

Prey dynamics and breeding performance in a generalist predator: The differential role of prey density, biomass, and effective consumption rates

Ignasi Torre^{a,b,*}, Joan Grajera^b, Fèlix Amat^{a,c}, Daniel Oro^d, Santi Mañosa^{e,f}

^a BiBio Research Group, Natural Sciences Museum of Granollers, Francesc Macià 51, 08402 Granollers, Spain

^b Small Mammal Research Area, Natural Sciences Museum of Granollers, Francesc Macià 51, 08402 Granollers, Spain

^c Herpetological Research Area, Natural Sciences Museum of Granollers, Francesc Macià 51, 08402 Granollers, Spain

^d Theoretical and Computational Ecology Group, Center for Advanced Studies of Blanes (CEAB-CSIC), Accés Cala Sant Francesc 14, 17300 Blanes, Spain

^e Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals. Institut de Recerca de La Biodiversitat (IRBio). Universitat de Barcelona. Facultat de Biologia, Avinguda Diagonal, 643, 08028-Barcelona, Catalonia, Spain

^f Institut de Recerca de La Biodiversitat (IRBio). Universitat de Barcelona. Facultat de Biologia, Avinguda Diagonal, 643, 08028-Barcelona, Catalonia, Spain

ARTICLE INFO

Keywords:

Environmental responses
Foraging strategy
Small mammals
Productivity
Trophic ecology

ABSTRACT

The breeding performance of predators is influenced by the differential consequences of prey density, prey biomass and effective consumption rates. Using camera traps at nests, we investigated whether changes in prey abundances caused functional and/or numerical responses of the common buzzard (*Buteo*) in a Mediterranean woodland region. After determining 1150 prey delivered to the nests by adults, we found that the biomass of prey caught was not a good indicator of its influence on individual life history traits such as productivity. Indeed, the consumption of small mammal prey, despite representing only 11% of the biomass delivered, had a much greater influence on buzzards' productivity than the consumption of snakes, which made up 47% of the biomass delivered. Live trapping evidenced that small mammals were roughly preyed according to its availability in the field, and their abundance in spring was directly related to buzzards' productivity and inversely related to hatching dates. Small mammals – mostly mice – can be considered as very suitable prey, owing quick handling times, profitability, and high energy intake. Our results pointed out the relevance of mice on buzzards' breeding performance, and altogether with the outstanding role of open-land small mammals on buzzards' demography during autumn-winter, suggested a key role of small mammals on buzzards' ecology throughout the year cycle in the Mediterranean area studied. These findings have important implications for our understanding of the foraging strategies of generalist species and the role that habitat and environmental factors play in shaping them.

1. Introduction

While specialized predators may be very sensitive to the fluctuation of the abundance of their specific prey (Arroyo and García, 2006; Llorente-Llurba et al., 2019), generalist predators are assumed to be more flexible in this respect, in some cases performing higher fitness as dietary breadth increases (Navarro-López et al., 2014). This was supposed to be the case for the common buzzard (*Buteo*), a generalist predator of small vertebrates, including small mammals, birds, and reptiles (del Hoyo et al., 1992). Dietary studies of the common buzzard in Europe revealed a very adaptable diet, dependent on the main prey availability in each area (Walls and Kenward, 2020), indicating the high plasticity of this species in terms of trophic behaviour. This high plasticity, observed at the continental and the population level, allows common buzzards to

live and perform very well in different habitats, from taiga to deciduous forest or Mediterranean woodlands, and from steppes to farmland (Walls and Kenward, 2020). One should expect to observe this dietary plasticity also at a more local scale, which should result in similar performance between pairs feeding on different prey within the same area. However, different research indicated that this was not the case, as breeding output (a proxy of performance or fitness) has been observed to fluctuate according to the temporal or spatial fluctuations of the availability or intake of one particular prey, usually voles (Francksen et al., 2017; Reif et al., 2001 2004; Selås et al., 2007; Swan et al., 2022) or rabbits (Graham et al., 1995; Rooney and Montgomery, 2013; Sim et al., 2001; Swann and Etheridge, 1995; Swan et al., 2022). This is a counterintuitive result that raised the question of why the high plasticity observed at the continental scale was not observed at more local scales. It seems as if,

* Corresponding author. BiBio Research Group, Natural Sciences Museum of Granollers, Francesc Macià 51, 08402 Granollers, Spain.
E-mail addresses: itorre@mcng.cat (I. Torre), famat@mcng.cat (F. Amat), d.oro@csic.es (D. Oro), smanosa@ub.edu (S. Mañosa).

in each area, there can only be one specific optimal prey on which to base the diet, and that switching to other prey inevitably results in a reduction of fitness. Previous studies determined this strong relationship between buzzard populations and specific prey, with buzzards responding functionally and numerically to the abundance of particular prey (Walls and Kenward, 2020). However, all these previous studies were conducted in northern continental Europe and Great Britain, in populations where the diet was dominated by a single abundant and profitable species, either voles or rabbits. Those are open-land mammals of optimal size for buzzards, which can become overabundant or experience population cycles (Hanski et al., 1991), generating a strong influence on buzzard populations. Nevertheless, no investigations in this regard have been conducted in areas where these optimal, locally, or temporally superabundant prey, do not exist. In such areas, buzzards were known to have a larger dietary breadth (Sergio et al., 2002), which included a wide range of prey such as birds, reptiles, and small mammals. In these areas, the question arises of how buzzards respond functionally to the availability of the different prey they consume, and whether buzzards exhibit or not a numerical response to the variation on some prey. This would allow us to better understand whether common buzzards behaved as generalist or specialist predators in these areas.

In Western Mediterranean, small mammals (rodents and shrews) are considered as key species for several generalists or specialists predators (Torre et al., 2018a), owing to their relevance in predators' diets. Indeed, some predators showed numerical responses to small mammal population changes (Torre et al., 2018b), and buzzards' demography was influenced by small mammals' dynamics during autumn-winter (Oro et al., 2021). In this study, we aimed to evaluate the existence of functional and numerical responses of common buzzards to changes in the abundance of some prey in a Mediterranean woodland region where neither voles nor rabbits are abundant. By setting camera traps at nests, the less biased available technique to evaluate and quantify provision rates (Francksen et al., 2016), we analysed whether annual breeding success (chicks raised per nest) was associated with the provisioning rates of different sorts of prey (mammals, reptiles, birds), and how variation in the diet was related to the annual changes in the availability of small mammals in live trapping plots. Buzzards are opportunistic predators (Graham et al., 1995; Reif et al., 2004), and we expected that their fertility to be influenced by the availability of the commonest prey species each year. Also, we expected higher dependency on small mammals during the pre-breeding and early breeding periods (late

winter-early spring), owing that alternative prey, such as reptiles, commonly consumed by buzzards during the breeding season in this area, are unavailable.

2. Material and methods

2.1. Study area and buzzard population

The study area is a transitional zone between two wooded and protected areas, Montnegre-Corredor and Serralada Litoral Natural Parks that comprises 70 km² of the Serralada Litoral of Barcelona (counties of El Maresme and El Vallès Oriental, Catalonia, NE Spain, Fig. 1). The study area is placed between 79 and 380 m above sea level (masl) and is covered by woodland (77%), mainly pine (*Pinus pinea*) and mixed oak-pine (*Quercus ilex* – *P. pinea*) Mediterranean forests, with the presence of riverside forests associated to small streams, as well as some farmland (15%), mainly devoted to cereal, set aside fields and orchards, and some urban areas (8%) (Otero et al., 2015). The area gives refuge to an estimated population of 54–125 common buzzard pairs (Macià et al., 2017). Between 2010 and 2019, we monitored the buzzards' annual productivity (number of chicks raised per nest) for a total of 50 breeding attempts (5 ± 1.49 SD nests/year).

2.2. Small mammal availability

Annual variation in small mammal availability was measured between 2010 and 2019 by eight SEMICE stations (www.semice.org; Torre et al., 2021) close to the study area (Fig. 1, Oro et al., 2021). Live trapping with a standardized sampling effort allowed the establishment of the relative annual abundance of common small mammal species in the study area. Each SEMICE station consisted of two live trapping sessions of three consecutive days each conducted in spring and fall, to account for seasonal population oscillations. At each site, we used 36 traps arranged in a 6 × 6 trapping grid, spaced 15 m, and were baited with a piece of apple and a mixture of tuna, flour and oil, including hydrophobic cotton for bedding (Torre et al., 2023). Traps were operated during three consecutive nights and revised during each early morning. The small mammals caught were identified to species, sexed, marked (rodents with ear tags – National Band Co. USA- and shrews with fur clips), and released at the point of capture. Only sampling sessions conducted in spring (mostly May) were used to characterize the small

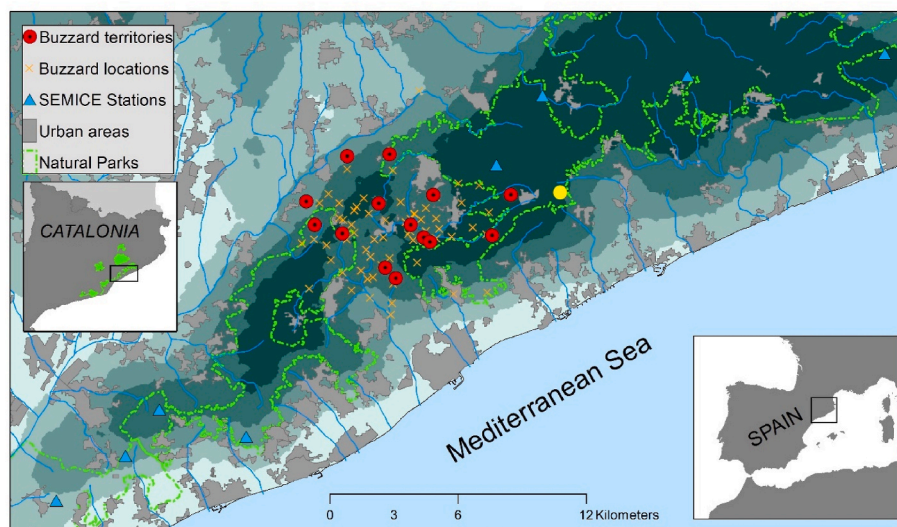


Fig. 1. Situation of nests (red dots) of the 14 territories of breeding buzzards monitored from 2010 to 2019. Blue triangles indicate the SEMICE stations that provided information on small mammal availability to breeding buzzards, and the yellow dot shows the bird station (Lorita). Green colours indicate interpolated forest cover (light green = low cover, dark green = high cover). Grey colours indicate urban areas.

mammals' availability to buzzards during the breeding period. Distance from the centre of the buzzard study area to the eight small mammal sampling stations ranged between 5 and 24 km, which is within the range of distances in studies of buzzards and synchronic small mammals' populations (Reif et al., 2004, for a similar approach). Small mammal species showed population spatial synchrony in the study area (Díaz et al., 2010; Stefanescu et al., 2020; Torre et al., 2022), and we expected that temporal (interannual) differences in abundance to be more relevant than spatial (plot/habitat) differences.

2.3. Buzzard diet analysis

Diet composition was studied using wildlife camera traps set on 24 nests between 2015 and 2019, corresponding to 10 different territories. Between four to six territories were studied every year. The cameras were fixed on branches near the nests (1–2 m apart), offering a complete view of the nest platforms (Selås et al., 2007; Tornberg and Reif, 2007). To avoid nest disturbances during the critical brood-rearing period (Robinson et al., 2017), cameras were installed when chicks were about 10 days old and were set for periods ranging from 2 to 43 days (median 11.5 days per nest, 279 camera-days). Information was recorded between May 15th and June 18th when the age of chicks ranged between 10 and 45 days. Photographs and measures (wing length and weight) of all the chicks were taken when cameras were first set on each nest, which were used to estimate their age and hatching date based on the criteria found on Dare (2015). This allowed determine the laying dates by subtracting an average of 35.5 days of incubation (33–38 days, Walls and Kenward, 2020). Only those files recorded between 5 a.m. and 10 p.m. were considered since no deliveries were detected outside that period (Selås et al., 2007). Prey were mostly identified by expert criteria owing that authors are specialists on the three main groups of prey species (e.g., birds: JG; reptiles: FA; small mammals: IT). Preys were classified to the lowest possible taxonomic level, although difficulties in specific identification from the images recorded limited identification to the Class or Family level in many cases. In the case of birds, we only were able to identify feathered individuals. The biomass of each delivered item was assigned according to its taxon, relative size or age and, eventually, sex. For rabbits, we assumed that consumed biomass represented a fraction of the original weight of the prey (Dare, 2015; Walls and Kenward, 2020), so we considered that a more realistic figure of rabbit biomass delivered to the nest would be between 150 and 350 g (Dare, 2015), depending on the obvious differences in the size of individuals delivered to the nests (small = 150 g, medium = 250 g, large = 350 g). Small mammals were identified by morphology and fur colouration (Selås et al., 2007), and were gathered in three main groups (mice, voles, and shrews), averaging the weight from captures obtained in the SEMICE stations around the study area (see below). In the case of rats, we considered three weight classes (small = 62 g, medium = 125 g, large = 187 g) according to the relative size of the individuals delivered to the nests, and for other mammals, we used standard weights in the area (squirrel: Gosálbez, 1987; weasel: Camps and Llimona, 2000). The biomass of reptiles was assigned according to evident differences in size (i.e., related to age and sex) of individuals identified in the videos/photos (appendix 1). For unidentified birds, an average biomass was assigned, according to the relative abundance in the field of different passerine species from annual censuses performed in May–June (SIOC, www.sioc.cat) in the only sampling station within the study area (Lorita, Fig. 1).

2.4. Data analyses

Generalized Linear Mixed Models (GLMM, Bolker et al., 2009) were used to ascertain variations in the number of prey items delivered daily by adults to the nests in the period 2015–2019 as a function of two fixed factors (Year, Month) and a covariate (age of chicks, in days). We considered territory as a random factor since adults selected every year

different nests within their territories. Response variables were the number of prey daily delivered to the nests (Poisson/Negative Binomial error distribution, see below), considering several prey categories (see Table 2).

Population indices of small mammals were obtained using TRIM software (Pannekoek and Strien, 2005), which allows the analysis of time series of counts with missing observations. Since TRIM uses linear models for the logarithm of expected counts in contingency tables, indices of abundance of the species were $\text{Log}(X + 1)$ transformed to avoid error in calculations (Torre et al., 2018a). GLMMs were used to analyse annual variations in spring abundance/availability of common small mammals (Poisson or Negative Binomial error distribution, see below) in the period 2010–2019, considering the year as a fixed factor, and the sampling plot as a random factor. Annual variations in buzzards' productivity were analysed for the same period of small mammals' abundance (2010–2019) by a GLMM considering mean productivity as the response (Gaussian error distribution), year as a fixed factor, and buzzards' territory as a random factor.

Species models showing dispersion irregularities (underdispersion, with scaled deviance <0.5 or overdispersion, with scaled deviance >1.5) were built with negative binomial instead of Poisson error distribution, to adapt better the models to the data (Zeileis et al., 2008). For the selected models, we calculated pseudo- R^2 values (Nakagawa and Schielzeth, 2013) using the R function *r.squaredGLMM* and the delta method for variance estimation. R-functions used were available in the packages *MuMIn* (Barton, 2015) and *lme4* (Bates et al., 2015). Multiple regression analysis was performed to ascertain whether mean annual productivity was related to mean annual small mammals' availability for the period 2010–2019, using mean productivity as the response, and the abundance of three groups of small mammal species (e.g., shrews, mice, and voles) as predictors. We used logarithmic fit owing that productivity was asymptotic and showed better adjustment than the linear fit. Associations between the number and biomass of prey items of each category delivered per day and buzzards' productivity (chicks/nest-year) were conducted using Pearson correlations and logarithmic regression.

3. Results

3.1. Diet composition and delivery rates

A total of 1150 prey deliveries were recorded using camera trapping (2015–2019), and 955 (83%) were identified at least to class level (including carrion) (Table 1). According to the number of items delivered to the nest, the diet of chicks was mostly based on mammals (55.6%), followed by reptiles (28.8%), birds (12.4%) and other sorts of prey (amphibia, invertebrates and carrion, 3%). Mice accounted for the bulk of identified small mammals delivered to the nest (69.9%), followed by voles (16.6%) and shrews (13.5%). Delivered reptiles comprised lizards (51%) and snakes (49%), meaning that lizards accounted for 14.7% and snakes for 14.1% of total prey deliveries to the nest.

When considering the biomass delivered to the nests, reptiles (52.6%) largely outweighed mammals (26.5%), birds (12.5%), amphibians (3.1%) or carrion (5.3%) (Table 1). The global contribution of snakes and lizards to the diet in terms of biomass was 47.3% and 5.3% respectively. The mammal biomass delivered to the nest mostly consisted of small mammals (mice, voles and shrews; 52.3%), and the main single contributions were due to mice (76.4%), followed by voles (17.2%) and shrews (6.3%). Mammal biomass delivered to the nest was 10.6% mice, 4.7% rats, 5.6% rabbits, 2.4% voles, 1.3% squirrels, 0.87% weasels, and 0.6% shrews.

Daily delivery rates (items/day) (Table 2) of total mammals, small mammals, and mice, decreased with the age of chicks, whereas bird deliveries increased with the age of chicks. Total prey delivery rates (preys/day) were minimum in 2017 (2.98 ± 0.26) and maximum in

Table 1
Number and biomass of prey delivered to the nests (2015–2019). Percentages are computed excluding unidentified prey or biomass.

Mammals	N	%	Biomass (g)	Biomass (%)
	531	55.60	17,535.5	26.50
<i>Crocicidura russula</i> (9 g)	36	3.77	324	0.49
<i>Sciurus vulgaris</i> (294 g)	3	0.31	882	1.33
<i>Rattus</i> sp. (62–187 g)	23	2.41	3113.5	4.71
<i>Apodemus/Mus</i> sp. (21 g)	186	19.48	3906	5.90
<i>Microtus/Clethrionomys</i> (20 g)	44	4.61	880	1.33
Undetermined small mammals (19 g)	218	22.83	4142	6.26
<i>Mustela nivalis</i> (196 g)	3	0.31	588	0.89
<i>Oryctolagus cuniculus</i> (150–350 g)	18	1.88	3700	5.59
Birds	118	12.36	8262.1	12.49
<i>Columba palumbus</i> (320.2 g)	9	0.94	2881.8	4.36
<i>Dendrocopos major</i> (75.7 g)	1	0.10	75.7	0.11
<i>Garulus glandarius</i> (109.5 g)	10	1.05	1095	1.65
<i>Turdus merula</i> (60.6 g)	5	0.52	303	0.46
<i>Strix aluco</i> (301.9 g)	1	0.10	301.9	0.46
<i>Tyto alba</i> (211.5 g)	2	0.21	423	0.64
<i>Buteo</i> (398.7 g)	2	0.21	797.5	1.21
Undetermined small birds (10.1 g)	61	6.39	619.9	0.94
Undetermined large birds (59.5 g)	27	2.83	1764.3	2.67
Reptiles	275	28.80	34,797.8	52.59
<i>Malpolon monspessulanus</i> (205.8–354 g)	25	2.62	7597.2	11.48
<i>Natrix astreptophora</i> (116.8–145.3 g)	11	1.15	1427.3	2.16
<i>Natrix maura</i> (38.9 g)	1	0.10	38.9	0.06
<i>Zamenis scalaris</i> (119.9–239.9 g)	61	6.39	14,014.1	21.18
<i>Coronella girondica</i> (23.1 g)	2	0.21	46.2	0.07
<i>Anguis fragilis</i> (16.9–20.1 g)	85	8.90	1561.9	2.36
<i>Timon lepidus</i> (213.2 g)	7	0.73	1492.4	2.26
<i>Psammotromus algirus</i> (7.5 g)	19	1.99	142.5	0.22
Undetermined snake (232 g)	35	3.66	8120	12.27
Undetermined lizard (17 g)	15	1.57	252.3	0.38
Undetermined small lizard (7.5 g)	14	1.47	105	0.16
Amphibia	16	1.68	2071.80	3.13
<i>Bufo spinosus</i> (146.3 g)	7	0.73	1024.10	1.55
<i>Epidalea calamita</i> (12.5 g)	1	0.10	12.50	0.02
Undetermined amphibia (129.4 g)	8	0.84	1035.20	1.56
Invertebrates	1	0.10	1.00	0.00
Carrion (250g)	14	1.47	3500	5.29
Unidentified small prey (16.7 g)	171	17.91	2855.7	4.32
Unidentified large prey (168.4 g)	24	2.51	4041.60	6.11
TOTAL	1150	—	73,065.50	100

2015 (5.34 ± 0.65). Small mammals (rodents and shrews) were the bulk of mammal prey daily delivered (1.79 ± 2.07), followed by reptiles (0.94 ± 1.07) and birds (0.42 ± 0.74). Predation rates on mice declined during 2016, especially in 2017 (0.08 ± 0.15), and increased in 2018, especially in 2019 (0.90 ± 0.12 , Table 3). Predation rates on shrews declined in years 2016, 2018, and 2019, but increased in 2017 (0.17 ± 0.04 , Table 3). Slow worms (*Anguis fragilis*) were less preyed in 2017 (0.21 ± 0.09) and 2019, and predation on birds decreased during 2019. Predation on snakes and whole reptile prey did not show interannual differences, but ladder snakes (*Zamenis scalaris*) were less preyed on in April than in May. Mean predation rates for the whole prey decreased in 2017.

3.2. Relationship between annual small mammals' abundance and small mammal delivery rates

During the study period (2010–2019) we captured 1395 small mammals of five species in eight SEMICE sampling stations. The wood mouse (*Apodemus sylvaticus*) was dominant with 63% of captures (879

individuals), followed by the Greater white-toothed shrew (*Crocicidura russula*, 14%), the Algerian mouse (*Mus spretus*, 10.8%), the bank vole (*Clethrionomys glareolus*, 2.6%), and the yellow-necked mouse (*Apodemus flavicollis*, 2.2%). The GLMMs testing for the interannual changes in abundance of wood mice and the whole mice indicated better fit and low overdispersion using the negative binomial instead of the Poisson distribution, but the contrary was true for the Algerian mouse and White-toothed shrew (Table 3). Considering the reference year (2015), wood mice abundance was significantly lower in 2013 ($\bar{x} = 2.25 \pm 2.81SE$, ind./plot), 2016 ($\bar{x} = 5.12 \pm 2.81SE$), and 2017 ($\bar{x} = 5.87 \pm 2.81SE$), and higher in 2011 ($\bar{x} = 20.75 \pm 2.81SE$) and 2019 ($\bar{x} = 20.37 \pm 2.81SE$), white-toothed shrews increased their abundance in 2013 ($\bar{x} = 4.25 \pm 1.36SE$) and 2017 ($\bar{x} = 4.0 \pm 1.36SE$), and Algerian mice increased in years 2011 ($\bar{x} = 3.87 \pm 1.90SE$), 2012 ($\bar{x} = 3.37 \pm 1.90SE$), 2018 ($\bar{x} = 2.75 \pm 1.90SE$), and 2019 ($\bar{x} = 4.0 \pm 1.90SE$). Wood and Algerian mice showed similar interannual variation in abundance ($r = 0.77$, $P = 0.01$, $n = 10$), but both rodents did not show similar population trends than white-toothed shrews ($r = -0.29$, $P = 0.42$, and $r = -0.19$, $P = 0.58$, $n = 10$; respectively).

The annual coefficients of the parameter estimates obtained in the GLMMs considering small mammal delivery rates (Table 2) and small mammal abundance in the field (Table 3) between 2015 and 2019 showed moderate association ($r = 0.82$, $P = 0.08$, $n = 5$), suggesting that this group could be preyed according to its availability in the field. Similar correlations were obtained from models considering mice alone ($r = 0.80$, $P = 0.1$). As a general pattern, in the years with the lowest small mammal abundance (2016–2017), buzzards preyed on less than 40% of this group, but during the year with higher small mammal abundance (2019), the frequency of predation increased to 50%. During 2017, the low predation rate on mice was compensated by the high predation rate on shrews.

3.3. Breeding success of buzzards: the role of prey delivery rate, small mammal availability, and laying date

Between 2010 and 2019 we documented the breeding success for a total of 50 buzzards' nests, from which 24 were also monitored for the diet. The mean number of breeding pairs detected per year in the area was 5.0 ± 1.5 (SD), ranging between three (years 2010 and 2013) and seven pairs (years 2015 and 2019). The laying dates of buzzards ranged between March 22 and April 3 ($\bar{x} = 03/27$) and the hatching dates between April 27 and May 9 ($\bar{x} = 05/02$). Average productivity was $1.88 \pm 0.66SD$ chicks/nest (range 1–3). The GLMM showed interannual variation in productivity (Wald $\chi^2 = 20.9$, $r^2 = 0.29$, $P = 0.01$, $df = 9$), with a significant decline in 2013 ($\bar{x} = 1.0 \pm 0.34$ S E chicks/nest) and 2017 ($\bar{x} = 1.20 \pm 0.26$ S E chicks/nest).

Mean annual chick productivity was strongly correlated to the mean number of daily mice deliveries to the nests ($r = 0.95$, $P = 0.014$, $n = 5$), mammals delivered ($r = 0.88$, $P = 0.049$, $n = 5$), and marginally correlated to total small mammals ($r = 0.85$, $P = 0.067$, $n = 5$), and total preys delivered ($r = 0.85$, $P = 0.065$, $n = 5$; Fig. 2). However, no other prey was correlated with productivity, and deliveries of other important preys such as reptiles ($r = 0.23$, $P = 0.71$, $n = 5$) or birds ($r = -0.34$, $P = 0.57$, $n = 5$), were not related to the average year productivity. These results were similar when considering the biomass delivered to the nests, which resulted in mammals being the most relevant category ($r = 0.99$, $P = 0.0006$, $n = 5$), followed by mice ($r = 0.94$, $P = 0.019$, $n = 5$), and small mammals ($r = 0.88$, $P = 0.049$, $n = 5$). No other prey had a positive effect on mean annual productivity, but small birds showed a negative association ($r = -0.90$, $P = 0.03$, $n = 5$).

For the total period (2010–2019), a multiple regression model indicated that mean annual productivity was strongly related to small mammal abundance in the eight sampling plots, showing a positive association to mice (coef. 0.02 ± 0.004 ; $t = 4.05$, $P = 0.005$) and a negative association to shrews (coef. -0.20 ± 0.03 ; $t = -6.15$, $P =$

Table 2

Generalized Linear Mixed Models (GLMM) of the number of preys delivered per day-nest by prey class, using year and month as fixed factors, age of chicks as a covariate, and buzzard territory as a random factor. Models were fitted by either Poisson or Negative binomial distributions (depending on overdispersion issues), selecting those showing higher fit (pseudo-R²) and lower AICc from a set of model candidates ($\Delta\text{AICc} \leq 2$). Overdispersion was tested by scaled deviance (ratio = residual deviance/df). Year 2015 was considered as the reference level (zeroed) by all the models. Standard error of estimates in parentheses.

	Mammals	Small mammals	Mice	Shrews	Voles	Rats	Rabbits
(Intercept)	1.58*** (0.31)	1.55*** (0.32)	0.55*** (0.01)	-1.80*** (0.00)	-2.63*** (0.66)	-2.91*** (0.73)	-3.03*** (0.44)
2016	-0.56* (0.24)	-0.59* (0.24)	-0.37*** (0.01)	-0.77*** (0.00)			
2017	-0.94*** (0.26)	-0.93*** (0.26)	-2.17*** (0.01)	0.85*** (0.00)			
2018	0.02 (0.26)	0.02 (0.27)	0.11*** (0.01)	-1.72*** (0.00)			
2019	0.01 (0.24)	0.05 (0.25)	0.36*** (0.01)	-0.53*** (0.00)			
Age of chicks (days)	-0.03*** (0.01)	-0.03*** (0.01)	-0.04*** (0.01)				
Log Likelihood	-470.75	-463.60	-277.38	-101.89	-117.51	-72.69	-66.08
AICc	958.02	943.74	571.30	216.09	241.10	159.78	136.20
R ² marginal	0.16	0.16	0.28	0.09	0.07	0.79	0.02
R ² conditional	0.44	0.45	0.42	0.20	0.32	0.792	0.04
Residual deviance (df 271)	281.58	280.65	213.69	117.53	102.54	95.04	86.3
Ratio	1.04	1.036	0.79	0.43	0.38	0.35	0.32
Num. Obs.	279	279	279	279	279	279	279
	Reptiles	Snakes	Ladder snake	Slow worm	Birds	Large birds	Small birds
(Intercept)	0.37* (0.16)	-0.68*** (0.20)	-1.65*** (0.21)	-0.54 (0.39)	-1.38** (0.42)	-3.63*** (0.76)	-1.53*** (0.19)
2016				-0.50 (0.38)	-0.36 (0.32)		
2017				-0.87* (0.42)	0.28 (0.32)		
2018				0.06 (0.43)	-0.28 (0.39)		
2019				-1.22** (0.43)	-0.72* (0.35)		
Month (May)			-0.96** (0.36)			0.62 (0.36)	
Age of chicks (days)					0.03** (0.01)	0.06** (0.02)	
Log Likelihood	-459.88	-265.10	-103.15	-209.71	-234.72	-144.81	-161.61
AICc	925.85	534.25	212.39	431.72	483.86	297.77	329.31
R ² marginal	0.03	0.03	0.05	0.08	0.08	0.07	0.03
R ² conditional	0.13	0.09	0.05	0.25	0.15	0.11	0.05
Residual deviance (df 271)	314.69	257.7	135.62	224.39	264.3	171.5	147.2
Ratio	1.16	0.95	0.5	0.83	0.97	0.63	0.54
Num. Obs.	279	279	279	279	279	279	279

Signif. Codes: ***p < 0.001, **p < 0.01, *p < 0.05, ·p < 0.1.

0.0004; Log-fit: adjusted $r^2 = 0.89$, $F_{2, 7} = 38.14$, $P = 0.0001$, Fig. 3). Interestingly, the mean annual hatching date was inversely related to mice abundance in the field (logarithmic fit: $r = -0.89$, $P < 0.01$, $n = 10$), and in the years with low abundance the hatching date was delayed for almost two weeks (Fig. 4). Furthermore, the buzzards' productivity decreased with the hatching date ($r = -0.84$, $P = 0.005$, $n = 10$). In years with high mice abundance (e.g., 2011 and 2019), females advanced laying (March 24) and hatching (April 29) dates. On the other side, in years with low mice abundance (e.g., 2013, 2016, 2017), females delayed laying (March 30 to April 3) and hatching (May 05 to May 09) dates.

4. Discussion

Obtaining accurate information on the demography of long-lived predators is puzzling mostly due to the difficulties in gathering data on prey and predators at suitable spatio-temporal scales (Korpimäki et al., 2020; Margalida et al., 2014; Oro and Furness, 2002; Rutz and Bijlsma, 2006). In this study, we investigated the role of nests' prey provisioning on buzzards' breeding performance over ten years (2010–2019), highlighting the positive role of mice abundance on

productivity (number of chicks raised per nest), and on advancing the laying dates. Using camera traps, a technique aimed at the obtention of relatively unbiased pictures of the diet composition of buzzards' diet during the breeding season (Francksen et al., 2016; Swan et al., 2022), altogether with data on small mammal abundance obtained in live trapping stations, allowed untangling the relevant role of these prey on buzzards' breeding performance.

Compared to previous research in other Mediterranean areas in Catalonia using more standard techniques (Mañosa and Cordero, 1992), our results showed a limited importance of rabbits and an outstanding importance of mice. The limited importance of rabbits was probably associated with the characteristics of the study area, dominated by forest, altogether with the rarefaction of this prey in Spain during the last decades (Virgós et al., 2007). However, we cannot rule out that differences in the composition of the diet were biased by different sampling methods used (i.e., video recordings vs. prey remains, Selås et al., 2007; Tornberg and Reif, 2007). The contribution of birds to the buzzard's diet was not globally important but increased significantly as the nestling period advanced, probably indicating a higher availability of newborn birds as the season progresses (Estrada et al., 2004), which makes them more attractive for a generalist predator. In fact, 91% of

Table 3

Generalized Linear Mixed Models (GLMM) of the abundance of *A. sylvaticus*, *M. spretus*, *C. russula*, mice, and the whole small mammals in the field during the period 2010–2019, using year as a fixed factor, and sampling station as a random factor. Models were fitted by either Poisson or Negative binomial distributions and showed pseudo-R² and AICc (see methods for details). The year 2015 was considered as the reference level (zeroed) by all the models. Standard error of estimates in parentheses.

	Small mammals (nbinomial)	Mice (nbinomial)	<i>A.sylvaticus</i> (nbinomial)	<i>M.spretus</i> (Poisson)	<i>C.russula</i> (Poisson)
	Estimate	Estimate	Estimate	Estimate	Estimate
Intercept	2.62*** (0.27)	2.34*** (0.30)	2.22*** (0.29)	−5.25 (3.46)	−1.45* (0.63)
YEAR: 2010	0.07 (0.24)	0.19 (0.28)	0.19 (0.30)	−0.19 (0.51)	0.15 (0.39)
YEAR: 2011	0.60* (0.23)	0.71** (0.27)	0.72* (0.30)	1.30*** (0.38)	0.56 (0.35)
YEAR: 2012	0.23 (0.24)	−0.12 (0.29)	−0.24 (0.32)	1.15** (0.39)	0.22 (0.38)
YEAR: 2013	−0.72** (0.26)	−1.47*** (0.34)	−1.61*** (0.38)	−0.75 (0.60)	1.04** (0.33)
YEAR: 2014	−0.27 (0.25)	−0.30 (0.29)	−0.34 (0.32)	0.42 (0.44)	0.40 (0.37)
YEAR: 2016	−0.68** (0.26)	−0.61* (0.30)	−0.65* (0.33)	−0.75 (0.61)	0.08 (0.39)
YEAR: 2017	−0.49 (0.25)	−0.75* (0.30)	−0.64* (0.33)	−1.04 (0.67)	0.98** (0.33)
YEAR: 2018	0.28 (0.24)	0.40 (0.27)	0.36 (0.30)	0.95* (0.40)	0.15 (0.39)
YEAR: 2019	0.70** (0.24)	0.66* (0.27)	0.67* (0.30)	1.32** (0.38)	0.60 (0.35)
Log Likelihood	−275.5	−257.4	−247.9	−94.2	−111.3
AICc	579.72	543.48	524.35	214.22	251.27
R ² marginal	0.29	0.37	0.41	0.03	0.51
R ² conditional	0.73	0.75	0.68	1	0.93
Residual deviance	90.02	95.19	90.27	99.38	64.93
Ratio	1.30	1.38	1.3	1.44	0.95
Df model	69	69	69	69	69

Signif. Codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '.' 1.

birds preyed by buzzards in northern Italy were nestlings or recently fledged (Sergio et al., 2002). The contribution of reptiles (mainly snakes and slow worms) was also very important (both in terms of relative frequency and biomass delivered), as already reported in other areas of Spain (Cordero and Mañosa, 1992; Tapia et al., 2007; Zuberogoitia et al., 2006), southern Norway (Selås et al., 2007), or northern Italy (Sergio et al., 2002).

Our results indicated that the average annual buzzards' reproductive output in the study area was mainly associated with the number of mice consumed which, in turn, was roughly related to the number of mice available in the field. The importance of mice was further supported by the relationship between spring mice abundance in the field and earlier hatching dates, which was also found to be related to higher breeding success, suggesting that the three parameters (small mammal abundance – laying/hatching dates – productivity) were interrelated (Korpimäki et al., 2020). Interestingly, delivery rates of mice were inversely related to the age of chicks, suggesting a relevant role of this prey during the early development phase. However, we are aware of the possibility of biases arising from our study not covering the entire development phase of the chicks in the nest (ages from 10 days old onwards, see Selås et al., 2007; Tornberg and Reif, 2007, for a similar approach). The buzzards also consumed large amounts of reptiles, which constituted more than half of the biomass delivered to the nests, largely above that of mammals or birds. However, variation in the consumption of reptiles did not explain the annual variation in breeding success, leading to an apparent paradox. This could be explained by mismatches between delivery and consumption rates in large prey (Slagsvold and Sonerud, 2007; Slagsvold et al., 2010).

Generalized diets at the species level can be the result of a sum of individual generalized diets or the sum of heterogeneously specialized diets at the individual or population level (Araújo et al., 2011). At the same time, specialization at the population level may arise because of the limited availability of different sorts of prey, or as a result of a real

preference for a given resource. In the first case, few intrapopulation variability in diet composition would be observed. In the second case, any intrapopulation variation in diet composition should be associated with some variation in survival or fecundity in favour of the individuals that consume the preferred prey (Arroyo and García, 2006; Llorente-Llurba et al., 2019). In the situation of common buzzards, previous research on the feeding and breeding ecology across Europe has revealed that breeding success in this species is tied to different prey in different areas, revealing the generalist character of this bird of prey at the species level, but its specialization ability at the population level. Indeed, the different patterns observed indicated different populations specializing in different prey, each exploiting a particular optimal prey. In Britain and Ireland, the rabbit (*Oryctolagus cuniculus*) is such an optimal prey (Graham et al., 1995; Sim et al., 2001; Swan et al., 2022), as well as in some Mediterranean areas in Spain (Mañosa and Cordero, 1992). Our results agreed with other dietary studies conducted in northern Spain, with mammals being dominant in front of reptiles (Tapia et al., 2007; Zuberogoitia et al., 2006). In the British Islands, many studies indicated a close relationship between rabbit abundance, rabbit intake, and breeding success (Rooney and Montgomery, 2013; Sim et al., 2001; Swann and Etheridge, 1995; Swan et al., 2022). Even in cases where the provisioning rates of voles and rabbits were both related to their abundance in the field (Swan et al., 2022), only the provisioning rate of rabbits was associated with a larger number of chicks. In this later study, even if the delivery rate of voles almost doubled that of rabbits, the biomass involved by the latter was almost six times higher, which would explain the observed relationship. In our study area, something similar could perhaps be expected to happen with reptiles, which are the most important prey delivered to nests in terms of biomass. However, this was not the case, and there was no relationship between the delivery rate of snakes or reptiles (nor in terms of numbers or biomass) and the number of chicks raised. Only the provisioning rate of mice (in terms of numbers or biomass) was significantly and positively associated with the number

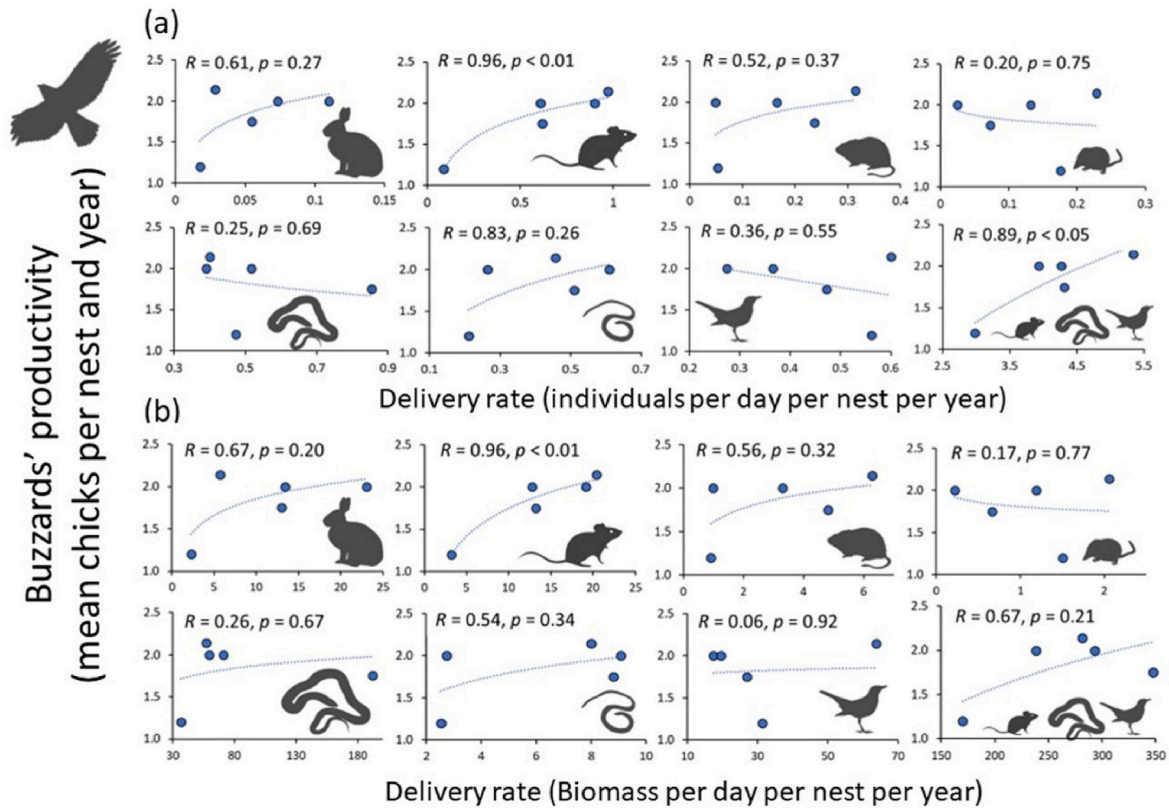


Fig. 2. Mean annual buzzard productivity (chicks raised per nest) related to the main prey items (a) and biomass (b) daily delivered to the nests during the period 2015–2019. From left to right: rabbits, mice, voles, shrews, snakes, slow worms, birds, and Total prey. Dots are mean values per day per year (n = 5). We showed the logarithmic fit (together with its coefficients of regression and p values) of the associations between variables. Only statistically significant associations (p < 0.05) with the categories “mice” and “total prey” were found.

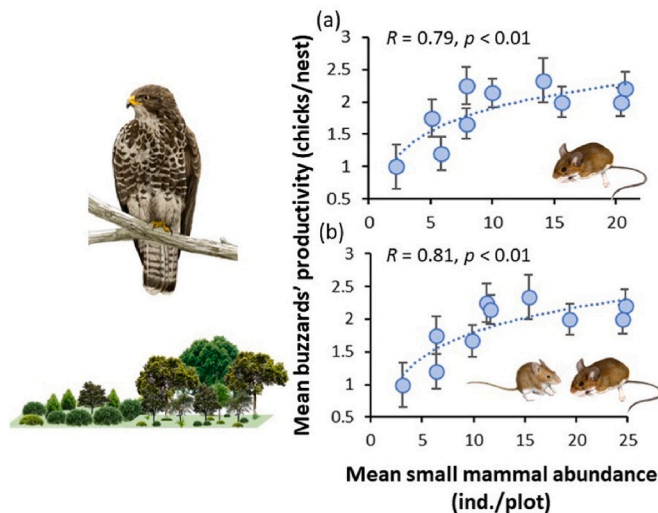


Fig. 3. Mean annual buzzard productivity (chicks raised per nest ± SE) related to the mean small mammal abundance – (a) wood mice and (b) all mice – in the eight sampling plots for the period 2010–2019. We show the fit of a logarithmic function (together with regression coefficients and p-values).

of chicks produced, contrasting with the above-mentioned studies, in which breeding success was associated to the most important prey in terms of biomass, being it rabbits (Swan et al., 2022) or voles (Tóth, 2014). In our study area, years with a higher abundance of mice roughly correlated with higher provisioning rates, indicating that the buzzards responded to the abundance of this prey. This resulted in a clear

association between mice abundance in the field or mice intake, with the number of chicks raised. It may seem intriguing why mice, a prey involving less than 11% of biomass delivered to the nest, have a relevant role in determining breeding success in front of snakes, which involved more than 47% biomass delivered. One possibility is the large difference in handling time and profitability of mice and reptiles in the nest. We observed that most mice delivered were ingested whole immediately by the chicks, while snakes (and other large prey) were hard to cut and could remain for hours or even days untouched. This hypothesis would agree with the findings of Selås (2001) in southern Norway, which suggested that the consumption of reptiles (mainly vipers and slow worms) by buzzards was somehow opportunistic, as the proportion of reptiles in the diet was higher in peak vole years, which was attributed to buzzards concentrated its hunting activity in habitats shared by voles and basking reptiles. Although we did not find such a relationship, the capture of reptiles may be also opportunistic, as suggested by the fact that the most important species identified (ladder snake, slow worm) are woodland inhabitants (Bas López, 1982; Valverde, 1967), as the preferred prey (wood mice, Torre et al., 2015). At the same time, this suggested that the buzzard, usually considered to prefer hunting in open land, may be well adapted to hunting within the forest – at least during the breeding period –, as has been already pointed out (Sergio et al., 2002).

In our study area mean laying dates (March 27) were similar compared to those reported for similar latitudes in northern Spain (March 28 in Bizkaia, Zuberogoitia et al., 2006). Nonetheless, laying dates were narrower (two weeks between the extreme dates) than in Bizkaia (six weeks). We hypothesised that the breeding phenology of buzzards was conditioned by prey availability in late winter when females start with the laying process (Sergio et al., 2002; Zuberogoitia et al., 2006). Since the pre-laying period is critical for females because

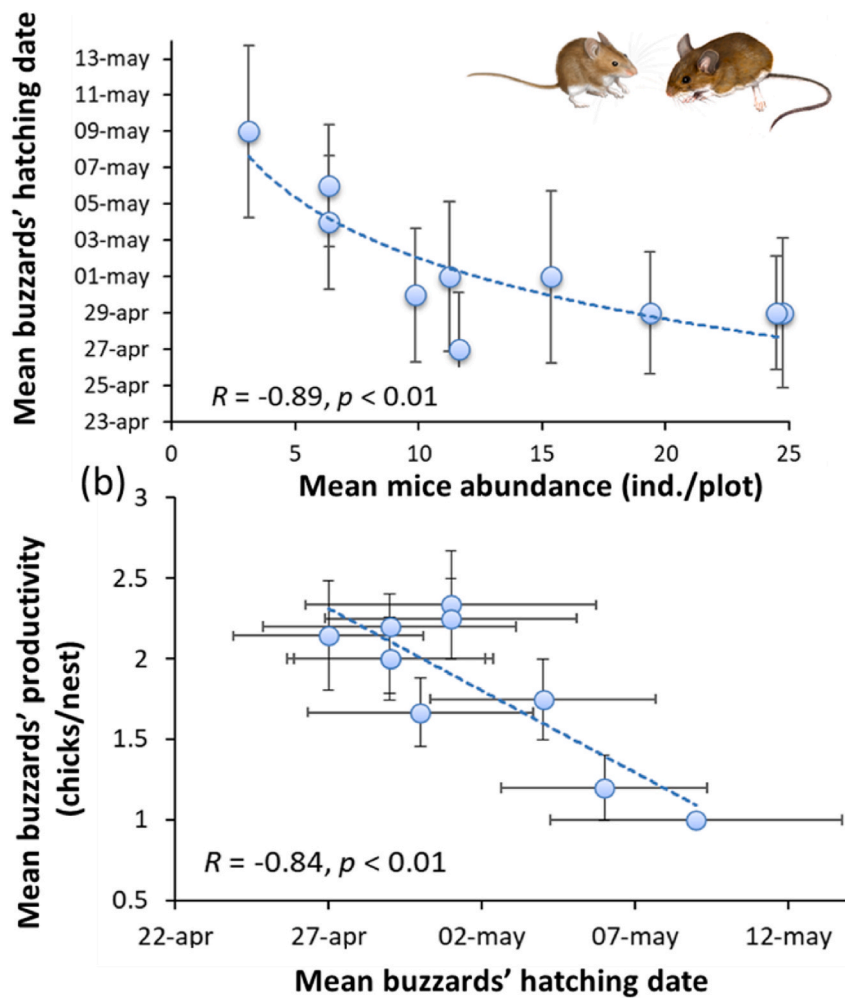


Fig. 4. Mean (\pm SE) annual hatching date (day-month) of buzzards related to (a) the mean mice abundance in the field, and (b) the mean annual productivity of buzzards in the period 2010–2019. We show the fit of a logarithmic function (together with regression coefficients and p-values).

they need energy for egg production and incubation (Newton, 1998; Hiron, 1982), food shortage will produce a delay in laying dates (Newton and Marquiss, 1981; Korpimäki et al., 2020). In this period of the year, only small mammals are available as potential prey, since reptiles are still hibernating, as well as other cold-blooded prey (invertebrates, amphibia). In years with high mice abundance, females reached earlier breeding conditions, advancing laying dates, as was observed in boreal owls feeding on voles (Korpimäki et al., 2020). On the other side, in years with low mice abundance, females delayed laying dates likely because they were not able to reach breeding conditions earlier (Hiron, 1982). Delaying breeding could increase the chance of feeding on alternative prey such as reptiles, which are more available in late spring as the breeding season progresses (Salvador, 2014). Nonetheless, more specific studies directly relating small mammals' availability (and other prey items) to the pre-laying period would be necessary to test such a hypothesis.

The relevant role of small mammals in the demography of buzzards was yet established during the autumn-winter in the study area, an especially unfavourable season for survival (Oro et al., 2021). These new results pointed out the importance of mice (mostly wood mice) on buzzards' breeding performance and owing to the outstanding role of open-land small mammals on buzzards' demography during autumn-winter, altogether suggested a key role of small mammals on buzzards' biology throughout the year cycle in the Mediterranean area studied. As revealed by this and another study (Oro et al., 2021), population asynchrony of mice and shrews allowed buzzards to predate on

particular species available during different years, and years with low predation rates on mice were compensated with high predation rates on shrews (e.g., 2017). Differential predation rates are a consequence of contrasting population dynamics, with wood mice populations increasing from autumn to spring, and white-toothed shrews showing the opposite pattern (Stefanescu et al., 2020; Torre et al., 2022). Our result agreed with other studies with diets based on voles, in which periods of voles' crash were compensated by provisioning other small mammals (Francksen et al., 2017). Small mammals can be considered as especially suitable prey for buzzards' chicks, owing to quick handling times, profitability, and high energy intake (Walls and Kenward, 2020). Indeed, we suggested small mammals as "biomass pills", in which chicks received a complete nutrition feeding on different tissues of the whole prey (e.g., flesh, bones, organs), thus increasing their survival and positively affecting buzzards' productivity. Despite the availability and limitation of the main food items can be a causal mechanism regulating the breeding phenology and success in buzzards and other generalist predators (Korpimäki et al., 2020; Rutz and Bijlsma, 2006), it is impossible to rule out that there were potentially other – non analysed – factors at play in our study system.

We provided evidence of the link between small mammal availability in the field and their predation rates, and between predation rates and the breeding phenology (i.e., hatching dates) and performance (i.e. productivity) of the common buzzard in a Mediterranean population. Also, we showed that large prey (in terms of biomass) played a secondary role, with small mammals, despite lower biomass delivered,

being more relevant owing to quick handling times, profitability, and high energy intake. Small mammals are also relevant prey for other generalist predators in the same area (Torre et al., 2018a), but in periods of low small mammal abundance generalist predators increased incidental predation on alternative prey (McKinnon et al., 2013; Reif et al., 2001). The dependence of buzzards' productivity on small mammals did not produce apparent breeding failure, but other raptors experienced complete failure (i.e., no breeding attempts or nest abandonment) in periods of scarcity of small mammals (Hirons 1982). In the case of buzzards, this successful breeding strategy was achieved by preying on alternative prey available in heterogeneous landscapes, combining either natural (i.e., forest and scrubland) or anthropized areas (i.e., crops). Indeed, most of the buzzards' territories studied were outside protected natural areas (9 out of 14, 64%), but all of them were placed in buffer zones (Lecina-Diaz et al., 2019), being considered as biodiversity hotspots in which buzzards can find a variety of prey items. As a forest generalist species, in our study area buzzards find more food resources in prey-rich landscapes, such as agro-silvo-pastoral mosaics found in the periphery of dense woodland (Gonçalves et al., 2012) outside protected areas, but benefit from more shelter for nests inside protected areas, owing the higher protection and surveillance by the authorities as well as the more forest cover available (Lecina-Diaz et al., 2019). Therefore, for the preservation of breeding buzzards, it is important to have conservation and management strategies encompassing both breeding and feeding territories.

Funding

Regional conservation agencies (Barcelona Provincial Council – Diputació de Barcelona – ref. 2015/3456, Dept. De Territori i Sostenibilitat – Generalitat de Catalunya) provided financial support to SEMICE (2010–2020). JG funded on his own all fieldwork research on buzzards.

Ethics approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. Investigations regarding small mammals followed the ethical guidelines for the use of wild mammals in research and education. All surveys were conducted with special permission for small mammals' scientific capture issued by the Catalan Government (Generalitat de Catalunya): 2010–SF/446; 2011–SF/389; 2012–SF/285; 2013–SF/519; 2014–SF/617; 2015–SF/778; 2016–SF/687; 2017–SF/891; 2018–SF/743.2019–SF/0554. Buzzards' populations were monitored under a special scientific permission of the Catalan Government (Generalitat de Catalunya).

CRediT authorship contribution statement

Ignasi Torre: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Joan Grajera:** Conceptualization, Data curation, Investigation, Methodology, Resources, Supervision, Validation, Writing – review & editing. **Fèlix Amat:** Investigation, Methodology, Validation, Writing – review & editing. **Daniel Oro:** Methodology, Supervision, Writing – review & editing. **Santi Mañosa:** Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We are grateful to the landowners and farmers who facilitated logistics, and to Institut Català d'Ornitologia (ICO), Raül Aymí, Francesc Carbonell, Héctor Andino, Mònica Alonso, and Andreu Carretero. We thank Diputació de Barcelona and Collserola Natural Park for providing financial and logistic support to the SEMICE program from 2008 until date, and Antoni Arrizabalaga for providing bureaucratic support. We want to acknowledge the volunteers and professionals in charge of SEMICE stations, who conducted fieldwork in the study area: Dolors Escruela, James Manresa, Marçal Pou, Tomàs Pulido, Alfons Raspall, Joan Manuel Riera, Cristina Terraza, and Marc Vilella (statistical support). Alfons Raspall and Toni Llobet kindly provided colour pictures of the small mammals and the buzzard. B/W images of buzzards' prey (Fig. 2) were taken from PhyloPic web (phylopic.org), available under the Creative Commons License. We also acknowledge the role of two reviewers and the editor to improve the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2024.103999>.

References

- Araújo, M.S., Bolnick, D.I., Layman, C.A., 2011. The ecological causes of individual specialisation. *Ecol. Lett.* 14, 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>.
- Arroyo, B.E., García, J.T., 2006. Diet composition influences annual breeding success of Montagu's Harriers *Circus pygargus* feeding on diverse prey. *Bird Study* 53, 73–78.
- Barton, K., 2015. MuMIn: multi-model inference. R Package Version 1 (15.6).
- Bas López, S., 1982. La Comunidad Herpetológica de Caurel: Biogeografía y Ecología. *Amphibia-Reptilia* 3, 1–26. <https://doi.org/10.1163/156853882X00121>.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67. <https://doi.org/10.18637/jss.v067.i01>.
- Bolker, B.M., Brooks, M.E., Clark, C.J., et al., 2009. Generalized linear mixed models: a practical guide for ecology and evolution - ScienceDirect. *Trends Ecol. Evol.* 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>.
- Camps, D., Llimona, F., 2000. Primeres dades sobre l'estudi de la mostela (*Mustela nivalis*) al Parc de Collserola. In: Llimona, F., Espelta, J.M., Guix, J.C., Mateos, E., Rodríguez-Tejedor, J.D. (Eds.), *I Jornades sobre Recerca en els sistemes naturals de Collserola: aplicacions a la gestió del Parc*, pp. 111–114.
- Del Hoyo, J., Elliott, A., Sargatal, J., 1992. *Handbook of the Birds of the World, vol. 1*. Lynx Edicions, Barcelona.
- Díaz, M., Torre, I., Arrizabalaga, A., 2010. Relative roles of density and rainfall on the short-term regulation of Mediterranean wood mouse *Apodemus sylvaticus* populations. *Acta Theriol.* 55, 251–260. <https://doi.org/10.4098/j.at.0001-7051.046.2009>.
- Estrada, J., Pedrocchi, V., Brotons, L., Herrando, S. (Eds.), 2004. *Atles dels ocells nidificants de Catalunya 1999-2002*. Institut Català d'Ornitologia (ICO)/Lynx Edicions, Barcelona.
- Francksen, R.M., Whittingham, M.J., Baines, D., 2016. Assessing prey provisioned to Common Buzzard *Buteo buteo* chicks: a comparison of methods. *Bird Study*. 63, 303–310. <https://doi.org/10.1080/00063657.2016.1183111>.
- Francksen, R.M., Whittingham, M.J., Ludwig, S.C., Roos, S., Baines, D., 2017. Numerical and uncensored responses of Common Buzzards *Buteo buteo* to prey abundance on a Scottish grouse moor. *Ibis* 159, 541–553. <https://doi.org/10.1111/ibi.12471>.
- Gonçalves, P., Alcobia, S., Simões, L., Santos-Reis, M., 2012. Effects of management options on mammal richness in a Mediterranean agro-silvo-pastoral system. *Agrofor. Syst.* 85, 383–395. <https://doi.org/10.1007/s10457-011-9439-7>.
- Gosálbez, J., 1987. *Insectívors i Rosegadors de Catalunya. Metodologia i catàleg faunístic*. Ketres editora, Barcelona, p. 241.
- Graham, I.M., Redpath, S.M., Thirgood, S.J., 1995. The diet and breeding density of Common Buzzards *Buteo buteo* in relation to indices of prey abundance. *Hous. Theor. Soc.* 42, 165–173. <https://doi.org/10.1080/00063659509477162>.
- Hanski, I., Hansson, L., Henttonen, H., 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 60, 353–367. <https://doi.org/10.2307/5465>.
- Hirons, G.J.M., 1982. The effects of fluctuations in rodent numbers on breeding success in the Tawny owl *Strix aluco*. *Mamm. Rev.* 12, 155–157. <https://doi.org/10.1111/j.1365-2907.1982.tb00011.x>.
- Korpimäki, E., Hongisto, K., Masoero, G., Laaksonen, T., 2020. The difference between generalist and specialist: the effects of wide fluctuations in main food abundance on

- numbers and reproduction of two co-existing predators. *J. Avian Biol.* 51 <https://doi.org/10.1111/jav.02508>.
- Lecina-Díaz, J., Alvarez, A., De Cáceres, M., Herrando, S., Vayreda, J., Retana, J., 2019. Are protected areas preserving ecosystem services and biodiversity? Insights from Mediterranean forests and shrublands. *Landsc. Ecol.* 34, 2307–2321. <https://doi.org/10.1007/s10980-019-00887-8>.
- Llorente-Llurba, E., Bota, G., Pujol-Buxó, E., Bonfil, J., Gálvez, M., Montés, G., Bas, J., Moncafé, F., Pont, F., Mañosa, S., 2019. Diet composition and breeding success of the Black-winged kite on the Lleida Plains in relation to population size. *ARDEOLA* 66, 33–50. <https://doi.org/10.13157/arla.66.1.2019.ra3>.
- Macià, F.X., Larruy, X., Grajera, J., Mañosa, S., 2017. Mida poblacional i densitat de rapinyaires forestals a la Serralada Litoral. III trobada d'Estudiosos de la Serralada Litoral Central i VII del Montnegre i el Corredor. Col·lecció Eines. Diputació de Barcelona, pp. 260–273.
- Margalida, A., Colomer, M.A., Oro, D., 2014. Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecol. Appl.* 24, 436–444. <https://doi.org/10.1890/13-0414.1>.
- Mckinnon, L., Berteaux, D., Gauthier, G., Bêty, J., 2013. Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos* 122, 1042–1048.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
- Navarro-López, J., Vergara, P., Fargallo, J.A., 2014. Trophic niche width, offspring condition and immunity in a raptor species. *Oecologia* 174 (4), 1215–1224. <https://doi.org/10.1007/s00442-013-2855-9>.
- Newton, I., 1998. Population Limitation in Birds. Academic Press, London.
- Newton, I., Marquiss, M., 1981. Effects of additional food on laying dates and clutch sizes of sparrowhawks. *Ornis Scand.* 12, 224–229.
- Oro, D., Furness, R.W., 2002. Influences of food availability and predation on survival of kittiwakes. *Ecology* 83, 2516–2528.
- Oro, D., Sanz-Aguilar, A., Carbonell, F., et al., 2021. Multi-species prey dynamics influences local survival in resident and wintering generalist predators. *Oecologia (Berl.)* 197, 437–446. <https://doi.org/10.1007/s00442-021-05042-2>.
- Otero, I., Marull, J., Tello, E., Diana, G.L., Pons, M., Coll, F., Boada, M., 2015. Land abandonment, landscape, and biodiversity: questioning the restorative character of the forest transition in the Mediterranean. *Ecol. Soc.* 20 <https://doi.org/10.5751/ES-07378-200207>.
- Pannekoek, J., Strien, A. Van, 2005. TRIM 3 Manual (Trends & Indices for Monitoring Data).
- Reif, V., Tornberg, R., Jungell, S., Korpimäki, E., 2001. Diet variation of common buzzards in Finland supports the alternative prey hypothesis. *Ecography* 24, 267–274.
- Reif, V., Jungell, S., Korpimäki, E., et al., 2004. Numerical response of common buzzards and predation rate of main and alternative prey under fluctuating food conditions. *Ann. Zool. Fenn.* 41, 599–607.
- Robinson, B.G., Franke, A., Derocher, A.E., 2017. Weather-mediated decline in prey delivery rates causes food-limitation in a top avian predator. *J. Avian Biol.* 48, 748–758. <https://doi.org/10.1111/jav.01130>.
- Rooney, E., Montgomery, I., 2013. Diet diversity of the Common Buzzard (*Buteo buteo*) in a vole-less environment. *Hous. Theor. Soc.* 60, 147–155. <https://doi.org/10.1080/00063657.2013.772085>.
- Rutz, C., Bijlsma, R.G., 2006. Food-limitation in a generalist predator. *Proc R Soc B Biol Sci* 273, 2069–2076. <https://doi.org/10.1098/rspb.2006.3507>.
- Salvador, A., Coordinador, 2014. Reptiles. 2ª edición revisada y aumentada. En: fauna Ibérica. In: Ramos, M.A., et al. (Eds.), Museo Nacional de Ciencias Naturales, vol. 10. CSIC, Madrid, p. 372, 1.
- Selås, V., 2001. Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey, voles. *Can. J. Zool.* 79, 2086–2093.
- Selås, V., Tveiten, R., Aanonsen, O.M., 2007. Diet of Common Buzzards (*Buteo buteo*) in southern Norway determined from prey remains and video recordings. *Ornis Fenn.* 84, 97–104.
- Sergio, F., Boto, A., Bogliani, G., 2002. Density, nest sites, diet, and productivity of common buzzards (*Buteo buteo*) in the Italian pre-Alps. *J. Raptor Res.* 36, 24–32.
- Sim, I.M.W., Cross, A.V., Lamacraft, D.L., Pain, D.J., 2001. Correlates of common buzzard *Buteo buteo* density and breeding success in the west midlands. *Hous. Theor. Soc.* 48, 317–329. <https://doi.org/10.1080/00063650109461231>.
- Slagsvold, T., Sonerud, G.A., 2007. Prey size and ingestion rate in raptors: importance for sex roles and reversed sexual size dimorphism. *J. Avian Biol.* 38, 650–661. <https://doi.org/10.1111/j.2007.0908-8857.04022.x>.
- Slagsvold, T., Sonerud, G.A., Grønlien, H.E., Stige, L.C., 2010. Prey handling in raptors in relation to their morphology and feeding niches. *J. Avian Biol.* 41, 488–497. <https://doi.org/10.1111/j.1600-048X.2010.05081.x>, 2010doi.
- Stefanescu, C., Soldevila, A., Gutiérrez, C., Torre, I., Ubach, A., Miralles, M., 2020. Explosions demogràfiques de l'eruga peluda del suro, *Lymantria dispar* (Linnaeus, 1758), als boscos del Montnegre el 2019 i 2020: possibles causes, impactes i idoneïtat dels tractaments per combatre la plaga. *Bull. Inst. Catalana Historia Nat.* (1901) 84, 267–279.
- Swan, G.J.F., Bearhop, S., Redpath, S.M., Silk, M.J., Padfield, D., Goodwin, C.E.D., McDonald, R.A., 2022. Associations between abundances of free-roaming gamebirds and common buzzards *Buteo buteo* are not driven by consumption of gamebirds in the buzzard breeding season. *Ecol. Evol.* 12, e8877 <https://doi.org/10.1002/ece3.8877>.
- Swann, R.L., Etheridge, B., 1995. A comparison of breeding success and prey of the Common Buzzard *Buteo buteo* in two areas of northern Scotland. *Bird Study* 42, 37–43. <https://doi.org/10.1080/00063659509477146>.
- Tapia, L., Domínguez, J., Romeu, M., 2007. Diet of Common buzzard (*Buteo buteo*) (Linnaeus, 1758) in an area of Northwestern Spain as assessed by direct observation from blinds. *Nov. Acta Cient. Compostelana* 16, 145–149.
- Tornberg, R., Reif, V., 2007. Assessing the diet of birds of prey: a comparison of prey items found in nests and images. *Ornis Fenn.* 84, 21–31.
- Torre, I., Gracia-Quintas, L., Arrizabalaga, A., Baucells, J., Díaz, M., 2015. Are recent changes in the terrestrial small mammal communities related to land use change? A test using pellet analyses. *Ecol. Res.* 30, 813–819. <https://doi.org/10.1007/s11284-015-1279-x>.
- Torre, I., Raspall, A., Arrizabalaga, A., Díaz, M., 2018a. SEMICE: an unbiased and powerful monitoring protocol for small mammals in the Mediterranean Region. *Mamm. Biol.* 88, 161–167. <https://doi.org/10.1016/j.mambio.2017.10.009>.
- Torre, I., Raspall, A., Arrizabalaga, A., Díaz, M., 2018b. Weasel (*Mustela nivalis*) decline in NE Spain: prey or land use change? *Mammal Research* 63, 501–505. <https://doi.org/10.1007/s13364-018-0388-7>.
- Torre, I., López-Baucells, A., Stefanescu, C., et al., 2021. Concurrent butterfly, bat and small mammal monitoring programmes using citizen science in Catalonia (NE Spain): a historical review and future directions. *Diversity* 13, 454. <https://doi.org/10.3390/D13090454>.
- Torre, I., Jaime-González, C., Díaz, M., 2022. Habitat suitability for small mammals in mediterranean landscapes: how and why shrubs matter. *Sustainability* 14, 1562. <https://doi.org/10.3390/SU14031562>.
- Torre, I., Bustamante, P., Flaquer, C., Oliveira, F.G., 2023. Is bedding material a more effective thermal insulator than trap cover for small mammal trapping? A field experiment. *J. Therm. Biol.* 118, 103738 <https://doi.org/10.1016/J.JTHERBIO.2023.103738>.
- Tóth, L., 2014. Numerical response of the common buzzard *buteo buteo* to the changes in abundance of small mammals. *Ornis Hung.* 22, 48–56. <https://doi.org/10.2478/orhu-2014-0010>.
- Valverde, J.A., 1967. Estructura de una comunidad mediterránea de vertebrados terrestres. *Monografías Estación Biológica de Doñana* 1, 1–218.
- Walls, S., Kenward, R., 2020. *The Common Buzzard*. T & AD POYSER, London, UK.
- Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. *J. Stat. Software* 27, 1–25. <https://doi.org/10.18637/jss.v027.i08>.
- Zuberogoitia, I., Martínez, J.E., Martínez, J.A., Zabala, J., Calvo, J.F., Castillo, I., Azkona, A., Iraeta, A., Hidalgo, S., 2006. Influence of management practices on nest site habitat selection, breeding and diet of the common buzzard *Buteo buteo* in two different areas of Spain. *ARDEOLA* 53, 83–98.