

Temporal and spatial variation in trophic scenarios affects population demographic heterogeneity in Bonelli's Eagle (*Aquila fasciata*)

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The recognition of individual variation has fundamental implications for ecological, evolutionary and biodiversity conservation. There is increasing theoretical interest in how spatial and temporal variation in the environment can create differences in the demographic contribution of individuals over space and time. However, empirical information about the characteristics of the environmental drivers of key vital rates and their spatio-temporal variation is still scarce. Here, we used data generated by a monitoring scheme (1990–2015) of a population of a long-lived territorial avian predator, Bonelli's Eagle *Aquila fasciata*, which included estimations of individuals' diet through stable isotope analysis (2008–15), to evaluate whether temporal consistency in spatially structured dietary patterns affects key demographic parameters, namely productivity and survival, at territory scales. We found strong within-population heterogeneity in survival and reproduction rates associated with Eagle territories, with territory average values ranging, respectively, from 0.58 to 1.00 and from 0 to 1.71 for the overall study period. Reproduction and survival were predictable over, respectively, 4- and 3-year periods for the bulk of the population, which suggests that the environmental drivers of these vital rates changed at these temporal scales. Interestingly, the characteristics of and the temporal variation in the diets of territorial individuals during these periods were associated with their survival and reproduction. Based on these findings, we suggest that spatial and temporal variations in trophic scenarios potentially act as meaningful drivers of intrapopulation demographic heterogeneity.

Keywords: bird predator, diet specialization, intrapopulation heterogeneity, raptors, stable isotope analysis.

Animal populations are not demographically homogeneous because of within-population variation in individual survival and reproduction rates,

a concept known as 'demographic heterogeneity' (Fox *et al.* 2006, Melbourne & Hastings 2008, Kendall *et al.* 2011). Variation in individual characteristics, linked either to developmental stages or to phenotypic traits, and environmental factors drive differences in individual vital rates (Shima *et al.* 2008, Gimenez *et al.* 2017). Demographic

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heterogeneity may therefore have profound ecological, evolutionary and conservation consequences for animal populations (Bolnick *et al.* 2002a, Schreiber 2006, Cam *et al.* 2012, Stover *et al.* 2012, Plard *et al.* 2019).

Both temporal and spatial variations in environmental characteristics can provoke demographic heterogeneity (Coulson 1968, McClaren *et al.* 2002, Shima *et al.* 2008). Temporal variation in vital rates driven by environmental conditions and its ability to affect individual fitness and population dynamics has received much attention in recent years. Changing environments may favour strategies that are based on greater yearly reproductive effort, greater dispersal rates or less niche specialization, whereas more stable environments potentially favour strategies relying on higher survival rates, less yearly reproductive effort, lower dispersal rates and greater niche specialization (Franklin *et al.* 2000, Reznick *et al.* 2002, Engen & Sæther 2016). At the population level, between-year environmental variation affecting vital rates reduces population persistence (Doak *et al.* 2005, Crone 2016).

Spatial variation in environmental conditions may enable individuals using areas with the most favourable conditions to make a greater contribution to the population growth rate than those using less favourable areas (Newton 1991, White 2000), thereby contributing seriously to within-population demographic heterogeneity. At the population level, spatial variation in individual fitness enhances population growth in dispersal-limited populations (Melbourne *et al.* 2007), an effect that can be diminished by dispersal as individuals from more productive areas may disperse to lower quality areas in density-regulated populations (Pulliam 1988).

Theoretical and empirical evidence has also underlined the powerful effect of the interplay between spatial and temporal environmental variation on population structuring and persistence (Schreiber 2010). However, most theory assumes that spatio-temporal heterogeneity occurs at patch scale and affects all individuals in a patch or local population (Plard *et al.* 2019). Nevertheless, although local conditions are known to significantly determine individual fitness (e.g. Rotenberry & Wiens 1991, Franklin *et al.* 2000, Maresh Nelson *et al.* 2023), there is a notable lack of literature exploring the role played by this fine-scale environmental heterogeneity in

generating demographic heterogeneity (but see Plard *et al.* 2019, Armstrong *et al.* 2021). In addition, little empirical data on the interplay between spatial and temporal heterogeneity at fine spatial scales actually exist (but see Sergio & Newton 2003).

Beyond its eco-evolutionary interest, recognizing the sources of demographic heterogeneity driven by environmental heterogeneity may also provide highly relevant insights for conservation planning. Spatial heterogeneity in demographic performance can help to identify targeted conservation actions to enhance a specific demographic parameter and maximize their effectiveness at the population level (Rollan *et al.* 2021). Understanding the relevant spatial scales at which populations are structured, as well as the temporal scales at which spatial heterogeneity is maintained, are key elements to be borne in mind when designing suitable cost-effective conservation or management actions (Ruggiero *et al.* 1994).

Trophic scenarios – that is, the conditions of food abundance and accessibility of different types of food resources – and individuals' food preferences determine patterns of trophic resource consumption in a population (Szigeti *et al.* 2019, Franco-Trecu *et al.* 2022). Consequently, diet composition can be used as a proxy of the trophic scenarios that an individual has to cope with (Futuyma & Moreno 1988, Moleón *et al.* 2012a, Resano-Mayor *et al.* 2016), though individual preferences may also influence diet composition (Bolnick *et al.* 2002a).

Several studies have revealed a link between diet and demographic characteristics at both individual and population levels (Resano-Mayor *et al.* 2014a, Costa-Pereira *et al.* 2019, Korpimäki *et al.* 2020). Therefore, variation in dietary patterns may affect demographic heterogeneity over both time and space. Although temporal variations in diet and demographic parameters in populations of avian predators have been well documented at the population level (Whitfield *et al.* 2009, Korpimäki *et al.* 2020), fine-scale spatio-temporal dietary variations and their contribution to demographic heterogeneity remain poorly understood, especially in complex ecosystems such as those found in the Mediterranean (Fargallo *et al.* 2009, Resano-Mayor *et al.* 2016). In addition, empirical evidence on the incidence, magnitude and temporal consistency of

within-population diet variation is still limited and much needed (Araújo *et al.* 2011, Bolnick *et al.* 2011, Novak & Tinker 2015, Ingram *et al.* 2018).

In this study, we assessed the link between spatial and temporal variation in trophic scenarios and demographic heterogeneity in a population of a sedentary, long-lived, territorial avian predator: the Bonelli's Eagle *Aquila fasciata* in Catalonia (north-east Spain). This Bonelli's Eagle population displays marked demographic spatial variation (Hernández-Matías *et al.* 2013, Resano-Mayor *et al.* 2014a, 2014b). Hence, the performance of territories can be characterized in terms of survival and reproduction, two key vital rates that in this population vary strikingly between neighbouring territories (Rollan *et al.* 2016). Bonelli's Eagle has a wide trophic spectrum and the European Rabbit *Oryctolagus cuniculus* is a key prey in our study population (Real 1991, Moleón *et al.* 2009, Resano-Mayor *et al.* 2011, 2014a). There is also a marked within-population heterogeneity in its diet composition, which has increased following the outbreak of virus haemorrhagic disease in rabbits in recent decades (Moleón *et al.* 2012b). Diet differences may indirectly reflect the local abundance of the main prey species and are linked to territorial performance and the growth rate of populations (Moleón *et al.* 2012a, Resano-Mayor *et al.* 2014a, 2014b, 2016). Bonelli's Eagle is therefore a very well-suited model species for examining the questions raised here.

Our specific aims were to study (1) whether or not there is demographic heterogeneity linked to the spatial location of breeding individuals; (2) whether or not this demographic heterogeneity has temporal consistency – understood as low interannual variation in breeding territories – and to what extent; and (3) whether or not temporal consistency in spatial demographic heterogeneity is linked to the characteristics and consistency of trophic scenarios in this long-lived predator. Based on current theory and on the biological characteristics of our study species, we predicted that (1) there would be marked demographic heterogeneity driven by spatial heterogeneity in territorial environmental features and, specifically, in trophic scenarios, and that (2) both vital rates of territorial individuals and diet composition would exhibit temporal consistency over time. Additionally, we predicted that (3) the territories with the best trophic conditions and the highest temporal

consistency (i.e. greater consumption of rabbits over longer time spans) would perform better. In our study system, diet can be estimated at the territorial level through stable isotope analysis of chick feathers (see Resano-Mayor *et al.* 2014a) and changes in the availability of rabbits are known to lead to important among-territory differences in the diet of the Bonelli's Eagle (Moleón *et al.* 2012b). We assumed here, therefore, that demographic and diet differences between territories were mainly driven by environmental conditions instead of individual quality or diet preferences.

METHODS

Study species

As is typical in a long-lived species, Bonelli's Eagle has low annual reproductive rates, high adult survival and late recruitment ages (Sæther & Bakke 2000). At the age of recruitment, usually between birds' second and fourth years, individuals begin to exhibit territorial behaviour. Given that mate fidelity and territorial fidelity are strong and last throughout birds' lifespans, breeding dispersal is rare (Hernández-Matías *et al.* 2010). In general, high human-induced mortality rates, habitat degradation and the decline in the species' main prey are currently the most important threats affecting this raptor (Real 2004, Hernández-Matías *et al.* 2011a, 2013). The European population was classified as Endangered after a marked decline in number and range that occurred in recent decades (BirdLife International 2004); however, more recently its populations appear to have stabilized and it is now listed as Least Concern (BirdLife International 2021).

In Western Europe, Bonelli's Eagles hunt a wide range of prey species (Palma *et al.* 2006, Moleón *et al.* 2009, Resano-Mayor *et al.* 2011), although they behave as specialist predators if rabbit densities are high (Moleón *et al.* 2012a). In fact, rabbit consumption has been shown to be positively correlated to breeding productivity at the territory level and to population growth rates (Resano-Mayor *et al.* 2014a, 2014b). Over the last decades, however, this key native prey species, which favours open habitats, has undergone serious population crashes in the majority of its European range due to the outbreak of diseases such as myxomatosis and viral haemorrhagic disease

(Virgós *et al.* 2007, Moleón *et al.* 2012b). As a consequence, rabbit populations are now very patchy and in certain lowland areas this lagomorph is regarded as a pest; as a result, in most areas of the studied population, rabbit abundances are low (Virgós *et al.* 2007, Moleón *et al.* 2009). Nevertheless, Bonelli's Eagle will consume many alternative prey items if they are highly and locally abundant (Resano-Mayor *et al.* 2014a), especially if rabbit numbers are low to moderate (Moleón *et al.* 2008).

Study area and demographic data collection

In 1990–2015, we monitored 75 Bonelli's Eagle territories (range 30–55; see Fig. 1) in the littoral and pre-littoral Catalan Mountain Range (north-east Spain, 41°20'N, 01°32'E) to estimate the breeding productivity and survival rates of each territorial pair. The study area has a typical Mediterranean climate and landscape features. Breeding territories were located at altitudes ranging from 0 to 1200 m above sea level in a wide variety of

habitats, but mainly in scrubland combined with Holm Oak *Quercus ilex* forests, Aleppo Pine *Pinus halepensis* plantations and crops (irrigated and non-irrigated) (Real *et al.* 2016).

Breeding success and productivity were recorded yearly by visiting each territory a minimum of five times during the breeding period (January to June). In January to March, we noted the presence of territorial birds and breeding activity. Then, in those territories with breeding attempts, in March/April the presence, numbers and ages of nestlings were recorded. Since 2008, when nestlings are 35–40 days old, we have visited nests to ring the chicks and collect a few mantle feathers from each one to be able to derive diet parameters using stable isotope analyses (SIA; see below) (Resano-Mayor *et al.* 2014a). Lastly, in May/June, a final visit to the territory confirmed whether or not the chicks had fledged.

At the same time, individual survival rates were estimated in 62 territories based on pair replacements. We compared for each territory the plumage-age (2nd year, 3rd year or adult) of the male and the female birds in two consecutive

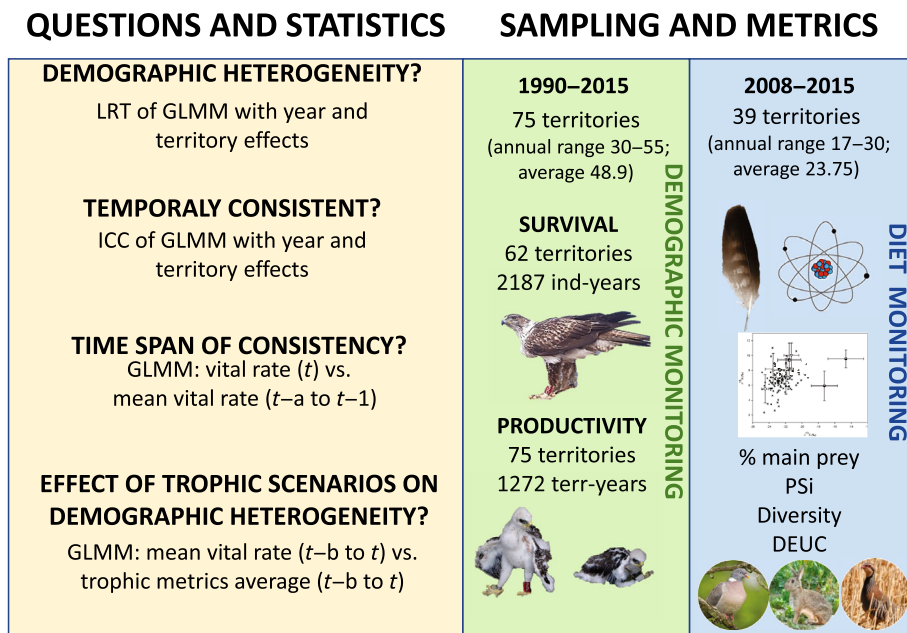


Figure 1. Diagram showing the main questions posed and the statistical methods (QUESTIONS AND STATISTICS), as well as the main characteristics of demographic monitoring and sampling and metrics for the diet analysis carried out (SAMPLING & METRICS). DEUC, Euclidean distance to centroid; Diversity, Shannon–Weaver index; GLMM, generalized linear mixed model; ICC, intraclass correlation coefficient; ind-years, number of individual-years of observations; LRT, likelihood ratio test; Psi, proportional similarity index; terr-years, number of territory-years of observations.

years: if there were no changes in the expected individual plumage-age from one year to another, we assumed the individual had survived (Hernández-Matías *et al.* 2011b). We also classified each pair in a given year as either 'adult' (i.e. both individuals with adult plumage) or 'non-adult' (i.e. at least one individual with a non-adult plumage).

Diet data and stable isotope analysis

In 2008–15 we analysed the stable isotope ratios of C (^{13}C : ^{12}C ; $\delta^{13}\text{C}$), N (^{15}N : ^{14}N ; $\delta^{15}\text{N}$) and S (^{34}S : ^{32}S ; $\delta^{34}\text{S}$) in feathers from 299 Bonelli's Eagle nestlings from 39 territories (range: 17–30; see Fig. 1). Nestling feathers were processed following the method described in Resano-Mayor *et al.* (2014b). Using the SIAR package (Parnell *et al.* 2010), diet estimates were obtained at territory-year level for the following main prey categories: European Rabbit, Red-legged Partridge *Alectoris rufa*, Eurasian Red Squirrel *Sciurus vulgaris*, Common Wood Pigeon *Columba palumbus*, Rock Pigeon *Columba livia*, Yellow-legged Gull *Larus michahellis*, Ocellated Lizard *Timon lepidus* and Passeriformes (Resano-Mayor *et al.* 2014a). The isotopic ratios from international standards were used for $\delta^{13}\text{C}$ (Pee Dee Belemnite: PDB), $\delta^{15}\text{N}$ (atmospheric nitrogen: AIR) and $\delta^{34}\text{S}$ (Canyon Diablo Troilite: CDT). Measurement precisions for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ were $\leq 0.15\text{‰}$, $\leq 0.25\text{‰}$ and $\leq 0.40\text{‰}$, respectively. All isotopic measurements were conducted at the Scientific and Technological Centres of the University of Barcelona (CCiTUB).

Data analyses

Temporal consistency of demographic heterogeneity

To assess whether or not demographic heterogeneity exists in productivity and survival, we used Generalized Linear Mixed Models (GLMMs) with a Poisson distribution and a logarithm link function for productivity, and a binomial distribution with a logit link function for survival. GLMMs allowed us to account for the non-independence of observations from the same territories and years by including these two variables as random factors. For each vital rate (productivity and survival, hereafter referred to as, respectively, PROD and SURV), the effects of temporal and spatial variation were assessed by comparing four models in which the dependent variable was the vital rate in

question that included the null model and three models with random factors: (1) year, (2) territory or (3) year + territory. Therefore, if spatial and temporal variation had a relevant effect on the vital rate in question, we would expect that the likelihood ratio test of the most complex model against the model including one random factor was significant (Bates *et al.* 2023). We calculated the intraclass correlation coefficient (ICC) as a measurement of repeatability in demographic performance at the territory level, as it can be interpreted as the within-territory correlation among years (Nakagawa & Schielzeth 2013).

We also employed GLMMs to explore the temporal scale at which there was consistency for each vital rate. We used only the territories that had been monitored consecutively for at least 11 and up a maximum of 26 years, which allowed us to assess temporal consistency over a long time period. Here, the response variable was the vital rate in question (either PROD or SURV) at time t , and the explanatory variables PROD or SURV at $(t-1)$, and their average between $(t-1)$ and $(t-2)$, $(t-1)$ and $(t-3)$, and so on, up to the average value between $(t-1)$ and $(t-10)$. We used this procedure to address whether conditions in a given year can be explained by the average conditions in the preceding years in a given time span. For each analysis (PROD and SURV), we evaluated a set of models, each of which contained only one explanatory variable referring either to PROD or SURV in the previous time lags (11 models, see Table 1). Age of pair (i.e. adult or non-adult) was also included as a fixed factor in the productivity analysis (Hernández-Matías *et al.* 2011a, Resano-Mayor *et al.* 2014a), whereas territory and year were included as random factors in the two analyses.

Defining trophic scenarios

For each territory and year (period 2008–15), we obtained a single isotopic signature either using the values for single nestlings or averaging the values of siblings. Based on the stable isotope analysis, we calculated several dietary variables to describe the trophic scenario in a given territory-year: (1) the proportion of main prey consumed, (2) diet diversity calculated using the Shannon–Weaver index (H') (Shannon & Weaver 1997) and (3) a proportional similarity index (PSi), which estimates nestlings' prey-consumption specificity, that is, the diet overlap between nestlings in a territory-year and the mean population diet in the

Table 1. Model selection assessing the time lag during which there was temporal consistency in productivity and survival ($n = 48$ and $n = 42$ territories, respectively).

Vital rate	Model	AICc	Δ AICc	AICcw	
PROD	PROD (previous 4 y) + AGE	919.939	0.000	0.478	
	PROD (previous 3 y) + AGE	921.957	2.018	0.174	
	PROD (previous 5 y) + AGE	923.169	3.230	0.095	
	PROD (previous 6 y) + AGE	924.050	4.111	0.061	
	PROD (previous 8 y) + AGE	924.172	4.233	0.058	
	PROD (previous 2 y) + AGE	924.378	4.439	0.052	
	PROD (previous 7 y) + AGE	924.737	4.799	0.043	
	PROD (previous 10 y) + AGE	926.101	6.162	0.022	
	PROD (previous 9 y) + AGE	926.864	6.925	0.015	
	PROD (previous 1 y) + AGE	931.511	11.572	0.001	
	AGE	937.038	17.099	<0.001	
	SURV	SURV (previous 3 y)	502.789	0.000	0.601
		SURV (previous 4 y)	505.206	2.417	0.180
SURV (previous 5 y)		506.179	3.389	0.110	
SURV (previous 2 y)		508.355	5.566	0.037	
SURV (previous 6 y)		508.639	5.850	0.032	
SURV (previous 7 y)		509.832	7.042	0.018	
SURV (previous 8 y)		511.204	8.415	0.009	
SURV (previous 1 y)		512.057	9.267	0.006	
SURV (previous 9 y)		512.986	10.197	0.004	
SURV (previous 10 y)		514.339	11.550	0.002	

The response variable was the vital rate in question (either PROD or SURV) at time t . The explanatory variables were the average values of the considered vital rates in the previous n years. All models included territory and year as random factors and in the productivity analysis, age of the pair was also included as a fixed factor. Δ AICc refers to the difference in corrected Akaike's Information Criterion (AICc) between model i and the best model. AICcw explains the probability that a given candidate model is the best of the proposed set. Selected models with Δ AICc < 2 are shown in bold type.

whole set of territory-years. PSi tends towards 1 in those territories where nestling prey consumption is similar to the mean population diet, but declines when prey consumption differs from the mean diet (see Bolnick *et al.* 2002b, Resano-Mayor *et al.* 2014a). Finally, based on the isotopic values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ represented in a three-dimensional space, we calculated the mean Euclidean distance to centroid (DEUC) as a

measure of diet consistency at territory level (i.e. short distances indicate temporal consistency in diet, while long distances indicate more variable trophic scenarios). To do so, we first defined the territory centroid point from the cloud of points when considering the whole set of years of a given territory, and then estimated the Euclidean mean distances from each year point to its centroid. In our analyses, we used dietary data for all periods of either four or three consecutive years for each territory, according to the best time lag obtained in the consistency analysis of the demographic heterogeneity of, respectively, productivity and survival.

It is worth mentioning that our territorial diet estimates only included successful breeding pairs because nestlings can only be sampled if breeding pairs are successful in hatching and rearing chicks. In the analyses we used territories with at least 2 years of diet information (Resano-Mayor *et al.* 2014a), which could be done safely because the mean Euclidean distance was not correlated to the number of sampled years (Kendall's Tau-b rank coefficient = 0.006, $P = 0.915$, $n = 184$; and coefficient = 0.013, $P = 0.839$, $n = 159$ for productivity and survival datasets, respectively). Based on this, we performed the analysis beginning in either 2006 and 2007 for, respectively, productivity and survival as long as diet information was available for at least 2 years for the territory and period in question.

Effect of trophic scenarios on demographic heterogeneity

We used GLMMs to test whether or not – and how – different trophic scenarios modulated demographic heterogeneity in terms of productivity and survival. We defined mean productivity (PROD) as the response variable for the time periods of 4 years to coincide with the time period for which we detected temporal consistency (see Results). The explanatory dietary variables (OC = rabbit consumption; H' = diet diversity; Psi = prey consumption specificity; DEUC = mean Euclidean distance to centroid) were also estimated for each territory as the mean values during the same period as productivity. PROD was modelled as a Gaussian response variable. The proportion of years with an adult territorial pair was included as a covariate because the age of the breeding individuals may affect productivity (Carrete *et al.* 2006, Hernández-Matías *et al.* 2011a,

Resano-Mayor *et al.* 2014a). Time period (a different set of years) was included as a covariable as we noted a temporal trend in productivity across the study period. Territory was included as a random factor. Collinearity was inspected by correlation analysis and we excluded H' from the analysis because it was highly correlated to OC ($r_p = -0.89$) and PSi ($r_p = 0.58$) (Moleón *et al.* 2012a). We evaluated all possible models containing the main effects of the explanatory variables. In addition, we included the quadratic effects and interactions that were considered potentially relevant based on previous studies and the graphic inspection of the data.

We used GLMMs following a similar procedure to determine survival. Rather than use mean survival, which produced an abnormal distribution, we defined SURV as the binomial response variable for the 3-year time periods, a time span based on temporal consistency analyses: a score of 1 if territorial individuals survived the 3-year period or 0 if at least one territorial individual disappeared during the 3-year period. The explanatory variables were the same as in the productivity analysis (OC, H' , PSi and DEUC) but were estimated for each territory-period as the mean values over the 3-year period. Period was included as a covariate rather than a random factor because we detected a marked temporal trend in survival during the study period. Territory was included as a random factor. The set of considered models was analogous to that of the productivity analyses.

For all linear model analyses, model selection was based on Akaike's Information Criterion or Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002). Models within 2 AICc points of the best model were selected to construct averaged models. Akaike weights were also used to assess the probability that each candidate model was the best of the proposed set. All models were fitted using R software (<https://www.r-project.org>). Generalized linear models were fitted with the functions `lmer()` and `glmer()` of the *lme4* package (Bates *et al.* 2015). AICc, Akaike weights and model average coefficients were estimated using the `dredge()` and `model.avg()` functions in the *MuMIn* package (Barton 2017). Marginal and conditional R^2 values were estimated using the `r.squaredGLMM` function in the *MuMIn* package (Nakagawa & Schielzeth 2013, Barton 2017). Intraclass correlation coefficients were calculated using the

`icc` function() in the *performance* package (Lüdtcke *et al.* 2021).

RESULTS

Temporal consistency of demographic heterogeneity

Spatial demographic heterogeneity was present in the studied Bonelli's Eagle population given that the models that included 'territory' as a random factor in both the productivity and the survival analyses fitted better than the null model ($\chi^2 = 27.56$, $df = 1$, $P < 0.001$ and $\chi^2 = 5.54$, $df = 1$, $P = 0.018$, respectively) or the model including 'year' as random factor only ($\chi^2 = 27.37$, $df = 1$, $P < 0.001$ and $\chi^2 = 5.54$, $df = 1$, $P = 0.018$). In both cases, spatial heterogeneity was more relevant than temporal heterogeneity because the random factor 'territory' had a greater effect than the random factor 'year', which did not show significant differences compared with either the null model ($\chi^2 = 0.33$, $df = 1$, $P = 0.564$ and $\chi^2 = 0$, $df = 1$, $P = 1$, for productivity and survival, respectively) or the model including 'territory' as a random factor only ($\chi^2 = 0.15$, $df = 1$, $P = 0.698$ and $\chi^2 = 0$, $df = 1$, $P = 1$). Average productivity per territory ranged from 0 to 1.71 fledglings per pair and year (mean = 0.908) and average survival per territory ranged from 0.583 to 1.00 (mean = 0.903). Despite these marked differences, we found low ICC values associated with the factor 'territory' (0.103 for productivity and 0.045 for survival) suggesting low repeatability of territory performance over the whole period.

Our analysis of temporal consistency showed that productivity in year t was best explained by the average value of productivity between $t-1$ and $t-4$, although the model that considered the average value of this vital rate between $t-1$ and $t-3$ as an explanatory variable was also quite well supported (Table 1). Similarly, survival in t was best explained by the value of survival between $t-1$ and $t-3$ (Table 1).

Effects of trophic scenarios on demographic heterogeneity

When modelling mean productivity in 4-year periods (range 0.25–2 fledglings per territory) in response to different trophic scenarios, the model average of the top three models included the

Table 2. Model selection assessing the effects of trophic scenarios on productivity at territory level ($n = 184$ territory-periods of observations).

Model definition	df	AICc	Δ AICc	AICcw
AGE + DEUC + PSi + PERIOD + DEUC * PSi	8	72.58	0.00	0.25
AGE + DEUC + RABB + RABB2 + PSi + PERIOD + DEUC * PSi	10	72.61	0.03	0.24
AGE + DEUC + RABB + RABB2 + PSi + PERIOD + DEUC:RABB + DEUC * PSi	11	73.76	1.19	0.14
AGE + DEUC + RABB + PSi + PERIOD + DEUC * PSi	9	74.63	2.05	0.09
AGE + DEUC + DEUC2 + RABB + RABB2 + PSi + PERIOD + DEUC * PSi	11	75.17	2.59	0.07
AGE + DEUC + DEUC2 + PSi + PERIOD + DEUC * PSi	9	75.63	3.05	0.05
AGE + DEUC + RABB + PSi + PERIOD + DEUC:RABB + DEUC * PSi	10	75.77	3.19	0.05
AGE + DEUC + DEUC2 + RABB + RABB2 + PSi + PERIOD + DEUC:RABB + DEUC * PSi	12	76.37	3.79	0.04
AGE + DEUC + DEUC2 + RABB + PSi + PERIOD + DEUC * PSi	10	77.37	4.79	0.02
AGE + DEUC + DEUC2 + RABB + PSi + PERIOD + DEUC:RABB + DEUC * PSi	11	78.55	5.97	0.01

The response variable was the mean number of fledglings per territory in a 4-year period. Independent variables included average values of dietary variables in each territory during the same time period (DEUC, mean Euclidean distance to centroid; DIVERS, diet diversity; PSi, prey consumption specificity; RABB, rabbit consumption). All the models included the proportion of years in which a pair was adult (AGE) as a fixed factor, and territory and period as random factors. Δ AICc refers to the difference in corrected Akaike's Information Criterion (AICc) between model i and the best model. AICcw explains the probability that a given candidate model is the best of the proposed set. The best models are shown in bold type.

effects of PSi and DEUC, along with the interaction between them, the quadratic effect of DEUC, the linear and quadratic effect of rabbit consumption and the interaction between this variable and DEUC, as well as the effects of the age of the pair and the time period (Tables 2 and S2 in Supporting Information). The most important effects related to trophic scenarios were PSi and DEUC, and the interaction between them (Fig. 2), which had Akaike weights of 1. The model predicted higher productivity in territories with consistent trophic scenarios (i.e. low DEUC) in which fewer highly consumed prey types were consumed (i.e. low PSi) than in consistent trophic scenarios with a diet similar to the average diet in the population. The model also predicted high productivity in territories with inconsistent diets that were similar to the mean population (i.e. high PSi values), although this prediction was not supported by any observation (see Fig. 2a). In addition, territories where diets were similar to the population average (high PSi) and consistent over time (low DEUC) showed lower productivity than those with intermediate levels of these variables. Also, most territories with inconsistent diets (very high DEUC) had low productivity values (Fig. 2a). Conversely, the linear and quadratic effects of rabbit consumption, as well as the interaction of rabbit consumption with DEUC, had less effect on productivity (Fig. 2b) and lower Akaike weights (0.76, 0.74 and 0.27, respectively). Nevertheless, productivity

was higher in territories with either a very high or very low proportion of rabbits in their diets, which were also territories in which few prey types were consumed (i.e. low PSi) (Fig. 2c).

All considered models included the age of territorial individuals and the time period, and all also had Akaike weights of 1. Nevertheless, the magnitude of the estimated coefficients and their standard errors also indicated that these effects were relevant: territories with a higher proportion of adults and during the initial time periods had higher productivity values. Nonetheless, the r^2 analysis of the best model illustrated that fixed effects captured much less variance in the response variables (marginal $r^2 = 0.183$) than random effects (conditional $r^2 = 0.707$).

When modelling survival during 3-year periods in response to different trophic scenarios during the same time period, we found that the best model included rabbit consumption, the time period and the interaction between them (Tables 3 and S3 in Supporting Information). Graphics showed that in earlier time periods, survival was lower in territories with greater rabbit consumption but that the opposite trend was true in later time periods in which the highest survival rates were found in territories with intermediate or high rabbit consumption (Fig. 3). In spite of these results, most variance in the response variable was explained by the effect of territory (marginal r^2 of the best model = 0.092, conditional $r^2 = 0.737$).

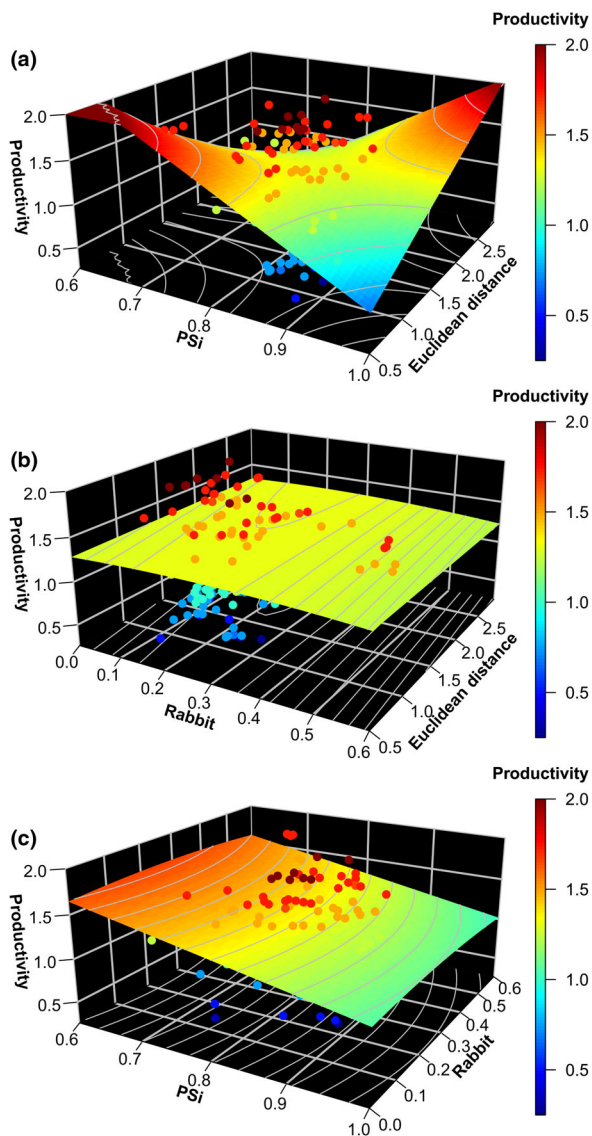


Figure 2. Predicted (coloured surface and grey isolines) and observed (coloured dots) response (i.e. mean productivity in 4-year periods) in relation to the explanatory variables in the average model. (a) Response in relation to mean prey consumption specificity (PSi, proportionally similarity index, range: 0–1) and mean distance to centroid (Euclidean Distance: distance in the three-dimensional space of stable isotopes signature of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰)). (b) Response in relation to the mean percentage of rabbit consumption (Rabbit) and the mean distance to centroid (Euclidean Distance). (c) Response in relation to the mean proportion of rabbit consumption (Rabbit) and mean prey consumption specificity (PSi).

Accordingly, the Akaike weights of the variables present in the selected models were relatively low (rabbit consumption = 0.70, interaction rabbit *

period = 0.57) but higher than the non-retained variables (DEUC = 0.24; PSi = 0.24).

DISCUSSION

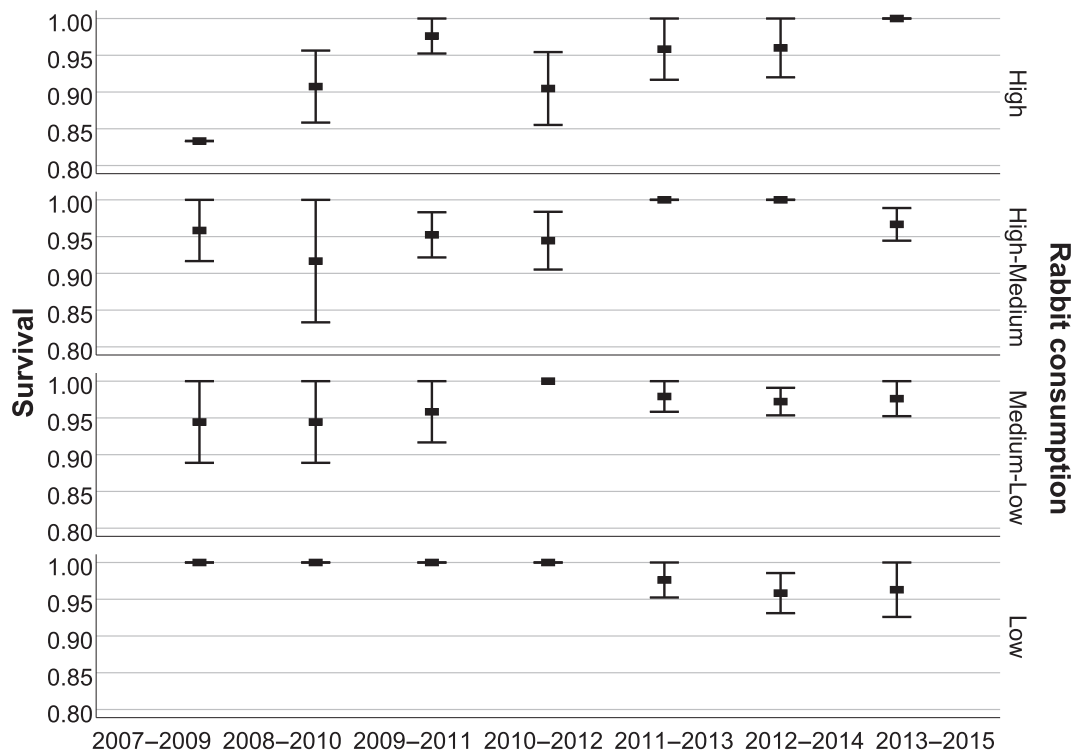
Environmental variation at multiple spatiotemporal scales can create marked differences in the demographic contribution of individuals and populations over space and time. Individuals facing different trophic scenarios may exhibit differential fitness, which eventually may affect population dynamics (Bolnick *et al.* 2002a, Resano-Mayor *et al.* 2014b, 2016, Ingram *et al.* 2018). Thanks to the continued monitoring of a Bonelli's Eagle population carried out over a large spatial range (Hernández-Matías *et al.* 2013), which included estimations of individuals' diets through stable isotope analysis (Resano-Mayor *et al.* 2011, 2014a), we show that, in a long-lived territorial avian predator, characteristics and the spatiotemporal variation in diet of individual territorial holders is correlated to their performance in terms of survival and reproduction. Therefore, we suggest that spatial and temporal variation in trophic scenarios act as meaningful drivers of intrapopulation demographic heterogeneity.

Fitness differences between individuals in a single population play a central role in evolutionary theory (Darwin 1859, Ridley 1997). Yet, fine-scale variation in the contribution of apparently similar individuals to the dynamics of local populations is commonly overlooked in ecological studies. In recent years, efforts to understand within-population differences in key aspects of individuals' vital activity have increased (Bolnick *et al.* 2002a, Schreiber 2006, Cam *et al.* 2012, Plard *et al.* 2019). However, we still have only a limited understanding of how widespread this intrapopulation demographic heterogeneity is and its consequences in terms of population and community structure and dynamics (Bolnick *et al.* 2011, Gimenez *et al.* 2017). Here, we found that there is great variation in the average values for vital rates in territorial pairs within a single Bonelli's Eagle population (see also Rollan *et al.* 2021), which vary much more than the range observed between different local populations. For example, average values of productivity in territories in our study population ranged from 0 to 1.71 fledglings, while the observed values of this vital rate in a sample of 12 populations in western Europe ranged from 0.60 to 1.42.

Table 3. Model selection assessing the effects of trophic scenarios on survival at territory level ($n = 159$ territory-periods of observations).

Model definition	df	AICc	Δ AICc	AICcw
RABB + PERIOD + RABB * PERIOD	5	137.15	0.00	0.30
PERIOD	3	138.22	1.07	0.18
DEUC + RABB + PERIOD + RABB * PERIOD	6	139.25	2.10	0.11
RABB + PSi + PERIOD + RABB * PERIOD	6	139.31	2.16	0.10
RABB + PERIOD	4	140.18	3.03	0.07
PSi + PERIOD	4	140.28	3.13	0.06
DEUC + PERIOD	4	140.31	3.16	0.06
DEUC + RABB + PSi + PERIOD + RABB * PERIOD	7	141.41	4.26	0.04
RABB + PSi + PERIOD	5	142.19	5.05	0.02
DEUC + RABB + PERIOD	5	142.28	5.13	0.02
DEUC + PSi + PERIOD	5	142.37	5.22	0.02
DEUC + RABB + PSi + PERIOD	6	144.23	7.08	0.01

The response variable was survival, that is, whether over a 3-year period all territorial individuals survived (1) or did not (0). We used as independent variables the average values of dietary variables in each territory and during the same time period (DEUC, mean Euclidean distance to centroid; DIVERS, diet diversity; PSi, prey consumption specificity; RABB, rabbit consumption). All models included territory as a random factor and the time period (PERIOD) as covariable. Δ AICc refers to the difference in corrected Akaike's Information Criterion (AICc) between model i and the best model. AICcw explains the probability that a given candidate model is the best of the proposed set. The best model is shown in bold type.

**Figure 3.** Mean survival over the study period in territories that had different levels of rabbit consumption in a given 3-year period. Rabbit consumption levels corresponded to the quartiles of the observed distribution of rabbit consumption (OC). Error bars show standard errors.

Similarly, average observed values of local survival in our territories ranged from 0.583 to 1.00, while this vital rate ranged from 0.868 to 0.940 at European population level. Despite having a much narrower range, this implies that local populations act either as sinks or as sources at an overall western European scale (Hernández-Matías *et al.* 2013).

This heterogeneity is consistent over time for territories that perform either very well or very poorly. Interestingly, the performance of most territories was not constant over time, which suggests that their performance was shaped by environmental conditions, which provides partial support for our predictions. In particular, when all territories were considered together, the current values of both productivity and survival were best predicted by the average values of these rates in, respectively, the four and three previous years. For long-lived birds such as Bonelli's Eagles, which have relatively high adult survival rates (Hernández-Matías *et al.* 2011a), these time spans are fairly short, especially if we bear in mind that, once recruited, individuals are sedentary and show a strong attachment to their territories (Hernández-Matías *et al.* 2011a, 2011b). This implies that the breeding conditions at the time of recruitment will not necessarily be stable in the mid- or long term.

The main causes of mortality in our study population are non-natural (e.g. electrocution; Hernández-Matías *et al.* 2015, 2020). However, the fact that the time spans that best predict current survival and reproduction rates are similar suggests that the environmental conditions that affect reproduction are also affecting survival. This could occur if the abundance and distribution of certain basic prey species determine the exposition to threats to survival (López-Peinado *et al.* 2023). It is to be expected that the temporal consistency of environmental conditions will play a less relevant role in short-lived than in long-lived species (Engen & Sæther 2017). Indeed, available data show that passerines display relatively low fidelity to their breeding sites between consecutive years, a characteristic that is known to be driven by nest predation but also possibly by variation in the environmental characteristics of breeding areas (e.g. Paradis *et al.* 1998, Citta & Lindberg 2007). In our study population, individuals may be subject to a trade-off between the benefits of recruiting early because potential territories are limited in

large long-lived territorial predators and the costs of delayed recruitment in an attempt to recruit in the few very high-quality territories that exist (Kokko & Sutherland 1998).

Increasing theoretical and empirical evidence suggests that individual trophic specialization may have important consequences at population and community levels (Araújo *et al.* 2011, Bolnick *et al.* 2011, Dall *et al.* 2012, Layman *et al.* 2015, Ingram *et al.* 2018). Nonetheless, individual differences in resource consumption are generally assumed to be caused by individual preferences or characteristics rather than spatial differences driven by the environmental conditions where individuals live; the extent to which ecological opportunities can generate within-population variation in trophic consumption and whether or not this variation may cause within-population demographic heterogeneity still remain little studied (but see Votier *et al.* 2004, L'Hérault *et al.* 2013, Layman *et al.* 2015, Szigeti *et al.* 2019). Bonelli's Eagle may exploit quite diverse environments and prey resources (del Hoyo *et al.* 1992, Moleón *et al.* 2009) and in our study area there are remarkable differences in the composition of habitats used and the species preyed on by these eagles (Resano-Mayor *et al.* 2011, Real *et al.* 2016). Here, we addressed diet composition using mixing models on stable isotope analysis, a method that, although it presents limitations for the identification of all prey at the species level, has shown good agreement with conventional methods in our study system (Resano-Mayor *et al.* 2014b).

Our results show that resource consumption patterns differ markedly between the territories in our study population and that these differences have significant consequences for birds' key vital rates (Resano-Mayor *et al.* 2014b, 2016). Interestingly, our results also illustrate that, in addition to diet composition, both niche specialization (measured as P_{Si}) and the temporal consistency of resource consumption in Bonelli's Eagle are correlated to breeding performance. In vertebrates, diet-specialist individuals are often more efficient or have greater fitness than generalists (Bolnick *et al.* 2002a, Svanbäck & Eklöv 2003, Tinker *et al.* 2012; but see Woo *et al.* 2008, Whitfield *et al.* 2009), particularly when their preferred prey items are abundant (Terraube *et al.* 2011). Available evidence suggests that rabbits and partridges are key prey species for Bonelli's Eagle in southern Europe (Moleón *et al.* 2007, 2012a); however,

since the outbreak of haemorrhagic disease in rabbits that has caused a drastic fall in this prey species' populations in recent decades in western Europe, Bonelli's Eagles have shifted their diets and have begun to consume fewer rabbits and increase their diet diversity (Real 1991, Moleón *et al.* 2009, 2012b, Resano-Mayor *et al.* 2014b, 2016). Furthermore, diets with little diversity, due to high consumption of either rabbits or pigeons, were correlated to higher productivity at the territory level (Resano-Mayor *et al.* 2014b) and, in the case of rabbits, to higher growth rates at the population level (Resano-Mayor *et al.* 2016). Here, we found that highly specialized diets have the greatest productivity levels. As Resano-Mayor *et al.* (2014b) state, when prey other than rabbits, such as partridges and pigeons, are consumed in great number, productivity responds positively. This suggests that when the main prey species exploited by Bonelli's Eagles are highly abundant, this eagle will consume them in preference to other items, a choice that has a positive effect on reproduction.

On the other hand, we found that the temporal pattern of survival varied between territories with low rabbit consumption, where survival has been poor in recent years, and territories with mid- to high rabbit consumption, where survival has increased in recent years. Overall, rabbit consumption has decreased over time and eagles in territories with higher survival rates do in fact consume fewer rabbits. Although this finding does not match our predictions, it could be due to the fact that in our study area rabbits are currently most abundant in intensively humanized open areas, which are also where the greatest non-natural threats such as power lines, dangerous ponds and illegal persecution are concentrated. Hence, it is to be expected that the eagles that exploit most intensively the areas in which rabbits are abundant will be more exposed to the non-natural threats that are the main cause of adult mortality in this species (Hernández-Matías *et al.* 2015). Although the relationship between spatial use by individuals and exposure to risk is still poorly understood in most species, available evidence in several raptor species shows that spatial use and exposure to risk factors may be strongly modulated by the availability, distribution and predictability of food resources (Martínez-Abraín *et al.* 2012, López-López *et al.* 2014, Arrondo *et al.* 2020, López-Peinado *et al.* 2023).

Beyond the characteristics of trophic scenarios, our results reveal that the temporal consistency of these trophic conditions is also relevant – in a complex fashion – when attempting to explain the within-population demographic heterogeneity of territorial individuals. Identifying the timescale over which trophic specialization is manifest is very challenging and, indeed, there are very few empirical assessments of the temporal variation of individual specialization and its consequences for fitness (Layman *et al.* 2015, Costa-Pereira *et al.* 2019, Szigeti *et al.* 2019). Novak and Tinker (2015) showed that analyses of feeding observations of sea otters during short timeframes (e.g. hours) overestimate the degree of individual specialization and, although we did not explicitly quantify this aspect, our measures of mean distance to centroid (a proxy of temporal variation of diet) do indicate that some territories show very marked changes in trophic scenarios over relatively short periods of time. In agreement with our observations and Novak and Tinker's (2015) findings, Fodrie *et al.* (2015) highlight how the timescales of studies can greatly influence the degree of niche specialization.

In our study, the territories that had the most constant diets also had high productivity values if diets were highly specialized (low P_{Si} values), a pattern previously observed at the population level (Reznick *et al.* 2002, Engen & Sæther 2016) and one that agrees with our predictions. By contrast, we found intermediate values of productivity at intermediate levels of diet specialization and low values of productivity at low levels of diet specialization. A possible explanation for this pattern is that the majority of the population feeds on a moderately diverse range of prey items (Fig. S2 in Supporting Information), inhabits environments with relatively stable conditions, consumes average numbers of rabbits (Fig. S3 in Supporting Information) and has intermediate reproductive performance (Amar *et al.* 2003, Korpimäki *et al.* 2005). On the other hand, territories with low rabbit consumption and highly diverse diets show low performance. Finally, intermediate levels of temporal consistency in diet composition coincided with fairly good reproductive performance; likewise, the territories with the most variable diets were also those that reproduced most poorly.

Beyond environmental conditions, the intrinsic characteristics of individuals (e.g. individual trophic preferences and hunting abilities) may have

also contributed to the patterns we observed (Newton 1989, Ferrer & Donázar 1996, Bolnick *et al.* 2002b, Araújo *et al.* 2011). In this context, we would anticipate high-quality individuals to preferentially select high-quality territories, thereby contributing to the observed intrapopulation heterogeneity. However, disentangling individual characteristics from territorial characteristics presents significant challenges in long-lived territorial raptors, as individuals typically occupy the same territory throughout their entire lifespan. Further insights into this issue could be gained by incorporating information on prey availability into our approach. Unfortunately, acquiring such information for the main prey species of Bonelli's Eagles is very challenging, especially considering the diverse census techniques required for such study (Gil-Sánchez 1998), the large territories of this raptor species (Moleón *et al.* 2011) and the influence of habitat structure on its hunting success (Ontiveros *et al.* 2005). Nevertheless, the Bonelli's Eagle in southwestern Europe exhibits a clear preference for rabbits (Moleón *et al.* 2009, 2012a, 2012b, Resano-Mayor *et al.* 2014a, 2014b, 2016). Hence, individual prey preferences and hunting abilities are expected to manifest primarily towards those prey that need to be taken in the absence of abundant rabbit populations.

Overall, our results highlight the idea that spatial and temporal variation in trophic conditions can have a meaningful impact on within-population demographic heterogeneity. Our study illustrates that monitoring diets over time – for example by sampling feathers from chicks and stable isotope analyses – is a powerful way of detecting within-population variation in prey consumption and, consequently, of detecting temporal and spatial shifts in trophic consumption, information that, along with demographic data, provides excellent insights into the determinants of within-population demographic heterogeneity. However, the period for which we investigated these questions is relatively short for a long-lived species. Therefore, further studies considering longer time spans on the relationship between trophic characteristics and vital rates will be helpful to further support the patterns described here. In terms of conservation, managers should aim to improve habitat and prey stocks to promote those trophic scenarios, either to sustain good performances in territories and local areas that contribute positively to the population growth rate, or to restore

territories or local areas that contribute negatively to the population growth rate. By incorporating this source of information into long-term monitoring schemes, it may be possible to detect environmental changes before they impact negatively on the population, and provide further insights into the complex relationships between the environmental drivers of vital rates and their potential effect on shaping the eco-evolutionary fate of animal populations.

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AUTHOR CONTRIBUTIONS

Antonio Hernández-Matías: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision; resources. **Iván Peragón:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis. **Jaime Resano-Mayor:** Conceptualization; investigation; writing – review and editing; methodology; formal analysis. **Marcos Moleón:** Conceptualization; investigation; writing – review and editing. **Emilio Virgós:** Conceptualization; investigation; writing – review and editing. **Joan Real:** Conceptualization; investigation; funding

acquisition; writing – original draft; methodology; writing – review and editing; project administration; data curation; supervision; resources; validation; visualization.

CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest in this research.

ETHICAL NOTE

None.

Data Availability Statement

The authors agree to make data and materials supporting the results or analyses presented in their paper available upon reasonable request.

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SUPPORTING INFORMATION

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

Table S1. Mean consumption estimates (%) of main prey categories and diet diversity estimated by isotopic mixing models at the population level ($n = 185$ territory-years).

Table S2. Model average and parameter estimates with their standard errors of generalized linear mixed models ($\Delta\text{AICc} < 2$) for the mean productivity in 4-year periods of territories of Bonelli's Eagle ($n = 184$).

Table S3. Model average and parameter estimates with their standard errors of generalized linear mixed models for survival in 3-year periods of territories of Bonelli's Eagle ($n = 159$).

Figure S1. Relationship between distance to centroid (DC, x -axis) and rabbit consumption (OC, y -axis) measured in periods of 4 years at the territory level.

Figure S2. Relationship between diet diversity (H' , x -axis) and prey consumption specificity (PSi , y -axis) measured in periods of 4 years at the territory level (see Resano-Mayor *et al.* 2014a).

Figure S3. Relationship between rabbit consumption (OC, x -axis) and prey consumption specificity (PSi , y -axis) measured in periods of 4 years at the territory level.