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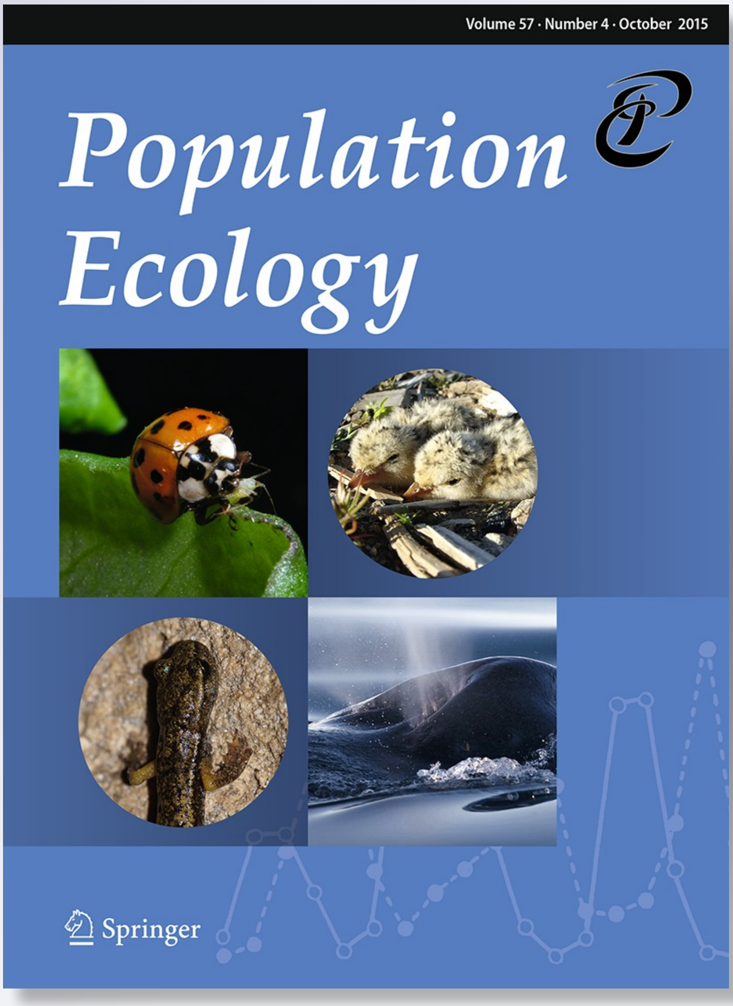

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ORIGINAL ARTICLE

Evaluating the influence of diet-related variables on breeding performance and home range behaviour of a top predator

Rui Lourenço[1] · **Maria del Mar Delgado**[2,3] · **Letizia Campioni**[4] · **Erkki Korpimäki**[5] · **Vincenzo Penteriani**[2,6]

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Abstract Diet composition is linked to reproductive performance directly or indirectly by other life-history traits, including home range behaviour. The relationships between prey abundance, diet and individual fitness have often been explored. However, these relationships are complex and difficult to disentangle, especially in vertebrate top predators. Here, we present the results of a long-term study using multi-model inference procedures to elucidate the influence of diet-related variables on breeding parameters and home range behaviour of a top predator, the eagle owl *Bubo bubo*. Superpredation, diet diversity, rat biomass and rabbit mean weight were the most important variables when analysing reproductive parameters, suggesting that less diverse diets with greater rabbit biomass percentage may benefit reproductive performance, whereas rat biomass percentage is apparently associated with greater variation of breeding success. Earlier laying dates seem to be associated with the consumption, on average, of smaller rabbits. On the other hand, edge density was the most relevant factor determining the variation in home range behaviour, with individual characteristics, such as age and sex, also being important. Although the relative importance of the diet-related variables was generally low, mean weight of alternative prey, diet diversity and rabbit biomass also helped to explain home range parameters. In an optimal foraging context, centred on the abundance of the main prey species, our results suggest that when rabbits are less available eagle owls may increase home range size in order to obtain alternative prey, increasing at the same time their dietary diversity, which may also require higher movement speed.

Keywords Diet diversity · Foraging theory · Optimal diet · Predator–prey relationships · Prey size variation

Introduction

The study of diet is a primary subject in animal ecology since it is related to crucial aspects of life-history and, ultimately, to individual fitness. The relationships between diet and fitness have often been studied in the framework of optimal foraging theory (MacArthur and Pianka 1966; Schoener 1971; Perry and Pianka 1997), being generally accepted that the reproductive performance of an animal should be explained in part by its food intake and the effort associated with obtaining it (Perry and Pianka 1997). Despite the fact that optimal foraging theory fails in explaining several cases, it still holds some robust

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✉ Rui Lourenço
lourenco@uevora.pt

[1] Labor-Laboratory of Ornithology, Instituto de Ciências Agrárias e Ambientais Mediterrânicas, Universidade de Évora-Núcleo da Mitra, Ap. 94, 7002-554 Évora, Portugal

[2] Department of Conservation Biology, Estación Biológica de Doñana, CSIC, c/Americo Vespucio s/n, 41092 Seville, Spain

[3] Metapopulation Research Group, Department of Biosciences, University of Helsinki, 00014 Helsinki, Finland

[4] MARE, Marine and Environmental Sciences Centre, ISPA Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal

[5] Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland

[6] Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University-Campus Mieres, 33600 Mieres, Spain

predictions (MacArthur and Pianka 1966; Schoener 1971; Perry and Pianka 1997; Sih and Christensen 2001): (1) predators should prefer more profitable prey, i.e., those that yield more energy per time spent in search, pursuit, handling and eating; (2) when the abundance of a higher value prey increases, the lower value prey should be less frequently consumed, and consequently diets should be broader in times of food scarcity; and (3) predators should follow a quantitative threshold rule for when specific prey types should be included or excluded from the diet.

Life-history studies of vertebrate predators (e.g., breeding biology, diet, home range behaviour) have traditionally been common in the literature [we present a literature review in Electronic Supplementary Material (ESM)], and from them we have learned that prey abundance may influence individual fitness directly, and indirectly by affecting other individual characteristics such as home range behaviour, foraging, and diet (Korpimäki 1986, 1992a, b; Korpimäki and Norrdahl 1991; Moleón et al. 2009; Terraube et al. 2011; Santangeli et al. 2012; Penteriani et al. 2013). However, the relationships between prey abundance and other life-history traits are not always direct and simple to interpret. For example, in food-specialist species, variations in prey abundance may not alter feeding ecology (detected mostly by changes in diet composition), yet change the parameters related to reproductive performance and home range and movement behaviour, often resulting in a numerical response reflected in the predator's density (Korpimäki and Norrdahl 1991; Dupuy et al. 2009; Terraube et al. 2011). In food-generalist species, variations in prey abundance may frequently cause a functional response, with changes in dietary characteristics, such as prey frequency and diversity (Korpimäki and Norrdahl 1989, 1991; Dupuy et al. 2009; Moleón et al. 2012). To the best of our knowledge, only a few ecological studies in raptors have considered more specific diet features (e.g., diet diversity, prey mean weight; see Table S2 in ESM), yet these factors may sometimes provide a deeper understanding of the relationship between prey abundance and individual fitness. Considering specific dietary features may be especially relevant when: (1) the estimates of prey abundance are not completely reliable because of methodological limitations (Fernández-de-Simon et al. 2011); (2) prey abundance does not fully reflect prey availability (Janes 1984; Ontiveros et al. 2005); (3) prey is not consumed in proportion to its occurrence in the field; and (4) the main prey species shows considerable differences in size and behaviour which influences profitability (Werner and Hall 1974). Still, individual fitness and home range behaviour can be influenced directly or indirectly by several other factors besides diet, which can also interact among themselves, particularly: (1) landscape characteristics; (2) intra- and interspecific interactions; (3) human disturbance; (4) individual characteristics; (5) weather; and (6) physiological condition (see ESM for references).

As dietary studies are very common in vertebrate predators (Herrera and Hiraldo 1976; Marti et al. 1993; Virgós et al. 1999; Lourenço et al. 2011; Díaz-Ruiz et al. 2013), which are often threatened species, understanding how diet composition is related to other individual characteristics (e.g., home range behaviour) and their associated fitness represents a useful tool in ecology and conservation. In a previous study, we demonstrated that the home range behaviour of eagle owls *Bubo bubo* is influenced by both internal and external factors, with a relevant role played by habitat structure and composition (dense vegetation, sparse scrubland, and edge density), phenology, sex, age, and health state (Campioni et al. 2013). In that same study, we also found that reproductive success is influenced by the biomass percentage of its main prey (rabbits *Oryctolagus cuniculus*) in the diet, whereas we observed no relevant effects influencing laying date. An unexpected result in Campioni et al. (2013) was the absence of an obvious effect of rabbit abundance on home range behaviour and reproductive parameters. This may have been due to the fact that (1) this prey is very abundant in the study area and, thus it is not a limiting factor (Campioni et al. 2013); or (2) the result of methodological constraints of abundance estimates (Fernandez-de-Simon et al. 2011). Therefore, in some cases, can diet-related variables explain reproductive performance and home range behaviour better than prey abundance? From our literature review (ESM), we obtained good indication that, despite only seldom used, diet-related variables (e.g., diet diversity, mean prey weight, proportion of juvenile individuals) can contribute to explaining variations in breeding performance and home-range behaviour.

Here, taking advantage of a long-term study of the eagle owl, we specifically focused on analysing the relative effect of less frequently explored diet-related variables on reproductive performance and home range behaviour of a top predator. In particular, we were interested in testing if under conditions of high abundance of a profitable prey where diet composition is spatially homogeneous, the individual differences in reproductive performance and home range behaviour could be explained by variations in the mean size of the main prey (rabbits) or the alternative prey species. Therefore, more profitable prey weights should increase breeding performance and, at the same time, should reduce home range size and movement rates. To provide a context for analysing the relative importance of diet-related variables, we have also included in our analysis those variables that resulted relevant to understanding breeding performance and home range behaviour in Campioni et al. (2013).

Methods

Study species and study area

The eagle owl is a large nocturnal raptor that occupies the top of terrestrial food webs in Palearctic ecosystems. It is often considered a generalist predator that can locally specialize in abundant and profitable prey species, such as rabbits, hares *Lepus* spp., rats *Rattus* spp., and microtine rodents (Herrera and Hiraldo 1976; Korpimäki et al. 1990; Lourenço et al. 2011). In Mediterranean ecosystems of south-western Europe, rabbits are frequently the most important prey of eagle owls (Martínez and Calvo 2001; Martínez and Zuberogoitia 2001; Lourenço 2006), which is also the condition in our study area (Campioni et al. 2013; more details in the section below "Diet-related variables"). Rabbits show considerable size variation, and eagle owls seem to prefer easier prey individuals, namely young rabbits (Donázar and Ceballos 1989) and substandard individuals (Penteriani et al. 2008).

From 2003 to 2010, we studied a population of eagle owls located in the Sierra Norte of Seville, a hilly area comprising two river valleys and an artificial lake, located in south-western Spain. Altitude ranges between 60 and 200 m, and the landscape is dominated by sparse woodlands, Mediterranean scrubland and small eucalyptus plantations. Climate is typically Mediterranean, temperate with dry and hot summer (annual average mean temperature = 17.5 °C; average total annual precipitation = 500 mm). Most of the area is managed for small-game hunting, primarily rabbit and red-legged partridge *Alectoris rufa*.

Breeding performance

During the entire study period, we regularly monitored the reproduction at 26 breeding sites, recording egg laying date and the number of fledglings. We determined egg laying dates by estimating the age of nestlings following Penteriani et al. (2005) and assuming 33 days of incubation. Breeding performance was characterised per breeding site by three variables: (1) mean breeding success (i.e., mean annual number of fledglings); (2) coefficient of variation of breeding success; and (3) mean egg laying date (Table 1).

Home range behaviour

We radio-tracked 26 breeding individuals (17 males and 9 females) belonging to 16 breeding sites. Each individual was fitted with a 30-g radio-transmitter using a Teflon ribbon backpack harness (Biotrack; Wareham, Dorset, UK; http://www.biotrack.co.uk). The mass of the backpack was less than 3 % of the mass of the smallest adult male (1550 g) in our population. We trapped breeding individuals using two methods: (1) simulating an intrusion with a taxidermic mount and playback of a male call (see Penteriani et al. 2010 for more details); and (2) a bow-net placed in the nest when nestlings were 20–35 days old (see Campioni et al. 2013 for more details). We followed breeders individually throughout the night (from 1 h before sunset to 1 h after sunrise) during 258 continuous radio-tracking sessions (mean ± SD sessions per individual = 9.9 ± 5.9). We recorded a new location (total number of locations = 4296; mean ± SD locations per individual = 165.2 ± 99.0) each time we detected a change in the position of the focal individual (for more details on movement detections, see Penteriani et al. 2008). Therefore, the number of recorded locations represented the effective number of movements for an individual during each night. The continuous radio-tracking sessions were performed year-round until either the individual died or the battery of the transmitter was drained (139 sessions from January to June, and 119 sessions from July to December; see Penteriani and Delgado 2008; Delgado et al. 2009; and Campioni et al. 2013 for more details on radio-tracking procedures). We estimated home range size through fixed-kernel methods (Worton 1989) using the Animal Movement Extension for ArcView 3.2 (Hooge and Eichenlaub 2000). We calculated the 90 % fixed kernels using the least squares cross-validation (LSCV) procedure (Silverman 1986; see Campioni et al. 2013 for more details). Home range behaviour was characterised by four variables (Table 1): (1) mean nightly total distance; (2) mean nightly home range; (3) mean step length; and (4) mean movement speed.

Diet-related variables

The diet of eagle owls was determined by analysing prey remains and pellets collected at the end of the breeding season (April–June) from 2003 to 2008 during visits to nests and roosting or feeding perches in 26 breeding sites. We pooled all samples from each breeding site and determined the minimum number of individuals of each species by counting the most frequent bone, generally long bones from front and hind limbs. We identified 4184 prey individuals using identification keys for bones and feathers and a reference collection (Laboratory of Archaeo-sciences, IGESPAR, Portugal). We calculated the biomass percentage of each prey group using its mean weight value from bibliographic references or bone measurements to estimate the weight of each individual (ESM). We then derived seven variables characterizing diet composition per breeding site: (1) rabbit biomass percentage; (2) mean

Table 1 Response variables describing breeding performance in 26 eagle owl breeding sites and home range behaviour of 26 eagle owl individuals

Variable	Description	Mean ± SD (range)
Mean breeding success	Mean number of fledglings per year during the period 2004–2010	2.52 ± 0.54 (1.50–4.00)
Coefficient of variation of breeding success	Coefficient of variation of the mean number of fledglings produced each year	0.32 ± 0.21 (0.00–0.89)
Mean laying date	Mean laying date for all studied years, expressed as an ordinal date (Julian calendar)	32.26 ± 17.47 (2.50–79.25)
Mean nightly total distance	Mean of the total distance covered by each individual during each night, calculated as the sum of all consecutive step lengths (m)	7199.4 ± 2012.9 (4106.1–11746.4)
Mean nightly home range	Mean of the home range size covered each night, estimated using the 90 % kernel (ha)	254.78 ± 273.77 (56.61–1479.12)
Mean step length	Mean distance between consecutive locations during each night (m)	429.9 ± 100.9 (288.1–682.9)
Mean movement speed	Mean speed of movements, calculated as the step length divided by the time interval between successive locations (m/min)	32.8 ± 12.4 (12.5–65.4)

Table 2 Description of the variables used to explain eagle owl reproductive performance and home range behaviour

Variable	Description	Mean ± SD (range)
Diet composition (*n* = 26 eagle owl breeding sites)		
Rabbit biomass	Percentage of biomass in the diet composed of rabbits	63.3 ± 15.8 (24.8–93.7)
Rabbit mean weight	Mean weight of all rabbits consumed (g). The weight of each rabbit individual was estimated using humerus, femur or tibia length (Donázar and Ceballos 1989)	468.3 ± 91.7 (262.0–670.6)
Proportion of juvenile rabbits	Number of juvenile rabbits divided by the total number of rabbits consumed. Age was estimated considering bone size and ossification of the distal and proximal epiphyses	0.43 ± 0.15 (0.24–0.75)
Rat biomass	Percentage of biomass in the diet composed of rats (*Rattus* spp.)	9.5 ± 11.0 (1.8–53.5)
Mean weight of alternative prey	Mean weight of all prey species other than rabbits (g). Most frequent species were rats, hares, partridges and pigeons	271.7 ± 72.3 (161.8–436.0)
Diet diversity	Shannon diversity index applied using the numeric percentage of each prey taxonomic order in the diet	0.506 ± 0.110 (0.280–0.726)
Superpredation	Numeric percentage of mesopredators (owls, diurnal raptors, mammalian carnivores) from the total prey (Lourenço et al. 2011)	1.5 ± 1.3 (0.0–3.8)
Landscape characteristics (*n* = 26 eagle owl home ranges)		
Sparse scrubland	Percentage of sparse scrubland with trees (dehesa) in the home range	19.2 ± 15.3 (0.0–56.2)
Dense scrubland	Percentage of scrubland without trees in the home range	17.3 ± 21.8 (0.0–69.2)
Edge density	Length of all edge segments involving the patch types (land cover classes) divided by the total landscape area (m/ha)	178.3 ± 55.1 (99.1–299.3)
Individual characteristics (*n* = 26 individuals)		
Sex	Male (0)	17 males
	Female (1)	9 females
Age	Younger individuals—3 years old or less (0)	7 younger
	Older individuals—4 years old or more (1)	19 older
Internal state (*n* = 26 individuals)		
Haematocrit	Volume percentage of erythrocytes in blood	51.47 ± 7.72 (41.70–66.70)

weight of rabbits; (3) proportion of juvenile rabbits; (4) rat biomass percentage; (5) mean weight of alternative prey; (6) diet diversity; and (7) superpredation (see Table 2 for variable description).

In exploratory analysis we found no annual differences in diet parameters within breeding sites, therefore we pooled the data from all years to obtain a representative sample size for each breeding site (range 47–239 prey). Rabbits were the

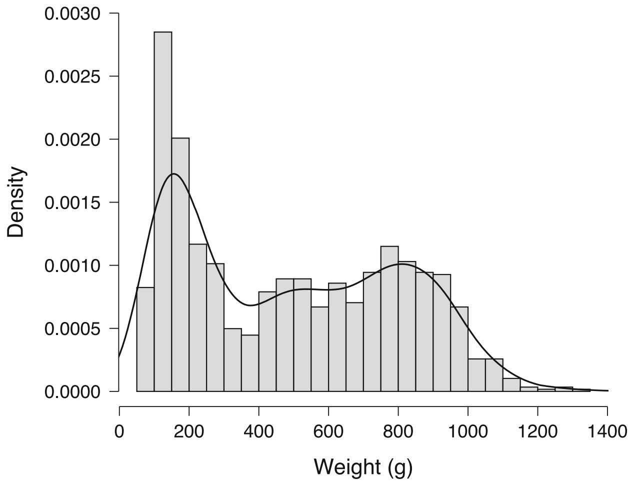

Fig. 1 Weight distribution of the rabbits captured by eagle owls in the study area ($n = 1166$ rabbit individuals). *Histogram* with density estimate *curve*

main prey in our study area, with a mean biomass contribution of 63.3 ± 15.8 % (mean ± SD; range 24.8–93.7 %). The remaining prey groups had smaller biomass contributions to the diet of eagle owls: rats (*Rattus* spp.) = 9.5 ± 11.0 % (mean ± SD; range 1.8–53.5 %); hares (*Lepus granatensis*) = 7.2 ± 6.6 % (mean ± SD; range 0.0–27.5 %); red-legged partridges = 8.8 ± 5.0 % (mean ± SD; range 0.0–23.1 %); pigeons (Columbiformes) = 2.7 ± 4.0 % (mean ± SD; range 0.0–17.6 %); and passerine birds (Passeriformes) = 0.8 ± 1.1 % (mean ± SD; range 0.0–5.4 %). Eagle owls showed a bimodal pattern in terms of the size of captured rabbits, with a greater frequency of juvenile rabbits weighing between 100–250 g, and a moderate peak of adult/sub-adult rabbits weighing between 700–900 g (Fig. 1).

Landscape characteristics of home ranges

We determined landscape characteristics by intersecting the home range boundaries of each owl with a map of land-cover elements (scale 1:25000, Junta de Andalucía, Consejería de Medio Ambiente 2003). We included three variables (Table 2) considering our previous knowledge of the landscape characteristics most relevant to eagle owls (Campioni et al. 2013): (1) sparse scrubland with trees; (2) dense scrubland without trees; and (3) edge density. We used the GIS application ArcView 3.2 and its extension Patch Analyst (Elkie et al. 1999) to obtain the landscape variables.

Individual characteristics and internal state

Individuals were characterized by their: (1) sex, determined by molecular procedures using DNA extracted from blood (Griffiths et al. 1998); and (2) age, determined by the moult patterns of flight and body feathers, following Martínez et al. (2002). We considered two age groups based on breeding experience: (a) younger individuals, i.e., three years old or less (generally corresponding to the age of first breeding); and (b) older individuals, i.e., with four years old or more.

Following the results of Campioni et al. (2013), we estimated individual internal state using haematocrit values, i.e., the volume percentage of erythrocytes in blood, which has been frequently used as an indicator of physiological condition in wild birds (Brown 1996).

Data analysis

We analysed our data using multi-model inference to cope with model selection uncertainty (Burnham and Anderson 2002). We first performed a detailed screening of all our data to detect outliers and check distribution normality of the variables, and we accordingly applied the most suitable transformations: mean laying date was square-root transformed, mean nightly home range was log-transformed; and variables which were proportions were arcsine transformed, i.e., rabbit biomass percentage, proportion of juvenile rabbits, rat biomass percentage, superpredation, and the two habitat percentages. Then, we used Pearson correlation to detect high collinearity ($r_P > 0.7$) among the explanatory variables. In the analyses considering the breeding parameters, we excluded the variable “proportion of juvenile rabbits” because it showed strong collinearity with the variable “rabbit mean weight” ($r_P = -0.77$). In the data used in the analyses of home range behaviour, we excluded the variable “sparse scrubland” because it showed strong collinearity with the variable “edge density” ($r_P = 0.72$). Since the seven response variables were continuous (Table 1), we used linear regression models in all analyses. In the analyses of the relative importance of dietary features in determining the three parameters of breeding performance of the 26 eagle owl pairs, we considered the following six explanatory variables: rabbit biomass, rabbit mean weight, rat biomass, mean weight of alternative prey; diet diversity; and superpredation. In the analyses of the relative importance of dietary features in determining the four parameters of home range behaviour of the 26 radio-tracked eagle owls, we considered all explanatory variables except “sparse scrubland” (Table 2). In the models analysing home range behaviour, due to the small sample size and within-group representativeness, we assumed that different radio-tracked owls from the same breeding site were independent samples (in 7 breeding sites we radio-tracked 1 individual, in 8 breeding sites we radio-tracked 2 individuals, and in 1 breeding site we radio-tracked 3 individuals), and thus they were not treated as repeated measures, and as a result breeding site was not considered as a random effect in the models. This decision was also supported by: (1) our previous knowledge of the high inter-individual variation in home range parameters (Campioni et al. 2013); (2) exploratory analysis where we observed a great imprecision of the parameters of the random effect in mixed effect models (within-breeding site standard deviation, between-breeding site standard deviation); and (3) the poorer performance of linear mixed models when compared to linear models (Pinheiro and Bates 2000).

Given the number of cases available in all models ($n = 26$), and taking into consideration the rule of thumb of one explanatory variable for every ten cases, we limited the number of variables in each single candidate model to a maximum of two to avoid model over-fitting. We also ran the analyses establishing a maximum of three variables, but as the results were generally similar we chose the more conservative approach. We generated all possible models combining none (null model), one or two explanatory variables. This option, often classified as "data dredging" (Burnham and Anderson 2002), was used because according to our rationale all explanatory variables considered could potentially influence the response variables. Using all combinations guaranteed a balanced inclusion of the explanatory variables in the models used in the model-averaging procedure. The null model was included only as an indicator of model performance. We did not consider interactions among explanatory variables due to sample size limitations. Models were fitted one by one and ordered according to their $\mathrm{AIC_c}$ values. For each model we also calculated the number of parameters (degrees of freedom), log-likelihood value, $\mathrm{AIC_c}$ difference ($\Delta\mathrm{AIC_c}$), and Akaike weight ($\mathrm{AIC}w_i$). We calculated the model-averaged ("natural averaging") coefficients of all explanatory variables. Finally, as the main inference approach, we estimated the relative importance of each explanatory variable, by summing the Akaike weights of all models in which the variable appeared. The relative importance of variables that appear in all top models tends towards 1. In variables that only appear in less likely models, their relative importance tends towards 0. We then ranked the explanatory variables according to their relative importance, and the direction and magnitude of the effect of each variable was based on the model-averaged coefficients.

We found no spatial dependence in model residuals after analysing bicolour residual xyplots (bubble plots), and assessing statistical significance of Moran's I in model residuals using spatial correlograms (Dormann et al. 2007). We used model diagnostic plots to validate model results. All analyses were performed using the software R 3.0.2 (R Core Team 2013) with the packages gplots (Warnes et al. 2013), ncf (Bjørnstad 2012), MuMIn (Barton 2013), and sp (Bivand et al. 2013).

Results

Relative effects of dietary features on breeding performance

Superpredation was the most important variable affecting mean breeding success (Table 3), with lower breeding success associated with greater consumption of mesopredators (Fig. 2). Diet diversity, rabbit biomass percentage and rat biomass percentage were also included in the four best models ($\Delta\mathrm{AIC_c} < 2.00$), suggesting that greater mean breeding success was associated with less diverse diets, greater rabbit biomass and lower rat biomass in the diet. The null model was among the best models, indicating that the variables had poor explanatory power (ESM).

Rat biomass percentage was the variable with the greatest relative importance influencing the coefficient of variation of the breeding success (Table 3), suggesting that greater variation in breeding performance was associated with a diet with a greater percentage of rats (Fig. 3). Eight models represented the set of best models, including the null model (ESM).

Table 3 Results from the multi-model inference procedure for the parameters describing reproductive performance: relative variable importance (RVA) and trend of the relationship

	Mean breeding success		Variation coefficient of the breeding success		Mean laying date	
	RVA	Trend	RVA	Trend	RVA	Trend
Rabbit biomass	0.23*	+	0.26*	–	0.16	+
Rabbit mean weight	0.15	–	0.29*	+	0.48*	+
Rat biomass	0.17*	–	0.49*	+	0.30*	–
Mean weight of alternative prey	0.12	–	0.13*	+	0.13	–
Diet diversity	0.30*	–	0.15*	+	0.18*	+
Superpredation	0.43*	–	0.14*	+	0.22*	+

The asterisk indicates the variables included in the best models ($\Delta\mathrm{AIC_c} < 2.00$)

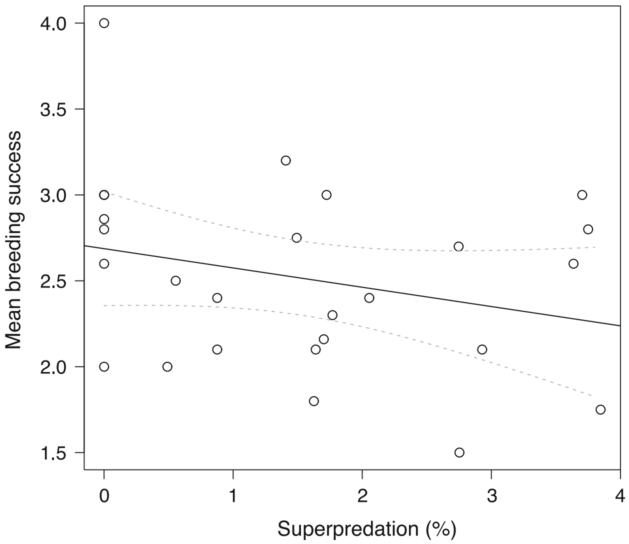

Fig. 2 Relationship between mean breeding success and superpredation—percentage of mesopredators in the diet of eagle owls ($R^2 = 0.13$). *Plot* showing linear regression trendline with lower and upper 95 % confidence intervals (*broken lines*)

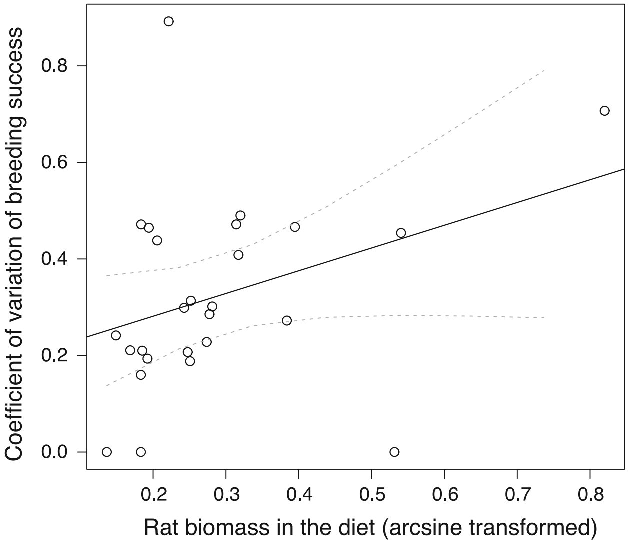

Fig. 3 Relationship between the coefficient of variation of breeding success and rat biomass in the diet of eagle owls ($R^2 = 0.12$). Plot showing linear regression trendline with lower and upper 95 % confidence intervals (*broken lines*)

Rabbit mean weight showed the greatest relative importance when analysing the relationships with mean laying date (Table 3), suggesting that earlier laying dates were associated with the consumption, on average, of smaller rabbits (Fig. 4). As with the two previous variables, the null model was included in the set of best models. The six best models also included the rat biomass percentage, superpredation and diet diversity, suggesting that earlier dates may be associated with less diverse diets, containing a greater proportion of rats and less mesopredators (ESM).

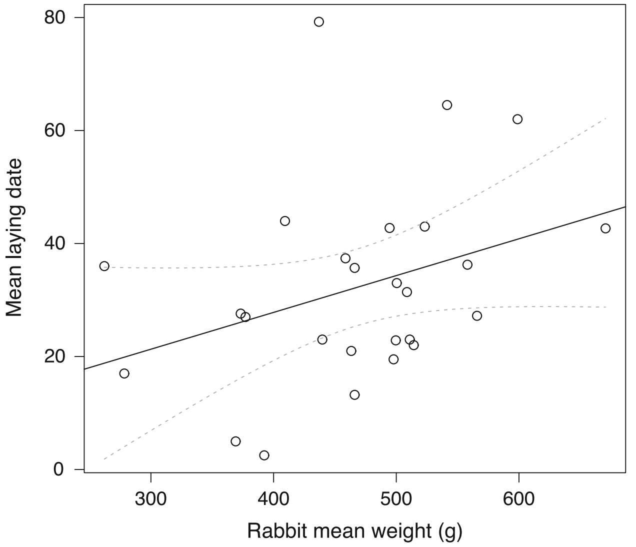

Fig. 4 Relationship between mean laying date and rabbit mean weight in the diet of eagle owls ($R^2 = 0.14$). Plot showing linear regression trendline with lower and upper 95 % confidence intervals (*broken lines*)

In summary, other variables besides rabbit biomass percentage showed the greatest relative importance in explaining breeding parameters, although, a large amount of variation remained unexplained. Despite considerable model uncertainty, our results seem to suggest that less diverse diets, with a greater rabbit biomass percentage, may benefit reproductive success, whereas a higher rat biomass percentage seemed to be associated with greater variation of breeding success, and earlier laying dates with the consumption of smaller rabbits.

Relative effects of dietary features on home range behaviour

Edge density and owl age had the greatest contribution in determining the total distance that eagle owls moved each night, as both were included in the single best model (Table 4). Greater edge density was associated with shorter mean nightly total distance, and older owls moved, on average, shorter distances during each night. The remaining variables showed low relative importance (ESM).

Edge density had the greatest relative importance in determining the mean nightly home range of eagle owls, with smaller home ranges showing greater edge density (Table 4). In addition, younger owls had larger mean nightly home range (ESM), and larger home ranges were also associated with larger mean weight of alternative prey (Fig. 5).

Edge density stood out from the remaining variables in its relative importance in determining the mean step length moved by eagle owls: mean step length was smaller in

Table 4 Results from the multi-model inference procedure for the parameters describing home range behaviour: relative variable importance (RVA) and trend of the relationship

	Mean nightly total distance		Mean home range per night		Mean step length		Mean movement speed	
	RVA	Trend	RVA	Trend	RVA	Trend	RVA	Trend
Rabbit biomass	0.04	–	0.05	–	0.07	+	0.20*	–
Rabbit mean weight	0.07	+	0.04	+	0.13*	+	0.07	+
Proportion of juvenile rabbits	0.04	–	0.03	+	0.08*	–	0.07	+
Rat biomass	0.04	–	0.04	–	0.13*	–	0.10	+
Mean weight of alternative prey	0.04	–	0.27*	+	0.06	+	0.07	+
Diet diversity	0.04	+	0.03	+	0.08	+	0.24*	+
Superpredation	0.04	+	0.03	–	0.07	+	0.08	+
Dense scrubland	0.12	+	0.03	+	0.12*	+	0.07	+
Edge density	0.62*	–	0.97*	–	0.83*	–	0.17*	–
Sex (female:male)	0.06	+	0.05	–	0.06	–	0.36*	–
Age (older:younger)	0.70*	+	0.33*	+	0.09*	+	0.19*	+
Haematocrit	0.06	+	0.03	–	0.06	+	0.09	+

The asterisk indicates the variables included in the best models ($\Delta AIC_c < 2.00$)

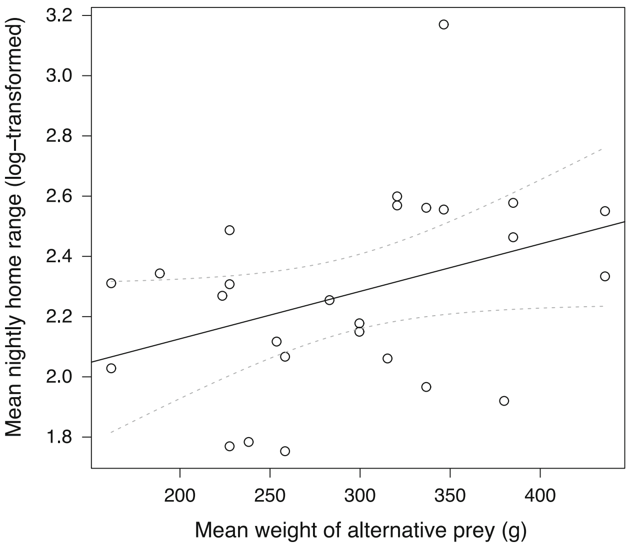

Fig. 5 Relationship between mean nightly home range and mean weight of alternative prey in the diet of eagle owls ($R^2 = 0.14$). Plot showing linear regression trendline with lower and upper 95 % confidence intervals (*broken lines*)

home ranges with greater edge density (Table 4). Although the set of the six best models included age, dense scrubland, proportion of juvenile rabbits, rat biomass, and rabbit mean weight, their relative importance was generally low (ESM).

Finally, sex showed the greatest relative importance in determining the mean movement speed of eagle owls (Table 4), with females moving faster than males. Although their relative importance was not high, diet diversity and rabbit biomass were also included in the set of the five best models, suggesting that faster movements may be associated with greater diet diversity, and lower percentage of rabbit biomass (ESM).

In summary, edge density was the most relevant factor determining the variations in home range behaviour, with individual characteristics, such as age and sex, also being relevant in some of the variables analysed. Although the relative importance of the diet-related variables was generally low, some of them also seemed to explain home range parameters, namely mean weight of alternative prey, diet diversity, and rabbit biomass. Moreover, diet-related variables were often included in the set of the best models ($\Delta AIC_c < 2.00$), reinforcing the idea that they are linked to home range behaviour.

Discussion

Our results indicate that diet-related variables less often explored could have some influence on both the reproductive performance and home range behaviour of predators whose main prey species show considerable intraspecific size variation. Despite the generally low explanatory power of our models, the three reproductive parameters were best explained by diet-related variables other than the biomass of the main prey (rabbits in this study), the most frequently studied effect in literature (ESM), namely superpredation, diet diversity, rat biomass and rabbit mean weight, which suggests that these factors can contribute to a better understanding of the variations in breeding performance within populations living in apparently homogeneous environments.

Higher levels of predation on mesopredators (i.e., superpredation) have often been related to lower availability of the main prey (Serrano 2000; Lourenço et al. 2011), and since this latter affects reproductive performance, superpredation may in fact act as a good surrogate of main prey availability as an alternative to its abundance in the field or its biomass in the diet. Dietary diversity and diet width are indices summarizing the contribution of different prey species to the diet. Despite being only seldom used in raptor studies (ESM), they can constitute informative variables (see for example Korpimäki 1986, 1992b; Korpimäki and Sulkava 1987; Marchesi et al. 2002; Penteriani et al. 2002; Moleón et al. 2012). In our case, breeding performance appeared to be negatively affected by a smaller proportion of the main prey in the diet (which is probably a function of prey availability), and, following the prediction of optimal foraging theory, it results in a search for alternative prey, such as rats, and an increase in dietary diversity. This relationship can be associated with two main explanations. First, increased reproductive success is associated with high availability of the main prey, and the resulting dietary specialization, i.e., “prey availability hypothesis” (Korpimäki 1986, 1992b; Steenhof and Kochert 1988; Whitfield et al. 2009). Second, specialized diets allow greater foraging efficiency, which in turn is associated with higher reproductive success, i.e., “diet specificity hypothesis” (MacArthur and Pianka 1966; Watson 1997; Katzner et al. 2005; Whitfield et al. 2009).

In some conditions, dietary diversity has been found to be positively correlated with reproductive performance, since specialization may in fact result from a restricted choice of prey types (Penteriani et al. 2002; Whitfield et al. 2009; Margalida et al. 2012). The eagle owl is a generalist predator that specializes on rabbits when they are abundant, with obvious benefits to its breeding success (Serrano 2000; Martínez and Calvo 2001; Martínez and Zuberogoitia 2001; Penteriani et al. 2002; Pérez-Garcia et al. 2012). In our study area, the spatio-temporal availability of a profitable prey (rabbits) can be considered predictable and stable, and thus a positive association between diet specialization and reproductive performance would be expected. The apparent negative relationship between dietary diversity and breeding success of eagle owls would also corroborate the well-established idea that rabbits are one of the most profitable prey for large predators in Mediterranean ecosystems (Delibes-Mateos et al. 2007; Moleón et al. 2009; Lourenço et al. 2011).

Earlier mean laying dates seemed to be associated with the consumption, on average, of smaller sized rabbits, which suggests that eagle owls could take advantage of the breeding season of rabbits. Consequently, those individuals that breed earlier should include a greater proportion of juvenile rabbits, which should be easier to capture and more numerous than adults. Earlier laying dates are generally associated with higher breeding success in eagle owls (Marchesi et al. 2002; Penteriani et al. 2002; Pérez-García et al. 2012) and other birds of prey (e.g., Newton and Marquiss 1984; Korpimäki and Hakkarainen 1991; Korpimäki and Wiehn 1998).

Home range behaviour was best explained by landscape structure (edge density) and individual characteristics (age and sex), effects already thoroughly discussed in Campioni et al. (2013). Edge density is a landscape index that summarizes the spatial organization of different habitat types, and in our study was also positively correlated with the percentage of sparse scrubland, a favourable habitat for rabbits. Thus, it appears that other simpler variables (e.g., rabbit biomass, rabbit mean weight, percentage of dense scrubland) may be outperformed when explaining home range parameters, which result from complex patterns of interacting factors. Nevertheless, it demonstrates the important role of landscape heterogeneity, fragmentation and complexity in generalist species (Kenward 1982; Penteriani et al. 2002; Campioni et al. 2013). It is important to mention that the known relationship between increased proportion of ecotones (reflected in greater edge density) and greater rabbit abundance (Moreno and Villafuerte 1995; Delibes-Mateos et al. 2010; Godinho et al. 2013) could have, in part, masked the effect of the rabbit-related variables so that these had lower relative importance in our analysis. We also found that older individuals required smaller home ranges and covered smaller areas per night, which is probably the result of greater experience related to greater hunting efficiency (Marchetti and Price 1989; Wunderle 1991; Penteriani et al. 2013).

In addition, our results also suggested that (a) greater home range size may reflect a greater mean weight of alternative prey, and (b) greater movement speed may be associated with greater diet diversity. Analysed under an optimal foraging context, centred on the abundance of the main prey, this can indicate that, when rabbits (especially juveniles) are less available, eagle owls need to increase home range size in order to obtain larger (and possibly more profitable) alternative prey (e.g., hares and rats). At the same time, this can lead to an increased dietary diversity, which requires greater movement speeds (i.e., more effort) in order to obtain alternative prey (Schoener 1971; Fernández et al. 2009; Santangeli et al. 2012; Penteriani et al. 2013).

The question is, why did the parameters describing prey size variations show a weak effect on both reproductive performance and home range behaviour, contrary to what would be expected considering the optimal foraging theory? Wild rabbits show great size variation (70–1400 g; Soriguer 1981a) and, although they may be generally considered easy prey for eagle owls when they reach high densities (Penteriani et al. 2008), different age classes should be associated with different capturing efforts, as a consequence of their abundance and behaviour. Juvenile rabbits are easier to capture due to their greater exposure and inexperience (Soriguer 1981a, b). As a result, several predators positively select this age class (Donázar and Ceballos 1989; Gil-Sánchez et al. 1999). However, the availability of young rabbits is more limited across seasons, and their relatively small size (70–300 g) makes them less profitable than adults (assuming theoretically that searching and capturing effort was similar in the two age classes). On the other hand, sub-adult and adult rabbits (500–1400 g) may be more profitable due to their larger size, although their lower abundance and more alert behaviour may require greater searching effort in terms of time and distance travelled. Still, adult rabbits are a more constant and predictable food source year-round. In areas where rabbits are very abundant, adults seem to be the most preyed upon age class (Hiraldo et al. 1975; Pérez-Mellado 1980). However, in our study area, most rabbits eaten by eagle owls were juveniles, and indeed the breeding season of this predator in Mediterranean ecosystems appears to be synchronized with the breeding season of rabbits in order to take advantage of this seasonally abundant food (V. Penteriani et al., unpublished data). The prevalence of juveniles in our study may be due to the fact that diet sampling primarily included material accumulated during the breeding period (January–June) of eagle owls, and only a part of the sample might correspond to the non-breeding period, when juvenile rabbits are less available and capture effort must focus on adults and sub-adults (Pérez-Mellado 1980; Donázar and Ceballos 1989; Gil-Sánchez et al. 1999). The pattern of the weight of the rabbits captured by eagle owls in our study is very similar to the age structure of rabbit populations studied in nearby areas during the period January–June (Soriguer 1981a), which may indicate that, in fact, eagle owls are not very selective in terms of rabbit size, but instead capture different age and size classes mostly as a function of their availability. In addition, we consider two other reasons that may explain the generally low relative importance of the variables expressing the role of rabbits in the diet of eagle owls, despite this species being the main prey. First, rabbit abundance is generally high in our study area, and consequently, availability of main prey may not be a limiting factor sufficient to cause strong variations in reproductive performance and home range behaviour (Campioni et al. 2013). Second, typical rabbit abundance estimates (based either on counting faeces or individuals) may not directly reflect prey availability, since the latter can result mostly from the interaction between prey abundance and prey detectability (Ontiveros et al. 2005). In this sense, habitat structure, besides directly affecting rabbit abundance, may also influence the ability of eagle owls to capture rabbits, which results in a complex interaction of factors that affects the interpretation of model results. Accordingly, we found a strong effect of edge density on home range behaviour, which in turn is correlated with rabbit abundance (Moreno et al. 1996) and possibly also with their availability to eagle owls.

In summary, our study illustrates what appear to be two non-exclusive directions taken by eagle owls to maximize breeding success in a scenario of relatively high prey abundance: (a) maximize the size of the rabbits captured, and (b) take advantage of the period when juvenile rabbits (easier age class to hunt) are most abundant. We hypothesize that these two “forces” may sometimes lead the owls to anticipate the laying date to synchronize with rabbit reproduction, but also to increase their home range (and related movements parameters) in order to obtain more profitable alternative prey (namely rats and hares). However, this process should, in large part, be mediated by rabbit abundance, which has direct implications on dietary diversity and superpredation. This rationale highlights the potential ecological role of the synchronization between the breeding seasons of rabbits and their predators, and should be explored in future studies.

In conclusion, our study provides new evidence supporting the fact that there may be complex interactions between prey size variation, prey abundance, and seasonal variations of both, which represent a particular challenge when explaining breeding performance and home range behaviour of vertebrate predators. Campioni et al. (2013) found that home range behaviour can be influenced by the biological cycle and by both external (i.e., habitat features) and internal (i.e., sex and health) factors, and our results are complementary by providing new research clues for studying the influence of prey size and profitability. However, due to a high degree of uncertainty in our results, further studies are necessary to confirm the role played by diet-related variables on breeding performance and home range. Since diet-related variables other than the most commonly used (i.e., the proportion of the main prey in the diet) may help understanding variations in breeding and home range parameters, we suggest that future studies should include information on both prey abundance and dietary data, and particularly variables describing dietary diversity and the mean size of prey.

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