebetina</i>)	0.27	2.29
Total reptiles	6			16.89	37.65
Birds		<i>Clivi</i>	Rock Pigeon (<i>Columba livia</i>)	0.54	1.22
		<i>Cpalu</i>	Common Woodpigeon (<i>Columba palumbus</i>)	0.27	0.76
		<i>Cmone</i>	Eurasian Jackdaw (<i>Corvus monedula</i>)	0.54	0.76
		<i>Ftinn</i>	Eurasian Kestrel (<i>Falco tinnunculus</i>)	0.54	0.55
		<i>Oscop</i>	Cyprus Scops-Owl (<i>Otus cypricus</i>)	0.54	0.24
		<i>Anoct</i>	Little Owl (<i>Athene noctua</i>)	1.09	0.98
		<i>Ccett</i>	Cetti's Warbler (<i>Cettia cetti</i>)	0.27	0.02
		<i>Gcris</i>	Crested Lark (<i>Galerida cristata</i>)	0.27	0.06
		<i>Msoli</i>	Blue Rock-thrush (<i>Monticola solitarius</i>)	0.27	0.08
Total birds	9			4.36	4.67
Mammals		<i>Rratu</i>	Black rat (<i>Rattus rattus</i>)	54.50	45.84
		<i>Mmusc</i>	House mouse (<i>Mus musculus</i>)	8.45	0.71
		<i>Leuro</i>	European hare (<i>Lepus europaeus</i>)	0.27	2.29
		<i>Haudo</i>	Long-eared hedgehog (<i>Hemiechinus auritus dorotheae</i>)	5.18	8.81
		<i>Csucu</i>	Lesser white-toothed shrew (<i>Crocidura suaveolens cypria</i>)	0.54	0.02
Total mammals	5			68.94	57.57
Total			23	100.00 (367)	100.00

Long-legged Buzzard diet study. To facilitate comparison of the Long-legged Buzzard diet with the Bonelli's Eagle diet and to discuss any possible interspecific competition, we calculated Pianka's diet overlap index (Pianka 1973) and Levins' standardized niche breadth index (Levins 1968, Hurlbert 1978).

Pianka's (1973) index of diet overlap is defined as:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where O_{jk} = Pianka's index of niche overlap between species j and k ; p_{ij} = the proportion of the i th prey item

in the diet of species j ; p_{ik} = the proportion of the i th prey item in the diet of species k ; and n = the total number of items. Pianka's index ranges from 0 (no resources used in common between the two species) to 1.0 (complete overlap in resources used between the two species). Diet overlap values were set at the following levels: high (>0.6), intermediate (0.4–0.6) or low (<0.4; Grossman 1986, Novakowski et al. 2008).

The Levins' standardized index that measures niche breadth is defined as:

$$B_i = \frac{1}{(n-1)} \left(\frac{1}{\left(\sum_j p_{ij}^2 \right)} - 1 \right)$$

Table 2. Comparison of diet composition of Long-legged Buzzard per taxonomic category during the nesting seasons of 2005, 2006, and 2018.

TAXONOMIC CATEGORY	2005			2006			2018		
	<i>n</i>	% FO	% B	<i>n</i>	% FO	% B	<i>n</i>	% FO	% B
Insects (Orthoptera and Coleoptera)	27	21.95	0.16	7	7.22	0.04	5	2.81	0.02
Amphibians	1	0.81	0.29	0	0	0	0	0	0
Reptiles									
Lizards	21	17.07	8.34	15	15.46	6.05	7	3.93	1.56
Snakes	9	7.32	44.84	9	9.28	46.64	6	3.37	16.83
Birds	6	4.88	4.19	4	4.12	3.58	7	3.93	5.67
Mammals	59	47.97	42.18	62	63.92	43.69	153	85.96	75.92

where B_i = standardized index of niche breadth; p_{ij} = proportion of diet of predator i on prey j ; and n = total number of items. B_i values vary from 0 (species consumes a single item) to 1 (species exploits available items in equal proportion). Values of B_i are considered high when higher than 0.6, moderate when between 0.4 and 0.6, and low when below 0.4 (Krebs 1989, Novakowski et al. 2008).

Both indices were calculated based on the total dietary data of the Long-legged Buzzard (sum of prey items) for the duration of the study (2005, 2006, and 2018) and for each year separately vs. the Bonelli's Eagle total dietary data (1999–2001). All analyses were performed in R software (version R 3.6.3, R Core Team 2020) using the packages *vegan* and *MASS* (Venables and Ripley 2002, Oksanen et al. 2019).

RESULTS

Long-legged Buzzard Prey Composition. We found a total of 398 prey items in the diet of Long-legged Buzzards from the 38 sites (35 nests and 3 roosts) for all years studied (2005, 2006, and 2018; Table S1, S2).

Because no year effect was observed for prey items between repeated sampling of the same sites in 2005 and 2006, and 2005 and 2018 (GLM: $z = -0.525$, $p = 0.60$; and $z = 1.151$, $p = 0.25$, respectively), six sites were excluded from most further analysis.

Our results included 367 prey items from 32 sites (29 nests and 3 roosts), which were represented by 21 prey species and 2 insect orders (Table 1). The most frequent prey species (% FO) in the diet of Long-legged Buzzard were in decreasing order: *Rattus rattus*, *Stellagama stellio*, and *Mus musculus*, followed by *Dolichophis jugularis* and *Hemiechinus auritus dorotheae*. There were more species of birds

found than in any other class but there were more individual items of mammals, reptiles, and invertebrates in the Long-legged Buzzard's diet. The mean prey biomass for the Long-legged Buzzard was $167 \text{ g} \pm \text{SE } 0.71$.

Mammals (68.9% FO) were the most frequent prey in the diet of Long-legged Buzzard, followed by reptiles (16.9% FO). Insects (Orthoptera and Coleoptera) were more frequent than birds (9.5% and 4.4% respectively. In 2005 and 2006, reptiles were the most important for biomass (53.2% and 52.7% respectively; Table 2), with *D. jugularis* being the most significant prey species biomass overall (36.9% and 46.6%, respectively; Table S1). In 2018, the contribution of reptiles declined to 18.4% B, with mammals being the most significant class (75.9% B; Table 2), and *R. rattus* the most important prey species in both frequency (76.4%) and biomass (63.6%; Table S1).

Effect of Year on Long-legged Buzzard Diet/Prey.

The DCA revealed a very strong clustering of nesting sites especially for 2018 (Fig. 2). The most common prey species found in this cluster was *R. rattus*. In addition, *S. stellio* and *D. jugularis* occurred more often at Long-legged Buzzard nesting sites. Prey species found at the edges of the ordination were the least common (mainly birds).

Although the GLMs revealed no substantial effects on prey between years, prey richness was lower in 2018 than in the other 2 yr (GLM: $z = -2.562$, $p = 0.01$, $D^2 = 21\%$). No significant difference was found in prey items between years 2005 and 2006 (t -test = 1.79, $p = 0.10$) and also for years 2005 and 2018 ($U = 61$, $p = 0.54$) and for 2006 and 2018 ($U = 56$, $p = 0.38$). Finally, prey composition did not differ in the sampling sites across the years (ANOSIM: $R = 0.06$, $p = 0.14$).

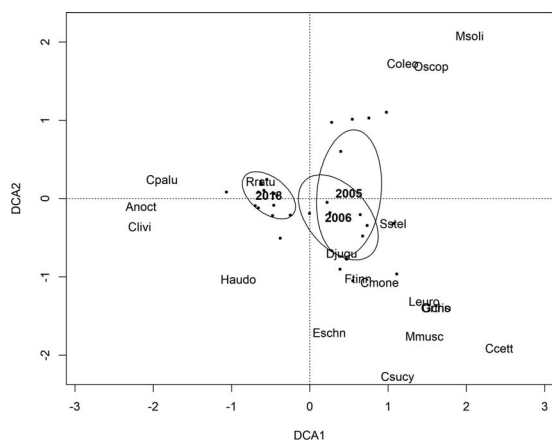


Figure 2. Detrended Correspondence Analysis (DCA) of prey species composition at 32 sites (abbreviations of prey species according to Table 1). Dots represent sampling sites and ellipses denote grouping obtained from the three sampling years (2005, 2006, and 2018). Eigenvalue: DCA 1 = 0.43; DCA 2 = 0.31.

Diet overlap/comparison for Long-legged Buzzards and Bonelli's Eagles. The diets of the two raptors were compared with the contribution of every class represented (Table 3.). The most important prey class for Bonelli's Eagles was birds (62.1% FO, 76.1% B), with mammals following (29.5% FO, 21.9% B), and reptiles third (8.4% FO, 1.7% B). The complete Bonelli's Eagle diet with the contribution from each prey species is shown in the Appendix (data pooled and analyzed taken from Iezekiel et al. 2004). Mean prey biomass was calculated at $350 \text{ g} \pm \text{SE } 0.74$.

Pianka's index (diet overlap index) between each Long-legged Buzzard sampling year and the overall Long-legged Buzzard diet for the 3 yr vs. the Bonelli's Eagle diet ranged from a minimum 0.468 in 2005 to a maximum 0.497 in 2006, with an

intermediate value in 2018 (0.476). The mean Long-legged Buzzard diet overlap (for the three sampling years) between the two species was intermediate at 0.492 (approaching 0.5).

Levins' index of niche breadth for the Long-legged Buzzard started at 0.485 in 2005, declined to 0.295 in 2006, and declined even more to 0.081 in 2018; the mean was 0.236 for the 3 yr. The Bonelli's Eagle Levins' mean index was 0.271 for the 1999–2001 sampling period.

DISCUSSION

Long-legged Buzzard Diet. The most abundant prey item found in the Long-legged Buzzard diet was the black rat in all years sampled. It seems that in the most recent year of analysis (2018), this rodent dominated the raptor's diet even more. The black rat is an abundant rodent and a common agricultural pest that reaches "plague" numbers in wet years, causing damage to crops and trees (Kryštufek and Vohralík 2009). The abandonment of agriculture along with the increasing depopulation of the countryside seems to favor this rodent, with large areas of abandoned vineyards and orchards being invaded by scrub and woodland (Hadjikyriakou 2005, Flint 2019), providing favorable habitat for this species and also for its predators. In fact, most of the high-density areas for the Long-legged Buzzard are in the *maquis*/olive-carob tree/higher scrub zone that coincides with areas with higher rat abundance. The increase of black rats in the Long-legged Buzzard's diet could also be attributed to the higher than average annual precipitation recorded in 2018 that may have enhanced food availability, prolonged the breeding season, and boosted rat populations on the island. It is known that rainfall patterns affect food resources, which also influence rat abundance (Madsen and Shine 1999).

Table 3. Diet composition summarized by taxonomic category and comparison between the Long-legged Buzzard (398 prey items from 38 sites) and the Bonelli's Eagle (1734 prey items).

TAXONOMIC CATEGORY	LONG-LEGGED BUZZARD DIET (THIS STUDY)			BONELLI'S EAGLE DIET (IEZEKIEL ET AL. 2004)		
	<i>n</i>	% FO	% B	<i>n</i>	% FO	% B
Insects (Orthoptera and Coleoptera)	39	9.8	0.06	0	0	0
Amphibians	1	0.25	0.08	0	0	0
Reptiles	67	16.8	36.3	146	8.4	1.7
Birds	17	4.3	4.6	1077	62.1	76.1
Mammals	274	68.8	58.9	511	29.5	21.9

A previous study from Cyprus conducted during 2005–2007 (Bakaloudis et al. 2012), which combined pellets and prey remains from 12 Long-legged Buzzard nesting sites, found mammals (50.6% FO), reptiles (42.3% FO), and birds (7.2% FO) in the diet, with no analysis provided for % B. Bakaloudis et al. (2012) stated that “the black rat (46.3% FO) was the most important prey species found in the pooled data, followed by the starred agama (30.4% FO), the large whip snake (5.0% FO), and the Schneider’s skink (*Eumeces schneiderii*; 4.7% FO).” Our results partly agree with these except in the significance of the large whip snake, identified as the most important reptile (in % B) and the most important prey species overall (in % B) for 2005 and 2006. Also, our results showed the significance of the long-eared hedgehog, the third most important prey species by % B. Finally, the first 2 yr of our sampling (2005 and 2006) were closer to the Bakaloudis et al. (2012) findings (in % FO) rather than to our findings for 2018, when small mammals dominated the diet and reptiles decreased substantially.

The Long-legged Buzzard can be considered a species of high dietary plasticity because it uses food items from different prey categories and adjusts its diet according to food availability (e.g., greater consumption of black rats was observed in 2018). Friedemann et al. (2016) stated that “this plasticity facilitates colonization of new areas in Judea, Israel, and the species expansion to new areas,” which is also the case in Cyprus. Furthermore, the dietary diversity of the Long-legged Buzzard (23 prey taxa) supports their common characterization as a generalist predator. Our results also indicate a high preference for small mammals and reptiles, which is also supported by other studies. For instance, in Israel, the Long-legged Buzzard’s main prey items are lizards (mostly starred agama and Schneider’s skink) and to a lesser degree snakes (Friedemann et al. 2016). In our study, starred agamas and large whip snakes dominated the reptilian prey, with the lizards being more abundant and the snakes contributing higher biomass. In Iran, the breeding season diet of the Long-legged Buzzard was dominated by reptiles (56.4% frequency of prey items), mammals (37.5%), and birds (6.2%). The Persian squirrel (*Sciurus anomalus*), with 29.9% frequency, was the most important individual prey species. Based on the total biomass of collected prey items, reptiles, mammals, and birds accounted for 56.8%, 41.4%, and 1.9% of the diet, respectively (Shafaeipour 2015).

Diet overlap between Long-legged Buzzards and Bonelli’s Eagles. Pianka’s index of diet overlap between the two sympatric raptors shows a mean intermediate level (Grossman 1986, Novakowski et al. 2008) of 0.492, mostly due to the consumption of an abundant food resource, the black rat. There was also some degree of overlap of reptilian prey, even though the Bonelli’s Eagle almost exclusively ate lizards, whereas in the Long-legged Buzzard diet, the most significant reptilian contribution (% B) came from the large whip snake, while lizards were more numerous. Steenhof and Kochert (1985) stated that “overlap should be especially reduced in ranges shared with interspecifics.” On Cyprus, diet overlap should be studied in more depth and researchers should explicitly examine the diet of neighboring pairs, as the two raptors seem to be utilizing similar resources to some extent. This will provide insight on whether neighboring pairs of the two species have reduced diet overlap (suggesting different food sources) to avoid competition (Korpimäki 1987).

Sa-Oliveira et al. (2014) suggest that Levins’ index values lower than 0.4 indicate a species with a relatively limited niche. The Levins’ index for the Long-legged Buzzard diet decreased during the 3 yr of sampling from 0.485 (indicating a more generalist diet) in 2005 to 0.081 (a more specialized diet) in 2018. This was attributed to the larger contribution of reptiles in 2005 and a broader diet vs. the larger contribution of small mammals (mainly black rats and long-eared hedgehogs) in 2018 that dominated the raptor’s diet (almost 86% FO) and the concomitant decline in the reptile prey (7.3% FO) in 2018, compared to 2005 (24.4% FO) and 2006 (24.7% FO; Table S1). The average Long-legged Buzzard Levins’ index for the 3 yr was 0.236, indicating a narrow niche. A narrow niche can occur in a generalist species when there is a super-abundance of a particular prey species (e.g., the black rat) across the entire distribution of the sampled area (Aguiar-Silva et al. 2014). In addition, the Bonelli’s Eagle’s relatively low Levins’ index of 0.271 showed that the eagle’s diet was mostly dominated by a single prey group, the birds (62.1% FO). Similarly, in a Bonelli’s Eagle study in Sicily, Italy, Di Vittorio et al. (2019) found that “birds were the most frequently predated items (61.6%), followed by mammals (36.9%) and reptiles (1.5%). However, in terms of biomass, mammals were the main prey (65.71%), followed by birds (34.12%) and reptiles (0.17%).” A study in

Greece (1997–1999) showed that Bonelli's Eagles' main prey species were birds, primarily the Rock Pigeon (*Columba livia*) and Chukar (*Alectoris chukar*), whereas mammals were the most important class (57.5%), followed by birds (39.4%) and reptiles (2.8%; Alivizatos and Bourdakos 2002).

The mean prey biomass two-fold difference calculated in this study reflects the body size difference of the two raptors and may indicate a food-niche differentiation. Similar results were documented for Hen Harriers (*Circus cyaneus*) and Montagu's Harriers (*Circus pygargus*) in Spain, with resource partitioning that might have decreased competitive interactions (Garcia and Arroyo 2005). Breeding season diets have been examined for several avian predator assemblages, with mixed results and interpretations. For example, a study on the sympatric Golden Eagle (*Aquila chrysaetos*) and White-tailed Eagle (*A. albicilla*) found no evidence for competitive interactions (Whitfield et al. 2013), whereas a high dietary overlap was found between Red-tailed Hawks (*Buteo jamaicensis*) and Northern Goshawks in parts of Arizona that was probably negatively affecting the latter (Gatto et al. 2005). Furthermore, a small degree of diet overlap was found in a diurnal raptor community in Mexico (Hiraldo et al. 1991), and some dietary overlap was reported for Wedge-tailed Eagles (*Aquila audax*) and Little Eagles (*Hieraaetus morphnoides*), although the latter's population decline seemed unrelated to this (Olsen et al. 2010).

In a study of diet overlap and breeding in owls in Israel, Charter et al. (2018) found that diet overlap between Barn Owls (*Tyto alba*) and Long-eared Owls (*Asio otus*) increased when the two species utilized the same abundant food resource (rodents) without being a source of interspecific competition, something that may be similar to the utilization of black rats in our study. The diet of a large predator such as the Bonelli's Eagle in an island environment has been examined in Sicily (Di Vitorio et al. 2019), with shifts in diet found between the 1990s and 2011–2017 due to changes in prey abundance.

Motion-activated cameras used to study the diet of cliff-nesting Golden Eagles recorded twice the number of prey compared to analysis of pellets and prey remains, and were "more likely to detect the smallest and largest prey" (Harrison et al. 2019). Neither the use of cameras nor pellet analyses are perfect for prey identification. However, trail cameras placed at nests during nestling-rearing require careful planning and installation, because sensitive

species may abandon their nests. Francksen et al. (2016) stated that "direct methods of assessing diet present the most accurate description of raptor diets, but are relatively time consuming and expensive." Harrison et al. (2019) wrote that "cameras should be used judiciously because camera installation creates a persistent manipulation at the nest, when eagles are sensitive to disturbance. Cameras should only be used as part of a well-planned study, and investigators should follow protocols that minimize disturbance to eagles during installation and should camouflage camera appearance." We recognize the advantages of direct methods, but because a combination of pellets/prey remains is still widely regarded as an acceptable method for describing diet and because we wanted to compare Long-legged Buzzard diet with the older Bonelli's Eagle study, we chose pellets/prey remains for this investigation.

Implications for Conservation. Black rats are important for both sympatric predators, but more so for Long-legged Buzzards. The major geographical area of the Long-legged Buzzard's distribution on the island, from lower scrubland (mainly *Pistacia* spp.) and cultivated fields to mid-level thorny scrub/olive and carob trees to higher elevation tall *maquis* (mainly *Quercus* spp.), vineyards, and fruit orchards consists of preferred habitats for black rats. In fact, the Long-legged Buzzard's expansion over the last 30 yr on the island may be due to the utilization of this abundant food resource, in addition to possible climatic factors and the availability of vacant nesting territories. Given the extent of anticoagulant rat poison applied in the countryside to control rodents, secondary poisoning could pose a potentially serious conservation problem for both raptors. In fact, recent tests on other rodent predators, the Barn Owl and Long-eared Owl, on Cyprus showed residues of anticoagulants in the majority of specimens tested (N. Kassinis unpubl. data). This must act as a warning sign to decrease the widespread chemical application and find environmentally safer ways to control rodents.

SUPPLEMENTAL MATERIAL (available online). Table S1: Percent frequency of occurrence (% FO) and percent biomass (% B) of Long-legged Buzzard prey species from pellets and prey remains collected during 2005, 2006, and 2018 breeding seasons for all original 38 sampling sites in Cyprus. Table S2: Cumulative prey composition of the diet of Long-legged Buzzard during 2005, 2006, and 2018 nesting

seasons at all original 38 sites. Note: % FO = percent frequency of occurrence, and % B = percent biomass.

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Appendix. Dietary composition of Bonelli’s Eagle in Cyprus. Data pooled and analyzed were taken from Iezekiel et al. (2004) and span from 1999 through 2001. Mean prey biomass was calculated as 350 g ± SE 0.74. Note: n = prey items, % FO = percent frequency of occurrence, and % B = percent biomass.

TAXONOMIC CATEGORY	PREY SPECIES	n	% FO	% B
Reptiles	Starred agama (<i>Stellagama stelio</i>)	140	8.1	1.6
	Schneider’s skink (<i>Eumeces schneiderii</i>)	7	0.4	0.09
Total reptiles			8.5	1.7
Birds	Chukar (<i>Alectoris chukar</i>)	557	32.1	45.8
	Common Woodpigeon (<i>Columba palumbus</i>)	190	10.9	15.6
	Rock Dove (<i>Columba livia</i>)	173	10	9.9
	Eurasian Magpie (<i>Pica pica</i>)	52	3	1.7
	Eurasian Jackdaw (<i>Corvus monedula</i>)	57	3.3	2.3
	Eurasian Jay (<i>Garrulus glandarius</i>)	11	0.6	0.3
	Northern Long-eared Owl (<i>Asio otus</i>)	5	0.3	0.2
	Common Kestrel (<i>Falco tinnunculus</i>)	4	0.2	0.1
	Eurasian Blackbird (<i>Turdus merula</i>)	2	0.1	0.05
	Little Owl (<i>Athene noctua</i>)	2	0.1	0.06
	Black Francolin (<i>Francolinus francolinus</i>)	1	0.06	0.08
Total birds	unidentified avian spp.	23	1.4	0
			62.06	76.09
Mammals	Black rat (<i>Rattus rattus</i>)	467	26.9	11.5
	European hare (<i>Lepus europaeus</i>)	30	1.7	9.8
	Long-eared hedgehog (<i>Hemiechinus auritus</i>)	13	0.7	0.6
	unidentified carcass	2	0.1	0
Total mammals			29.4	21.9