Diet-demography relationships in a long-lived predator: from territories to populations

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Understanding the mechanisms that shape animal population dynamics is of fundamental interest in ecology, evolution and conservation biology. Food supply is an important limiting factor in most animal populations and may have demographic consequences. Optimal foraging theory predicts greater consumption of preferred prey and less diet diversity when food is abundant, which may benefit key fitness parameters such as productivity and survival. Nevertheless, the correspondence between individual resource use and demographic processes in populations of avian predators inhabiting large geographic areas remains largely unexplored, particularly in complex ecosystems such as those of the Mediterranean basin. Based on a long-term monitoring program of the diet and demography of Bonelli's eagle *Aquila fasciata* in western Europe, here we test the hypothesis that a predator's diet is correlated to its breeding productivity and survival at both the territorial and population levels, and ultimately to its population growth rate. At the territorial level, we found that productivity increased with greater consumption of European rabbits *Oryctolagus cuniculus*, the Bonelli's eagle's preferred prey, and pigeons, an important alternative prey for this predator. The survival of territorial pairs was negatively affected by higher diet diversity, which probably reflected the inability to find sufficient high quality prey. Diet effects at the population level were similar but more noticeable than at the territorial level, i.e. a greater consumption of rabbits, together with lesser consumption of small-to-medium avian species ('other birds'; non-preferred prey), increased productivity, while greater diet diversity and lower consumption of rabbits was associated with reduced survival and population growth rate. Overall, our study illustrates how the diet of a predator species can be closely related to key individual vital rates, which, in turn, leave a measurable fingerprint on population dynamics within and among populations across large spatial scales.

Understanding the mechanisms that shape animal population dynamics is of fundamental interest in ecology, evolution and conservation biology (Begon et al. 2005). On a simple level, births, movements and deaths are the main demographic parameters conditioning animal population dynamics (Krebs et al. 2001) and, in turn, several abiotic and biotic factors potentially affect these parameters (Dempster 1975). A universal property of life is that organisms need energy and resources for survival and reproduction so food availability and consumption are expected to affect individual vital rates and hence are an important limiting factor in animal populations (Stephens and Krebs 1986, White 2008). In addition, the way resource consumption by individuals ultimately affects population demographic trends is closely related to the characteristics of species' life histories. In animal populations, fecundity has an important impact on population growth rates in short-lived species, while survival rates are more relevant to population dynamics in long-lived species (Sæther and Bakke 2000). Thus, the

effects of diet on individual vital rates within a population, along with the species' life-history traits, will determine how individual resource consumption ultimately affects the population growth rate.

Avian predators have been well studied as a way of assessing how prey consumption influences consumers' key demographic parameters such as breeding success and survival (Korpimäki and Norrdahl 1991, Millon and Bretagnolle 2008). In the case of territorial species whose populations range over large geographic areas, habitat heterogeneity is expected to influence prey abundance and availability, which will ultimately affect individual diet variation within a population (Whitfield et al. 2009) since organisms prefer environments in which their reproductive success and survival is good (Orians and Wittenberger 1991). Foraging theory predicts that animals will feed most efficiently by consuming a narrow range of preferred prey items when they are abundant, but will expand their range of food and consume less-preferred prey items when food becomes scarce (Emlen

1966, Futuyma and Moreno 1988). In this sense, species will prefer prey that benefits their individual fitness and key vital rates (Schoener 1971, Pyke et al. 1977), a choice that will seriously shape predator population dynamics (Vucetich and Peterson 2004, Millon and Bretagnolle 2008). For instance, high preferred prey abundance may increase its consumption and enhance predator breeding success and survival (Korpimäki and Norrdahl 1991, Millon and Bretagnolle 2008). By contrast, the scarcity of the preferred prey will force predators to expand their diet and to consume alternative prey (Schoener 1971, Pyke et al. 1977), which might constrain reproductive success and survival (Arroyo and Garcia 2006, White 2008).

Numerous studies have assessed the relationship between temporal variations in diet and demographic parameters in populations of avian predators, particularly in boreal and other northern ecosystems. These systems are characterized by cyclical prey regimes and both coupled and lagged variations in predator–prey population dynamics have been reported (Korpimäki and Krebs 1996, Krebs et al. 2001). By contrast, studies assessing the relationship between spatial variation in prey consumption patterns and demographic parameters of avian predators are comparatively scarce, particularly in temperate Mediterranean ecosystems that are more complex since they do not have clearly marked cyclical prey regimes (but see Salamolard et al. 2000, Fargallo et al. 2009). In such systems, the correspondence between individual resource use and demographic processes in populations (e.g. growth rates) remains largely unexplored, in part due to the scarcity of long-term monitoring data of resource consumption and demography over large spatio-temporal scales for most avian predator species.

Based on a long-term monitoring program in France, Spain and Portugal of Bonelli's eagle *Aquila fasciata*, a long-lived territorial raptor, here we test the hypothesis that a predator's diet is correlated to its breeding productivity and survival at both territorial and population levels, which ultimately influence its population growth rate. In western Europe, Bonelli's eagle predates on a wide range of prey that includes small-to-medium sized mammals (Lagomorpha and Rodentia), birds (Columbiformes, Galliformes, Passeriformes, Ardeiformes, Charadriiformes and others) and reptiles (mainly lizards) (Real 1991, Moleón et al. 2009). In this geographical area, marked differences in dietary patterns between territories have been described within single populations (Real 1991, Palma et al. 2006, Resano-Mayor et al. 2014a), a trend that increased after the outbreak of the Rabbit haemorrhagic disease in the late 1980s (Moleón et al. 2012a). Yet, despite the dietary differences between territories, European rabbits *Oryctolagus cuniculus* and, to a lesser extent, red-legged partridges *Alectoris rufa*, are thought to be Bonelli's eagle's preferred prey item, as they are positively selected and high consumption of these prey species leads to a decrease in this eagle's diet diversity (Real 1991, Moleón et al. 2009, 2012b). On the other hand, this raptor also shows marked intra- and inter-population demographic variations throughout its western European populations (Real and Mañosa 1997, Hernández-Matías et al. 2013). These variations are evident in terms of survival and reproduction both between territories and local populations, as well as in the contrasting demographic trends

occurring among local populations (Hernández-Matías et al. 2011a, 2013). Nevertheless, the potential effects of diet on the vital rates (e.g. breeding productivity and survival) of territorial pairs and whether dietary effects occurring at territorial scale also modulate local populations' growth rates are unanswered questions on a large spatial scale.

The main objective of this study was to test the effect of diet heterogeneity on vital and growth rates in Bonelli's eagle at territorial and local scale within its western European population. We assumed that the higher consumption of preferred prey reflects its greater availability while greater diet diversity is expected to occur when preferred prey availability is lower (Moleón et al. 2012b). Based on these assumptions, we predict that the consumption of preferred prey, e.g. rabbits, and greater diet diversity should positively and negatively correlate, respectively, with the productivity and survival of Bonelli's eagle at both the territorial and local population levels, and ultimately to its population growth rate. Given the life history traits of this species, we also predict that the dietary factors affecting survival will have a strongest effect on population growth rates.

Methods

Study period and area

In the period 1989–2006, we monitored both diet and demographic rates in 67 Bonelli's eagle breeding territories of five local populations within the species' western European range: Provence and Languedoc-Roussillon (southeast France; n = 8 territories), Burgos (north central Spain; n = 6), Catalonia (northeast Spain; n = 17), Granada (southeast Spain; n = 17) and southern Portugal (n = 19) (Fig. 1).

Diet analysis

The study of Bonelli's eagle diet was based on pellet analysis, with a total of 6908 identified items. Pellets were collected from breeding nests and perches. Pellet collection in each local population was conducted as follows: 1989–1995 in Provence and Languedoc-Roussillon, 1993–1996 in Burgos, 1990–2005 in Catalonia, 1993–2006 in Granada and 1992–2001 in southern Portugal (see Supplementary material Appendix 1 Table A1 for details at the territory level). Pellets were individually analysed and each prey item identified was counted as one item (Real 1996). Pellet contents (i.e. feathers, bones, hair, nails and scales) were identified using a $4 \times$ magnifying glass, reference collections and specialized guides. Prey items were identified to species level whenever possible.

Following Moleón et al. (2009), all items from pellets collected in the same breeding territory were pooled together even if they originated from different years. Therefore, our dietary estimates at the territorial level were representative of the whole monitored period for each local population. Prey items were then grouped into seven different taxonomic prey categories: European rabbits, 'other mammals', red-legged partridges, pigeons *Columba* spp., corvids, 'other birds' and reptiles (mainly Ocellated lizard *Timon lepidus*) to calculate
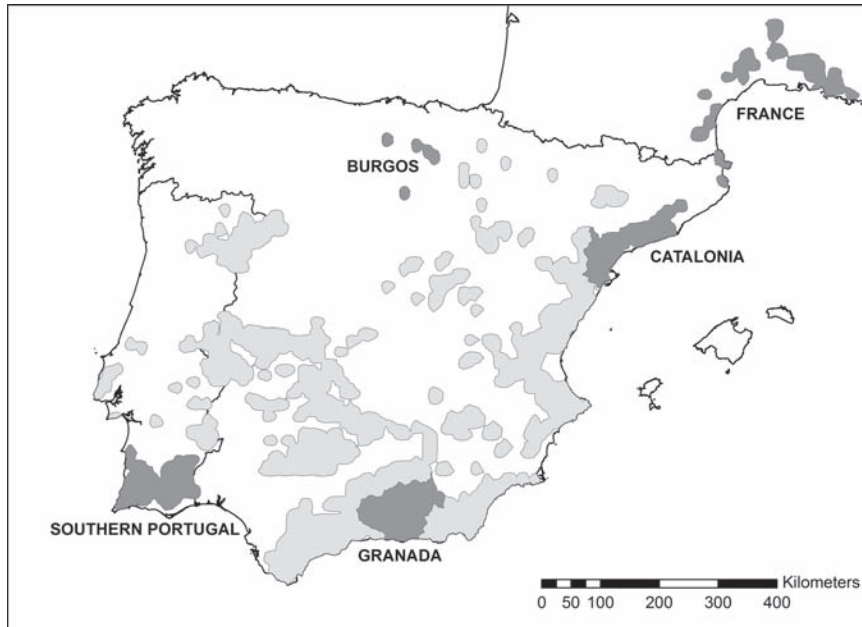
Figure 1. Distribution map of Bonelli's eagle in western Europe (modified from Hernández-Matías et al. 2013). The studied populations are shown in dark grey: France, Catalonia, Burgos, Granada and southern Portugal.

the consumption percentage of each prey category at the territorial level. These percentages were then used to estimate diet diversity by means of the Shannon–Wiener index (H') (Shannon and Weaver 1949).

Estimation of demographic parameters

We based our estimates of survival and breeding performance on basic monitoring information. To record this information, known breeding areas were visited several times per year from January to June. Between January and March we recorded breeding activity (i.e. flight displays, nest material transfers, copulation and incubation) as well as the combined information of plumage-age and the sex of territorial birds, which is required to obtain our estimate of survival. In late March and April, nests were checked to detect the presence, number and age of nestlings, which were estimated by feather development and backdating from the laying date. Between May and June, all breeding pairs were checked to record the number of chicks fledged (nestlings at an age of ≥ 50 days were assumed to have fledged successfully; Gil-Sánchez et al. 2004). Observations were always carried out away from nests using $10 \times$ binoculars and $20–60 \times$ spotting scopes.

At the territorial level, we first estimated yearly productivity and survival. Yearly productivity was calculated as the number of fledged chicks. Individual survival probability in a given territory was calculated from annual turnover rates of territorial birds, based on age classes but corrected for the proportion of non-detected replacements (i.e. the replacement of individuals of the same sex and age class). While this is an indirect measurement of survival it allows obtaining unbiased accurate estimates of this vital rate in our study species (Hernández-Matías et al. 2011a, 2013). In the analyses, we used as response variables the average values of

yearly productivity and survival data over a period of at least 10 years. In those territories in which pellet collection was conducted for ten or more years, productivity and survival were estimated for the same period as the pellet collection. If pellet collection had lasted for less than ten years, we still used a period of ten consecutive years to estimate both vital rates by placing the pellet sampling years in the middle of the ten-year interval. Considering a ten-year period allowed us to buffer variations of these vital rates caused by stochastic events in a given year (Resano-Mayor et al. unpubl.).

Beyond the territorial scale, estimates of productivity, survival and population growth rate (λ_p) for each monitored local population (n = 5) were obtained from a recent published study that estimated those demographic parameters for the same monitored populations during the period 1990–2009 (Hernández-Matías et al. 2013).

Statistical analysis

We used linear models to test the influence of diet on productivity at the territorial level (n = 67), and on productivity, survival and growth rate at the local population level (n = 5). To test the influence of diet on survival at the territorial level we used generalised linear models (GLMs) by considering a binomial family and a logit link function. In all these analyses, each demographic parameter was modelled as a response variable; the explanatory dietary variables were the four most consumed prey categories: rabbits and partridges (i.e. preferred prey), pigeons (i.e. important secondary prey) and 'other birds' (i.e. non-preferred prey), and diet diversity (H'). In order to control for the non-independence of territories within each local population, the categorical variable 'population' was considered as a fixed factor in all the models performed at the territory level. Moreover, when modelling productivity as the response

variable, we also considered a model with the probability of survival as the only explanatory variable (Carrete et al. 2006, Hernández-Matías et al. 2011b) to assess its potential effect on productivity compared with the dietary variables. Model selection was based on Akaike's information criterion adjusted for sample size (AIC$_c$); the Akaike weights (AIC$_{cw}$) were computed to assess the probability that each candidate model was the best for the proposed set (Burnham and Anderson 2002). To estimate the proportion of variance in the response variable explained by each linear model we calculated the coefficient of determination (R^2) (Draper and Smith 1998). For GLMs, the variation explained by each model was calculated using the Nagelkerke pseudo R^2 (Nagelkerke 1991). Linear and generalised linear models were fit using the 'lm' and 'glm' functions in R (ver. 2.14.0), respectively.

Results

Effects of diet on territorial demographic parameters

In the productivity analysis at the territorial level, the best supported model included the consumption of rabbits and pigeons as explanatory variables (Table 1, 2). This model had also the best explanatory power in terms of R^2 (Table 1). Productivity increased with greater consumption of rabbits and with the combined consumption of rabbits and pigeons.

Moreover, those breeding pairs with low rabbit consumption but remarkably high consumption of pigeons tended to increase productivity (Fig. 2). Survival alone had considerably less effect on productivity than the best supported dietary models (Table 1).

In the survival analysis at the territorial level, the best-supported model included diet diversity (Table 1, 2), so there was greater survival wherever the diet diversity was lower (Fig. 3). The best-supported model had also the highest explanatory power in terms of the Nagelkerke pseudo R^2 (Table 1).

Effects of diet on population demographic parameters

The best-supported models of productivity at the population level included either the consumption of 'other birds' or the consumption of rabbits (Table 3, 4). These prey categories, however, had contrasting effects on productivity: greater consumption of 'other birds' decreased productivity, while greater consumption of rabbits increased it (Fig. 4). These models had the highest R^2. We did not detect any effect of adult survival on productivity (Table 3).

Adult survival analysis at the population level showed that the model including diet diversity was the best supported by the data (Table 3, 4). As at the territorial level, but with higher model support, adult survival increased with lower diet diversity (Fig. 5). Moreover, the model including

Table 1. Ranking of the linear (productivity) and generalised linear (survival) models used at the territorial level. Dependent variables were productivity (i.e. mean number of fledglings/territorial pair) and survival (i.e. successes versus failures). The explanatory dietary variables considered were the consumptions of rabbits, partridges, pigeons, 'other birds', the combined sum of these prey categories and diet diversity (H'). For the productivity models we also considered a model including only survival. Models are ranked based on the parameter estimate AIC$_c$ (i.e. the lowest AIC$_c$ score, the best model). ΔAIC$_c$ refers to the difference in AIC$_c$ between model i and the best model. AIC$_{cw}$ explains the probability that a given candidate model is the best of the proposed set and so the sum of all models is 1.0. R^2 indicates the coefficient of determination of the models (i.e. explained variance of the dependent variable), which in the case of survival refers to the Nagelkerke pseudo R^2. Selected models with ΔAIC$_c$ < 2 are shown in bold type.

	Explanatory variables	AICc	ΔAICc	AICcw	R^2
Productivity models					
1	**population + rabbits + pigeons**	**−143.31**	**0.00**	**0.54**	**0.58**
2	population + pigeons	−141.18	2.14	0.19	0.55
3	population + survival	−139.65	3.66	0.09	0.54
4	population + other birds + pigeons	−139.47	3.85	0.08	0.55
5	population + partridges + pigeons	−139.44	3.88	0.08	0.55
6	population + other birds	−136.00	7.31	0.01	0.51
7	population + rabbits + other birds	−133.89	9.42	0.01	0.51
8	population + partridges + other birds	−133.68	9.64	0.00	0.51
9	population + rabbits	−132.27	11.05	0.00	0.48
10	population + diet diversity (H')	−131.81	11.51	0.00	0.48
11	population + partridges	−131.77	11.54	0.00	0.48
12	population + rabbits + partridges	−129.79	13.52	0.00	0.48
Survival models					
1	**population + diet diversity (H')**	**195.68**	**0.00**	**0.63**	**0.33**
2	population + pigeons	199.79	4.11	0.08	0.27
3	population + rabbits + pigeons	199.87	4.19	0.08	0.30
4	population + other birds	200.72	5.04	0.05	0.26
5	population + partridges + pigeons	200.91	5.23	0.04	0.29
6	population + other birds + pigeons	201.74	6.06	0.03	0.28
7	population + rabbits	202.41	6.73	0.02	0.23
8	population + partridges	202.47	6.79	0.02	0.23
9	population + rabbits + other birds	202.63	6.96	0.02	0.27
10	population + partridges + other birds	202.93	7.25	0.02	0.26
11	population + rabbits + partridges	204.14	8.46	0.01	0.25

Table 2. Selected models showing the relationship between productivity and survival with the dietary variables at the territorial level. The estimate of the parameters (including the sign), the standard error of the parameters (SE) and the degrees of freedom of the models (DF) are shown.

Best models	Explanatory variables	Parameter	Estimate	SE	DF
Productivity	population + rabbits + pigeons	intercept	0.682	0.194	60
		population (France)	0.310	0.164	
		population (S. Portugal)	−0.529	0.111	
		population (Granada)	0.178	0.115	
		population (Burgos)	−0.689	0.174	
		rabbits	0.009	0.004	
		pigeons	0.015	0.004	
Survival	population + diet diversity (H')	intercept	6.190	1.512	61
		population (France)	0.155	0.363	
		population (S. Portugal)	0.389	0.379	
		population (Granada)	0.909	0.393	
		population (Burgos)	0.686	0.502	
		diet diversity (H')	−2.355	0.899	

diet diversity showed the highest R^2 compared with all other models (Table 3).

Finally, the analysis of the population growth rate (λ_p) indicated that the models including diet diversity and rabbit consumption were the best supported by the data (Table 3, 4). Diet diversity had the same effect as previously reported for adult survival; those populations with greater growth rates had less diet diversity. Rabbit consumption had a positive effect on the population growth rate (Fig. 6). The models including diet diversity and rabbit consumption also had the highest explanatory power in terms of R^2 (Table 3).

Discussion

Our study shows how the diet of a long-lived predator is closely related to its demographic parameters at different spatial scales in complex ecosystems such as those in the Mediterranean basin. By using a large data set, we found

that several key demographic parameters of an endangered raptor such as Bonelli's eagle in western Europe are dependent on the consumption of preferred and alternative prey species and on diet diversity. This, in turn, leaves a measurable fingerprint on the population dynamics within and between populations, which may lead to different ecological, evolutionary and conservation implications.

Food supply is a typical limiting factor in animal populations and so an efficient exploitation of available food is a vital requirement for all animals (Emlen 1966, White 2008). According to optimal foraging theory, a greater consumption of preferred prey should maximize net energy and hence increase fitness parameters (Emlen 1966, Schoener 1971, Pyke et al. 1977). In our study, we found that Bonelli's eagle productivity at the territorial level was mainly determined by the consumption of rabbits and, to a lesser extent, the consumption of pigeons as an alternative prey (Table 1). As predicted, a greater consumption of rabbits, a preferred prey of Bonelli's eagle in western Europe (Real 1991, Moleón et al. 2009, 2012b), increased the mean productivity of territorial pairs (Fig. 2; see also Cheylan 1981, Real 1987, 1991). A positive association between preferred prey consumption and productivity has previously been found in
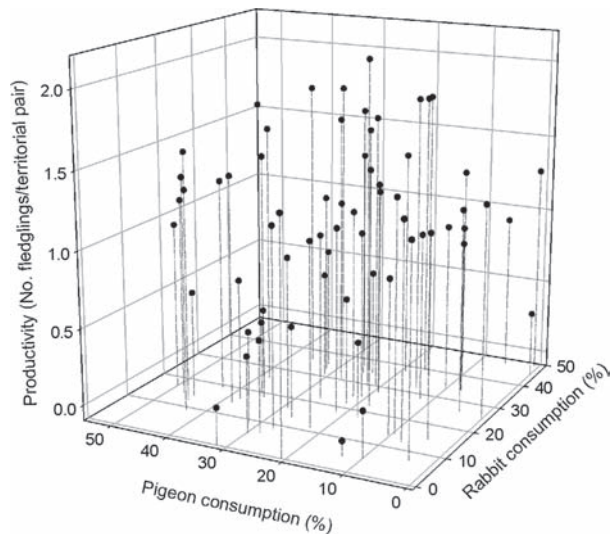

Figure 2. Three-dimensional scatter plot showing the relationship between Bonelli's eagles mean productivity (number of fledglings/ territorial pair, z-axis) and consumption (%) of European rabbits (x-axis) and pigeons (y-axis) at the territorial level. Each black dot represents data for each territory (n = 67).
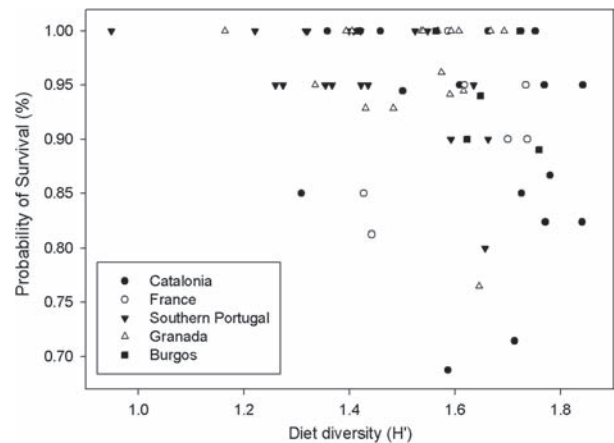

Figure 3. Relationship between the probability of survival (%) and diet diversity (H') at the territorial level (n = 67). Territories from the same population are denoted with the same symbol.

Table 3. Ranking of the linear models used at the population level. Dependent variables were productivity (i.e. mean number of fledglings/territorial adult pair), survival (i.e. probability of adult survival) and population growth rate. The explanatory dietary variables considered were the consumptions of rabbits, partridges, pigeons, 'other birds', and diet diversity (H'). For the productivity models we also considered a model including only survival. Models are ranked based on the parameter estimate AIC_c (i.e. the lowest AIC_c score, the best model). ΔAIC_c refers to the difference in AIC_c between model i and the best model. AIC_{cw} explains the probability that a given candidate model is the best of the proposed set and so the sum of all models is 1.0. R^2 indicates the coefficient of determination of the models (i.e. explained variance of the dependent variable). Selected models with $\Delta AIC_c < 2$ are shown in bold type.

	Explanatory variables	AICc	ΔAICc	AICcw	R²
Productivity models					
1	**other birds**	**−13.20**	**0.00**	**0.55**	**0.87**
2	**rabbits**	**−12.65**	**0.54**	**0.42**	**0.86**
3	partridges	−6.71	6.49	0.02	0.53
4	pigeons	−3.15	10.04	0.01	0.04
5	diet diversity (H')	−3.00	10.20	0.00	0.01
6	survival	−2.97	10.23	0.00	0.00
Survival models					
1	**diet diversity (H')**	**−36.33**	**0.00**	**0.81**	**0.79**
2	partridges	−31.70	4.63	0.08	0.47
3	pigeons	−31.38	4.95	0.07	0.43
4	rabbits	−28.95	7.38	0.02	0.08
5	other birds	−28.76	7.57	0.02	0.04
Pop. growth rate models					
1	**diet diversity (H')**	**−26.85**	**0.00**	**0.39**	**0.56**
2	**rabbits**	**−26.20**	**0.65**	**0.28**	**0.50**
3	other birds	−24.83	2.02	0.14	0.34
4	partridges	−24.72	2.13	0.13	0.33
5	pigeons	−23.07	3.78	0.06	0.06

several other avian predators (Steenhof et al. 1997, Catry et al. 2012). On the other hand, pigeons exerted a positive influence on productivity in those territories where their consumption was considerably high or combined with a moderate consumption of rabbits. Therefore, our results at the territorial level suggest that Bonelli's eagles may benefit in terms of productivity either from high consumption of preferred prey like rabbits, but also from moderate intake of preferred prey provided that they are abundantly complemented by certain alternative prey species, such as pigeons (Resano-Mayor et al. 2014b).

At the population level, the best-supported models indicated that lower consumption of 'other birds' and greater rabbit consumption increases eagles' productivity (Fig. 4).

Table 4. Selected models showing the relationship between productivity, survival and population growth rate with the dietary variables at the population level. The estimate of the parameters (including the sign), the standard error of the parameters (SE) and the degrees of freedom of the models (DF) are shown.

| Best models	Explanatory variables	Parameter	Estimate	SE	DF
Productivity	other birds	intercept	1.558	0.138	3
		other birds	−0.033	0.007	
	rabbits	Intercept	0.336	0.167	3
		rabbits	0.032	0.008	
Survival	diet diversity (H')	intercept	1.256	0.104	3
		diet diversity (H')	−0.223	0.067	
Pop. growth rate	diet diversity (H')	intercept	1.517	0.269	3
		diet diversity (H')	−0.336	0.172	
	rabbits	Intercept	0.923	0.043	3
		rabbits	0.003	0.002	
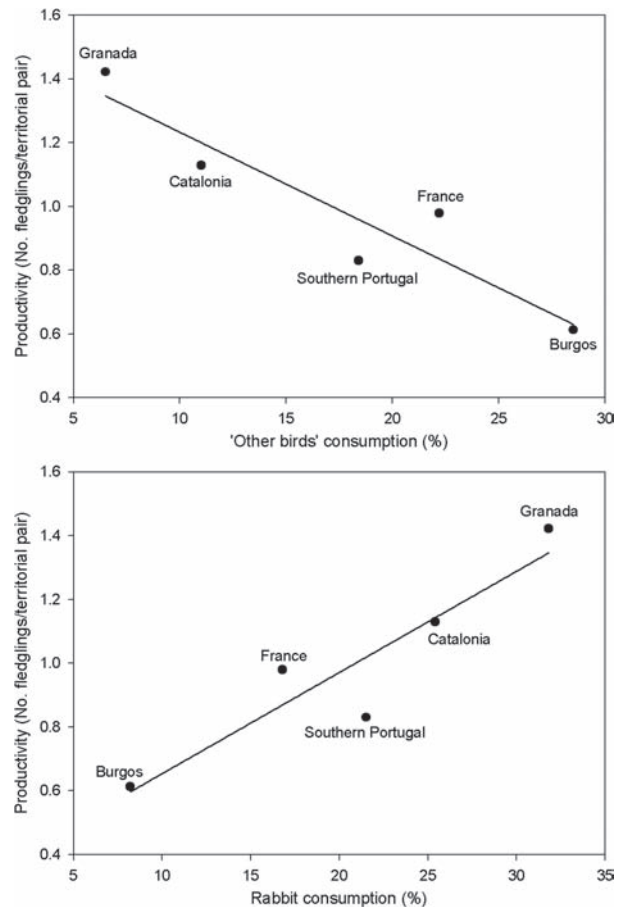
Figure 4. Relationship between adult productivity (number of fledglings/territorial pair) and 'other birds' consumption (%) and rabbit consumption at the population level (n = 5; each population labelled). Linear regression lines are shown.
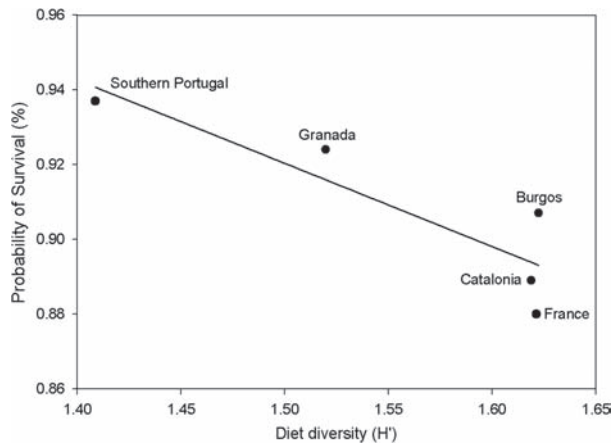
Figure 5. Relationship between the probability of adult survival (%) and diet diversity (H') at the population level (n = 5; each population labelled). The linear regression line is shown.

Figure 6. Relationship between population growth rate (λp) and diet diversity (H') and rabbit consumption (%) at the population level (n = 5; each population labelled). Linear regression lines are shown.

The prey category 'other birds' mainly included small-to-medium avian species (e.g. Passeriformes, Charadriiformes, Accipitriformes, Ardeiformes or Anseriformes), presumably more consumed when the preferred prey was scarce (Penteriani et al. 2002, Moleón et al. 2008, 2009). Supporting this idea, we detected both a negative correlation between the consumption of 'other birds' and rabbits and a positive correlation between 'other birds' consumption and diet diversity at the territory level. Our interpretation is also supported by the fact that the consumption of 'other birds' in the most northern populations of our study area increases considerably in the season when rabbits are scarcer (Real 1991, Moleón et al. 2007). On the other hand, the positive association between rabbit consumption and productivity showed that similar dietary parameters influencing the productivity of territorial pairs also modulate the diet–demography relationship at the population level (Sutherland 1996). Previous studies have revealed that rabbits are the main prey driving spatio-temporal patterns in the diet of Bonelli's eagles in the study area (Moleón et al. 2009). In this regard, rabbits, which are native to the Iberian Peninsula, are regarded as a keystone species for a large number of avian predators in southern Europe (Delibes-Mateos et al. 2007). Based on comprehensive dietary and demographic information, our study illustrates that the consumption of preferred prey (i.e. rabbits) may determine Bonelli's eagle breeding performance both in territories within populations and in local populations over a large geographical area.

Energy maximization when foraging allows for a better fulfilment of energetic demands, enhances body condition, and hence is expected to improve individual survival (Orians and Pearson 1979, White 2008). In our study, we found that the eagles' survival rates increased with lower diet diversity at the territorial (Table 1, Fig. 3) and the population levels (Table 3, Fig. 5). In general, lower diet diversity of breeding pairs was linked to greater consumption of the preferred prey (i.e. rabbits) (see also Moleón et al. 2012b). In some territories, however, breeding pairs were also highly specialized (i.e. had less diet diversity) on secondary prey items such as domestic pigeons, which may be consumed in abundance where they are common and predictable (Emlen 1966,
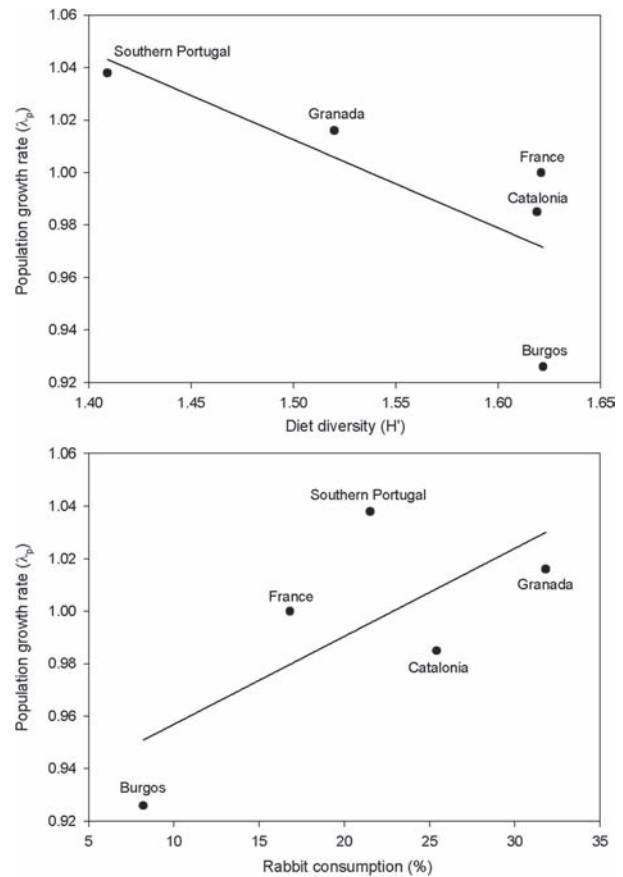
Palma et al. 2006). Greater consumption of preferred or predictable prey may imply a quicker fulfilment of energetic demands and less investment in foraging activities, what probably imply lower exposure to human-induced mortality risks such as electrocution, collision and persecution, the main causes of death in Bonelli's eagle (Real et al. 2001, Moleón et al. 2007). On the other hand, increases in diet diversity due to lower preferred prey consumption possibly reflects greater individual investment in foraging activities (e.g. both in terms of the time invested in moving around the territory and in the areas surveyed for hunting; Orians and Pearson 1979) that may lead to greater exposure to the main mortality risks. This would indicate an indirect effect of food scarcity on predator survival via a change in foraging behaviour (see also Martínez-Abraín et al. 2012).

Drivers of population dynamics depend on the life history characteristics of the species in question. In long-lived birds such as Bonelli's eagle, the population growth rate (i.e. lambda) is particularly sensitive to changes in adult survival (Sæther and Bakke 2000, Hernández-Matías et al. 2013). In this study, we found that diet diversity, which was the main dietary parameter determining survival, but also rabbit consumption, the main dietary parameter determining productivity, had the highest influence on population growth rates. Thus, populations with the lowest diet diversity (i.e. higher survival) and greatest rabbit consumption

(i.e. higher productivity) had the highest growth rates and vice versa (Fig. 6). In our study system, the abundance of key Bonelli's eagle prey items such as rabbits are mainly related to habitat characteristics, disease outbreaks and hunting practices (Delibes-Mateos et al. 2007, Moleón et al. 2009). Therefore, according to our results, Bonelli's eagle populations seem to be regulated by bottom–up processes where predators respond to prey dynamics (Moleón et al. 2012b, White 2013).

Population demographic parameters can be viewed as an emergent property of individual fitness (Sutherland 1996); however, the assessment of these links requires long-term, individual-based studies. In this regard, our study provides strong evidence of how diet can modulate individual (i.e. territorial) life history attributes such as productivity and survival and how it can eventually affect a predator's population growth rate. Our results highlight the fact that the processes relating diet and demographic parameters at individual level are also detectable at population level. That is, the main dietary parameters affecting productivity and survival were detected at both the territory and population levels. Overall, our study highlights the need for large long-term spatio-temporal monitoring programs recording dietary and demographic data of territorial predator species if we are to improve our knowledge of the processes driving population trends.

In the case of endangered predator species such as Bonelli's eagle in Europe (BirdLife International 2004), the relationships we found between diet and the main demographic traits have important implications on species conservation. In this sense, our results may guide conservation managers on how to improve the productivity of territorial pairs by, for example, undertaking habitat management practices that will increase abundances of preferred prey as the European rabbit near territorial breeding areas. Simultaneously, conservation actions should be applied in order to minimize human-related mortality risks of territorial birds since population growth rates have the highest sensitivity to this demographic trait. In this regard, an increase in preferred prey abundances in eagles' territories could reduce both their foraging effort and their exposure to potential mortality risks. All these practices must be given priority in populations with a negative demographic trend such as those in the northern part of the study area. Finally, we emphasize the importance of including comprehensive and coordinated dietary analyses in long-term multi-scaled monitoring programs of predator species. By doing so, we will be able to track how temporal and spatial variations in environmental characteristics affect the foraging habits of target species and to understand how these changes manifest themselves subsequently in observed population trends.

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Supplementary material (available online as Appendix oik.02468 at < www.oikosjournal.org/readers/appendix >). Appendix 1.