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ORIGINAL ARTICLE

Superpredation patterns in four large European raptors

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Abstract Predatory interactions among top predators, like superpredation or intraguild predation (IGP), can influence community structure. Diurnal raptors occupy high trophic levels in terrestrial food webs, and thus can regulate the presence of mesopredators. We studied superpredation (the killing and eating of another predator) in four large European raptors. We gathered 121 dietary studies, totalling 161,456 prey for the Goshawk *Accipiter gentilis* L., Golden Eagle *Aquila chrysaetos* L., Bonelli's Eagle *Aquila fasciata* Vieillot, and Eagle Owl *Bubo bubo* L. Results showed that superpredation: (1) is a widespread interaction in large raptors, but it can vary according to the top predator species; (2) is not an important energetic resource for large raptors, but rather seems mostly related to diet diversification when the main prey decreases; (3) is spatially clustered reflecting habitat heterogeneity, but shows no temporal or large-scale spatial trends; and (4) it is associated with lower breeding success of the top predator species. These findings support the food stress hypothesis as the main driving force behind increases in superpredation and IGP in raptors, with the decrease in breeding performance as a side effect. Superpredation by large raptors deserves future research to understand its effects on mesopredators, because on one hand it might contribute to promote biodiversity, while on the other hand, it can sometimes represent an additional risk for small populations of endangered mesopredators.

Keywords Food stress · Generalist diet · Intraguild predation · Mesopredators · Omnivory · Top predators

Introduction

Despite the very rare use of the expression "superpredation", the concept of superpredator, a predator that eats and kills another predator, has been frequently used in ecology. Superpredation can include acts of intraguild predation (IGP), when the top predator kills and eats another species that is a potential competitor (Polis et al. 1989), but it has a broader sense that includes predation on several other carnivorous species that are not direct competitors. Superpredation might also sometimes be associated with omnivory, defined by Pimm and Lawton (1978) in a food web theory context as the feeding by one species on

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resources at different trophic levels. Superpredation differs from interspecific killing among predators, because it assumes that the prey (mesopredator) is always consumed. The consumption of mesopredators as carrion also falls outside the concept of superpredation, because it lacks the killing act.

As apex predators in many terrestrial communities, large raptors often engage in superpredatory interactions with other carnivorous species (Herrera 1973; Insley and Dugan 1973; Mikkola 1976; Real and Mañosa 1990; Tella and Mañosa 1993; Bosch et al. 2007). Studies focusing on terrestrial vertebrates have shown that predatory interactions among top predators can play a crucial role in structuring vertebrate communities, through the suppression or release of either the mesopredator or the prey (Palomares et al. 1995; Crooks and Soulé 1999; Fedriani et al. 2000; Sergio et al. 2003; but see also Vance-Chalcraft et al. 2007). Superpredation seems to be a widespread phenomenon in raptor assemblages, though frequently overlooked (Sergio and Hiraldo 2008), and besides density-mediated effects (direct killing), a superpredator is also likely to produce behaviourally mediated effects (associated with predation risk) on other carnivorous species (Creel and Christianson 2008). Superpredation has also been considered as a helpful tool in conservation biology, because top predators can sometimes regulate the densities of common mesopredators (Valkama et al. 2005; Sergio and Hiraldo 2008).

There is a great amount of information available on the diet of large raptors in Europe, but it has seldom been used to examine predatory interactions among large carnivorous vertebrates. In studies of IGP, the emphasis has been mainly put on the consequences for the mesopredator (Sergio and Hiraldo 2008), and the superpredator has assumed a central role less often. Thus, there are no extensive analyses on both the importance and energetic contribution of mesopredators in the diet of superpredators, or the compensatory role of this kind of prey when the main prey groups decline (see Tella and Mañosa 1993; Serrano 2000). Also, despite known spatial–temporal variations in biodiversity and community stability (Pianka 1966; Järvinen 1979; Järvinen and Ulfstrand 1980), no one has ever looked for large-scale patterns in superpredation or IGP in vertebrate top predators. Moreover, although some studies have tried to link IGP and breeding performance in raptors (Martínez and Calvo 2001; Martínez and Zuberogoitia 2001), to our knowledge there are no studies objectively relating superpredation rates and superpredator's fitness.

So, for a better understanding of superpredation in vertebrate top predators, we present a review study of this interaction in four large raptors that are at the top of food webs in European ecosystems: (1) the Goshawk *Accipiter gentilis* L. is a large hawk (~500–2,100 g) with a widespread distribution across Europe, and mainly associated with forest habitats; (2) the Golden Eagle *Aquila chrysaetos* L. is a large eagle (~2,800–6,700 g) occurring in most European countries, although scarce from France to Poland; (3) the Bonelli's Eagle *Aquila fasciata* Vieillot is a large Mediterranean raptor (~1,500–2,500 g) occurring from Portugal to Turkey; and (4) the Eagle Owl *Bubo bubo* L. is the largest European owl (~1,500–4,200 g), being present in most countries (Cramp et al. 1977–1994).

This study had five main objectives: (A) to describe the frequencies of superpredation and the biomass contribution of carnivorous species in the diet of large raptors; (B) to analyse possible spatial and temporal variations in superpredation across Europe; (C) to understand the relations between superpredation and frequency of other prey in whole Europe, and then particularly in south-western Europe; (D) to relate superpredation with the apex predator's breeding performance; and (E) to analyse the results under the light of some proposed hypotheses for mechanisms behind IGP and superpredation.

Methods

Literature search

We searched for all the available studies covering the diet of Goshawk, Golden Eagle, Bonelli's Eagle and Eagle Owl, consulting several databases (e.g., IngentaConnect; Google Scholar), archives (e.g., JSTOR; SORA; BioOne) and publisher websites (e.g., ScienceDirect; SpringerLink; Wiley InterScience) (see S1 in Electronic Supplementary Material, ESM). As search terms, we used both the scientific and common names in the languages of most of the European countries where the four raptors occur. In each article, we also examined the cited references to look for other dietary studies which we might have missed in previous searches. Only the articles reporting: (1) the number of individuals consumed for all prey groups, or (2) the percentage of main prey groups (Class or Order level), were included in the analysis. Additionally, we only considered those studies that had a minimum sample size of 60 prey. Works presenting diet information for more than one study area, or for different time periods in the same area, were in most cases considered as different diet samples. We used the data about breeding success (total young fledged divided by pairs that started breeding) and population fecundity (total young fledged divided by total pairs in the population) if the studies also included this information for the same population, or if the authors cited a related article where the breeding data could be obtained.

Data analysis

In cases where authors only listed the number of individuals consumed, we calculated the numeric percentage of each prey group. Superpredation on large carnivorous vertebrates (hereafter designated as mesopredators) was considered as the sum of the percentages of the following prey groups: Orders Carnivora, Falconiformes, Strigiformes (taxonomy of birds according to *The Clements Checklist of Birds of the World*, 6th edn, 2008). The option of analysing prey data at the Order level was chosen to deal with results presented at different taxonomic level (Species, Family, Order or even Class), and also because several prey species do not occur widely in Europe, making it impossible to compare geographically distant studies. As just a few studies presented the percentage of prey in terms of biomass consumed, we calculated the percentage of biomass for all the studies reporting a complete and detailed prey list. We used prey weights according to Cramp et al. (1977–1994) and MacDonald and Barret (1993), and also the diet studies included here.

Since most diet samples are usually related to periods of a few years, we used the central year of the period for each study as an explanatory variable. Whenever the coordinates were not mentioned in the paper, we used the author's description to find the study area in Google Earth (http://earth.google.com) and extracted the central coordinates. With the central geographic point for each diet sample, we then obtained the correspondent biome according to the classification of Olson et al. (2001); see WWF website for a shapefile of the world ecoregions and biomes, http://www.worldwildlife.org//science/ecoregions/). We determined diet diversity for each sample study using the Shannon Diversity Index with the percentages of prey at the Order level. To correct the spatial autocorrelation among diet samples (neighbouring effects) we calculated an autocovariate term according to Augustin et al. (1996) and Dormann et al. (2007). Specifically for our objective B, we were also interested in quantifying the importance of the autocovariate as an effect influencing superpredation. In the remaining models, the autocovariate was used only to correct the spatial autocorrelation.

We used linear mixed-effects models (LMM; Pinheiro and Bates 2000) in objectives B and C, using the percentage of mesopredators as response variable, and in objective D using breeding success and population fecundity as response variables. The avian predator was included in the models as a random effect to account for the correlation between different diet samples within the same predator (Pinheiro and Bates 2000). Prior to each LMM procedure, we examined the data to detect non-normal distribution and outliers in explanatory variables (Zuur et al. 2007). We applied a squared root transformation to the variables Rodentia, and Lagomorpha, a logarithmic transformation to the variables Galliformes, Columbiformes, and Passeriformes, and a binary transformation to the variables Insectivora, Artiodactyla and Reptilia. In the analyses of breeding success and population fecundity, the explanatory variable mesopredators was square root transformed. To avoid multicollinearity among explanatory variables within each model, we performed pairwise Pearson correlations amongst all explanatory variables and, if $|r| > 0.7$, we excluded the one with lower correlation to the response variable, accounting for the biological meaning (Tabachnick and Fidell 2001). Models were fitted with restricted maximum likelihood (REML) that gives estimates of standard deviation generally less biased than the corresponding maximum likelihood (ML) estimates (Bolker et al. 2008). As heteroscedasticity, a common problem when analysing several studies (Gurevitch and Hedges 1999), was present in our datasets, we included a variance function to correct it (Pinheiro and Bates 2000). We used two variance function classes: power of variance covariate and exponential of variance covariate given by the fitted values (Pinheiro and Bates 2000). The choice was based on the best model (lowest AIC) and the analysis of the residual plots against fitted values and predictors (Zuur et al. 2007).

In the analysis of spatial and temporal patterns in superpredation (objective B), we tested the effects of central year, coordinate X, coordinate Y and autocovariate on the percentage of mesopredators ($n = 116$ diet samples). We initially considered nine fixed effects (see S2 in ESM), but due to collinearity, five explanatory variables had to be discarded. In the study of the relations between superpredation and the frequency of other prey in whole Europe (objective C), we tested the effects of 11 explanatory variables (prey groups and diet diversity) on the percentage of mesopredators ($n = 108$ diet samples). The variable "birds" was excluded due to collinearity problems. In the model for south-western Europe only (objective C), we tested the effects of the percentage of rabbits, central year and autocovariate on the percentage of mesopredators ($n = 45$ diet samples). To test the effect of the consumption of mesopredators on breeding performance of avian predators (objective D), we used two LMM, one with breeding success ($n = 30$ diet samples), and the other with population fecundity as the response variable ($n = 32$ diet samples). In both models, we only tested the effects of the percentage of mesopredators and the autocovariate. All statistical analyses were carried out using R 2.9.0 statistical software (R Development Core Team 2009) with the packages: nlme 3.1-90 (Pinheiro et al. 2008) and spdep 0.4-34 (Bivand 2009).

Table 1 Average percentage and biomass contribution of mesopredators in the diet of the four raptors

Superpredator	Carnivores	Raptors	Owls	Mesopredators
Goshawk (*Accipiter gentilis*)				
Average percentage	0.1 ± 0.2 (26)	1.0 ± 1.4 (25)	1.0 ± 0.9 (26)	2.1 ± 2.0 (25)
Average biomass (26,699 prey)	0.2 ± 0.6 (24)	1.7 ± 3.8 (24)	0.8 ± 0.9 (24)	2.7 ± 4.3 (24)
Golden Eagle (*Aquila chrysaetos*)				
Average percentage	5.3 ± 5.1 (23)	0.7 ± 1.0 (21)	0.5 ± 0.6 (23)	6.6 ± 5.6 (21)
Average biomass (21,357 prey)	7.5 ± 8.3 (20)	0.3 ± 0.4 (20)	0.3 ± 0.8 (20)	8.0 ± 8.5 (20)
Bonelli's Eagle (*Aquila fasciata*)				
Average percentage	0.9 ± 1.3 (16)	0.8 ± 2.6 (16)	0.3 ± 0.8 (16)	2.0 ± 1.6 (16)
Average biomass (6,503 prey)	1.1 ± 2.1 (16)	0.4 ± 0.5 (16)	0.2 ± 0.4 (16)	1.8 ± 2.0 (16)
Eagle Owl (*Bubo bubo*)				
Average percentage	0.8 ± 1.2 (50)	1.2 ± 1.6 (47)	2.4 ± 2.7 (47)	4.4 ± 3.9 (50)
Average biomass (61,782 prey)	1.6 ± 2.0 (44)	2.0 ± 2.4 (44)	2.3 ± 2.5 (44)	6.0 ± 4.7 (44)

Average percentages are presented with ±SD and number of diet samples in parentheses

Results

Our diet review comprised 27 Goshawk (28 diet samples and 49,377 prey), 21 Golden Eagle (23 diet samples and 22,296 prey), 16 Bonelli's Eagle (16 diet samples and 6,503 prey), and 50 Eagle Owl studies (54 diet samples and 83,280 prey). Overall, we had 121 diet samples used to describe diet, but had to discard five samples where we could not determine the mesopredator percentage, hence the sample size used for analyses was 116. Considering that superpredation in raptors may be a rare event that could be underestimated for diet samples with few prey, we first checked our data for a possible effect of the sample size (total number of prey in each diet study) on the percentage of mesopredators. The LMM ($n = 116$ diet samples) did not show any effect of the total number of prey on the percentage of mesopredators ($\beta = -0.18$, SE 0.18, $df = 111$, $t = -0.98$, $P = 0.33$), and thus we included all 116 diet samples in our review.

For an overview of the diet of the four predators in Europe, we present (S3 in ESM) the average percentage of the main prey groups (average percentage higher than 3.0% for at least one predator). The Goshawk is mainly ornithophagous, but sometimes mammals can have an important contribution to its diet. Pigeons, doves, partridges, grouses, corvids and thrushes are the main prey. The Golden Eagle preys mainly on medium-sized mammals, although partridges and grouses also play an important role. Bonelli's Eagle's diet is mainly based on lagomorphs, partridges and pigeons. The Eagle Owl is the most dependent on mammals, with important contributions coming from rodents and lagomorphs. Average diet diversity at the Order level is very similar among the four species. The detailed list of the carnivorous prey for the four raptors in Europe is shown in S4 in ESM.

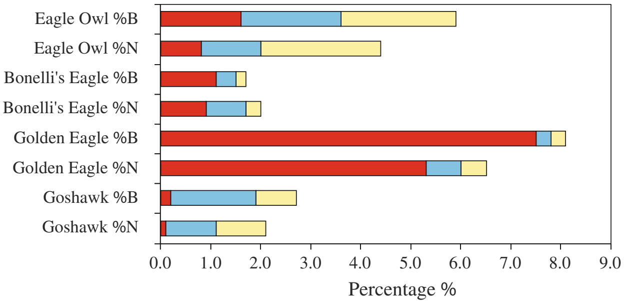

Fig. 1 Average numeric percentage (%N), average biomass percentage (%B), of mammalian carnivores (*red/dark*), diurnal raptors (*blue/grey*), and owls (*light yellow/light grey*) in the diet of the Goshawk *Accipiter gentilis*, Golden Eagle *Aquila chrysaetos*, Bonelli's Eagle *Aquila fasciata*, and Eagle Owl *Bubo bubo* in Europe

Objective A: frequency and biomass of mesopredators in the diet of large raptors

The consumption of other predators was a widespread event in the diet of the four top predators, as only 7 out of 116 studies (6.0%) had no mesopredators as diet items. The Golden Eagle showed the highest average percentage of mesopredators (6.6%), mainly due to the contribution of mammalian carnivores (5.3%). The Eagle Owl registered an average of 4.3% of mesopredators in the diet, capturing more owls (2.4%) than the other three large raptors. Goshawk and Bonelli's Eagle consumed comparatively low percentages of mesopredators (2.1 and 2.0%, respectively). The highest mesopredators percentage recorded in a diet sample was 8.1% for Goshawk, 20.2% for Golden Eagle, 5.8% for Bonelli's Eagle and 20.7% for Eagle Owl. The average biomass percentage of mesopredators in the diet of Golden Eagle (7.5%; $n = 20$) was the highest of the four raptors (Table 1; for clarity, results have also been plotted

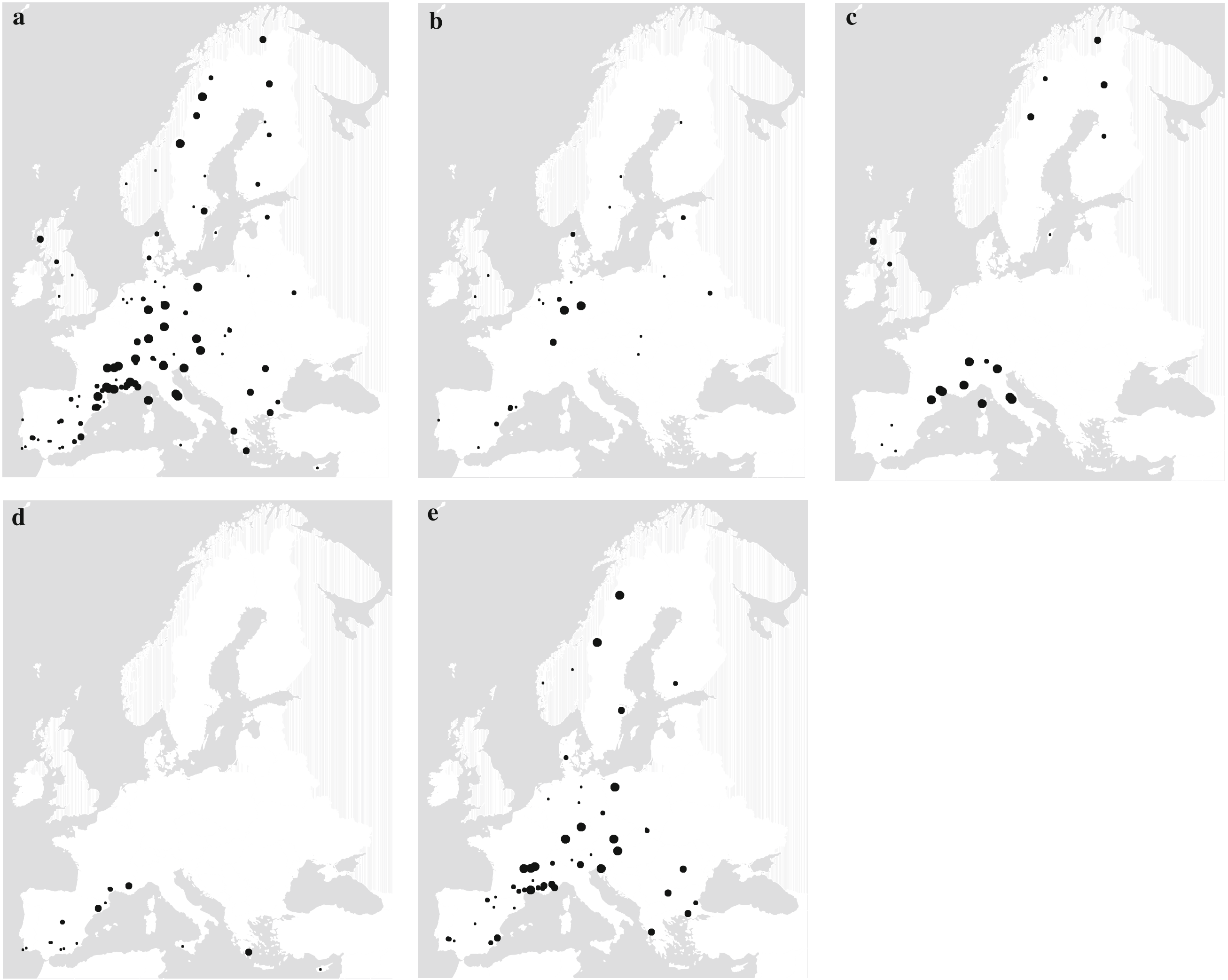

Fig. 2 Mapping of the diet samples with the percentage of mesopredators (*circles* correspond from smaller to larger to four classes of mesopredators percentage: 0.00–2.00, 2.01–3.93, 3.94–6.00, 6.01–21.00%). The value 3.93% was chosen for being the average mesopredators percentage for all the studies ($n = 116$). **a** All four raptors, **b** Goshawk *Accipiter gentilis*, **c**. Golden Eagle *Aquila chrysaetos*, **d** Bonelli's Eagle *Aquila fasciata*, **e** Eagle Owl *Bubo bubo*

in Fig. 1). The Eagle Owl showed an average biomass percentage of mesopredators of 6.0% ($n = 44$), while this value was 2.7% ($n = 24$) for Goshawk, and 1.8% ($n = 16$) for Bonelli's Eagle. The highest value of biomass percentage of mesopredators recorded in a diet sample was 33.1% for Golden Eagle, 19.9% for Goshawk, 17.7% for Eagle Owl, and 7.8% for Bonelli's Eagle.

Objective B: spatio-temporal patterns in superpredation

The LMM showed no evidence of temporal variation in the percentage of mesopredators ($\beta = -0.02$, $t = -0.92$, $P = 0.359$; see S5 in ESM). Also, we found no longitudinal ($\beta = 0.00$, $t = 0.11$, $P = 0.915$) or latitudinal spatial trend ($\beta = 0.01$, $t = 0.23$, $P = 0.822$) in the percentage of mesopredators. The autocovariate had a significant positive effect ($\beta = 0.75$, $t = 4.07$, $P = 0.000$), indicating a spatial aggregation of similar values, with some areas concentrating high percentages of mesopredators (e.g., Central Europe), and others low percentages of mesopredators (e.g., Iberian Peninsula, Fig. 2).

Objective C: relation between superpredation and main prey frequencies in the diet

The LMM for Europe showed that the decrease in the percentage of rodents ($\beta = -0.87$, $t = -3.99$, $P = 0.000$; see S5 in ESM), rabbits and hares ($\beta = -0.71$, $t = -3.23$, $P = 0.002$), partridges and grouse ($\beta = -0.63$, $t = -2.69$, $P = 0.009$), and pigeons and doves ($\beta = -0.80$, $t = -3.14$,

$P = 0.002$) had a significant effect in the increase of the percentage of mesopredators in the diet. On the other hand, the increase in the mesopredators percentage was related to a higher consumption of mammals ($\beta = 0.08$, $t = 3.00$, $P = 0.003$) and to more diversified diets ($\beta = 12.79$, $t = 5.97$, $P = 0.000$). The autocovariate had a positive significant effect ($\beta = 0.32$, $t = 2.65$, $P = 0.009$), indicating that the diet samples closer to each other had more similar mesopredators percentages. When we analysed only the samples from south-western Europe, there were no significant effects of the percentage of rabbits on the percentage of mesopredators in the diet ($\beta = 0.01$, $t = 0.52$, $P = 0.610$; see S5 in ESM). Also, there seemed to be no temporal trends in superpredation, given that the central year had no significant effect ($\beta = -0.02$, $t = -0.71$, $P = 0.48$). Once again, diet samples geographically close to each other had more similar percentages of mesopredators (autocovariate: $\beta = 0.77$, $t = 3.22$, $P = 0.003$).

Objective D: consumption of mesopredators and breeding performance

The decrease in breeding success of the four raptors was related to the increase in the percentage of mesopredators in the diet ($\beta = -0.09$, $t = -2.38$, $P = 0.026$; see S5 in ESM), while the mesopredators percentage showed no effect on the population fecundity of these top predators ($\beta = -0.08$, $t = -1.70$, $P = 0.10$). Areas closer to each other had similar breeding success (autocovariate: $\beta = -0.13$, $t = -2.12$, $P = 0.044$), but the same effect was not found for population fecundity ($\beta = -0.01$, $t = -0.06$, $P = 0.954$).

Discussion

General features and trends in superpredation by large raptors

This study shows that the capture of raptors and carnivores by large birds of prey and owls is a widespread phenomenon in most European study areas, although superpredation frequencies are highly variable between species and regions. From the studied predators, the Golden Eagle is the one consuming more mesopredators. Taking into account the amount of studies gathered, the obtained average percentages of mesopredators in the diet can represent good reference values of the level of superpredation by European large raptors to use in future studies. From these data, we can conclude that almost wherever large raptors occur, there can be a certain degree of effect on the populations of mesopredators. However, current knowledge does not allow the prediction of the effect of superpredation frequencies obtained from diet samples on mesopredator populations. This gap in our knowledge is a challenge for future studies and a research avenue that will surely lead to new monitoring tools in population and community ecology.

Superpredation frequencies can be influenced by many factors, such as the abundance and availability of the mesopredator. For example, the comparatively high percentage of mammalian carnivores in the diet of Golden Eagle were mainly associated with the predation on Red Fox *Vulpes vulpes* L. (e.g., Pedrini and Sergio 2001; Seguin et al. 2001; see S4 in ESM), which is a generalist and very common predator in Europe. When analysing the frequencies of superpredation (see S3 in ESM), it is possible to conclude that the most common mesopredators species in natural ecosystems are the ones that showed higher predation levels. Domestic populations of cats and dogs can sometimes represent profitable prey items, once they are common and less limited by food resources (generally provided by humans). Although these cases may inflate the role of superpredation on "natural" mesopredators, it is still worthwhile analysing them because this particular superpredation may assume an important conservation role, contributing to population control of alien species (Salo et al. 2008; Crooks and Soulé 1999). The overlap in the activity rhythms of predator and prey seems also relevant in determining levels of superpredation in different species, as for example, the Eagle Owl showed a higher average percentage of owls in the diet than the other three diurnal raptors. Still, there might be other factors causing distinct superpredation rates, but for which we cannot draw any conclusions, such as species-specific defence strategies (Palomares et al. 1996; Sergio et al. 2003, 2007; Zuberogoitia et al. 2008a).

Superpredation rate showed considerable spatial clustering at a small-scale but no large-scale spatial trends. So it seems that the known latitudinal and longitudinal trends in biodiversity and trophic diversity (Pianka 1966; Järvinen 1979; Korpimäki and Marti 1995) had no reflection on patterns of superpredation in Europe. Like IGP, superpredation also seems to be locally influenced by the community structure (e.g., diversity, habitat structure, productivity; Mylius et al. 2001; Holt and Huxel 2007; Janssen et al. 2007; Amarasekare 2008). The marked ecosystem patchiness that dominates Europe (Antrop 2004), creating a landscape mosaic and consequent variation in the structure of communities, appears to be the main driving force behind the spatial aggregation pattern in superpredation. In this sense, more thorough studies on how landscape and biodiversity affect interactions among top predators would be welcome.

We found no temporal trends at a large continental scale, but it does not mean that long-term temporal trends at a local scale do not exist. The diet of raptors and the superpredation rate can both change along short-time periods (Fernández 1993; Toyne 1998; Nielsen and Drachmann 1999; Martínez and Zuberogoitia 2001), but there are not enough data at a local scale to determine accurately the existence of long-term temporal trends. Moreover, the observed spatial heterogeneity in superpredation could have masked existing local-scale temporal trends. The Iberian Peninsula and southern France are areas where large raptors have been well studied, and where prey decline has been proved to cause large-scale temporal shifts in the diet (Moleón et al. 2009), but still we found no long-term temporal trends for south-western Europe. Considering all this, to address temporal variation in superpredation, future research should focus on long-term diet data on a local scale.

Trophic determinants of superpredation by large raptors

What drives large raptors to superpredation? The optimal diet of a predator results from the positive balance of the energy gained by the capture of prey compared to the energy spent searching and capturing it (MacArthur and Pianka 1966). Considering only their biomass, birds of prey, owls and carnivores should be worthwhile prey for the top predators examined in this study. But mesopredators normally do not make a profitable prey, because of the increase in time and energy needed to capture a scarce food resource and the risk associated in handling it. Nevertheless, any mesopredator that is of a size worth eating might be worth preying upon, if found by chance, and this might be especially true for predators under food stress caused by the decline of their main prey species.

Although variable, mesopredators represented a small contribution to the biomass ingested by the studied top predators, seldom reaching the same importance of other prey groups. The fact that mesopredators did not substitute main prey, together with the negative relations found between mesopredators and main prey percentages, and mesopredators percentage and breeding success of top predators, led us to conclude that increased superpredation in large raptors should mainly be a response to food stress, which causes, in generalist species, the widening of the diet breadth. Nevertheless, this might not be true for specialist species, unable to increase the trophic spectrum (Ferrer and Negro 2004).

In south-western Europe, rabbits are a staple prey of several apex predators (Delibes-Mateos et al. 2008), but their continuous decline could be a potential trigger for IGP and superpredation (Tella and Mañosa 1993; Serrano 2000). Despite the fact that the decline of rabbits can cause large- and local-scale shifts in the diet of raptors, with the increase in trophic diversity (Fernández 1993; Moleón et al. 2009), we found no evidence of a trend in superpredation in this region. Our results can have several interpretations: first, we could have had a sample size limitation for this particular analysis; second, we used diet at a large-scale, and perhaps superpredation trends could have been easier to detect by comparing diet at a territory-scale; third, these raptors could overcome the decrease of an important prey like rabbits turning to locally available alternative prey species (partridges, pigeons, hares, hedgehogs—Fernández 1993; Mañosa 1994; Moleón et al. 2008); and fourth, despite prey decline, diet may have remained similar, although causing the decrease in breeding success and territory occupancy (Martínez and Calvo 2001; Martínez and Zuberogoitia 2001). Consequently, the relation between the decline of rabbits and superpredation in south-western Europe does not seem to be as straightforward as it could be expected, with local nuances probably playing a role in this complex trophic interaction.

Some ecological mechanisms have been pointed out as potential triggers for IGP, which may also be related to superpredation: (1) in an opportunistic way, when their availability is high, carnivorous species can be seen merely as nutritionally profitable prey (Polis et al. 1989); (2) the decrease in main prey abundance (food-stress hypothesis) can lead apex predators to expand their diet and include mesopredators (Steenhof and Kochert 1988; Serrano 2000; Rutz and Bijlsma 2006); and (3) IGP facilitates the deliberate elimination of competitors, with additional energetic benefit (competitor-removal hypothesis; Serrano 2000). Another factor that might be in the origin of superpredation by raptors is the inherent risk that the top predator has to face when living near another predator that is also “built for the kill” (symmetrical IGP on adults and young, or mobbing; Mikkola 1976; Real and Mañosa 1990; Palomares and Caro 1999; Sunde et al. 2003; Zuberogoitia et al. 2008b), which could lead to a “kill before being killed” behaviour triggering IGP (that we designated as “predator-removal hypothesis”; R. Lourenço et al., in preparation). In this way, a potential predator or mobber might be a preferential target of IGP by large raptors.

Our findings support the food-stress hypothesis, where increased superpredation is associated with decrease in the percentages of typical prey groups. So overall, this could be the main mechanism behind superpredation and IGP in large European raptors. The negative relationship found between the consumption of mesopredators and top predator’s breeding performance also points to superpredation occurring mostly under food-stress situations, which are associated with a decrease in individual or population fitness. The absence of abundance data for the main prey and mesopredators in the study areas was a strong limitation to this study, because it could help to better understand the mechanisms behind superpredation. But food stress might not be the only determinant, and it would be important to determine the role of all factors. Moreover, because these determinants probably interact, it is difficult to explain and predict superpredation and IGP levels. To disentangle the role of these different causes behind superpredation it is necessary to design a holistic approach, which includes predator, mesopredators and prey abundance, but also experimental studies on the superpredator's behavioural mechanisms driving the competitor-removal and predator-removal hypotheses.

The potential superpredation-related effect on large raptors

Considering that a high frequency of superpredation in top predators is not to be expected (Arim and Marquet 2004), and may result from a diversification of the diet to include mesopredators caused by food stress (Polis et al. 1989), there can be an associated loss of individual fitness, with effects at the population level of the top predator. Reduced breeding performance is a common individual response to stress situations in the life history of raptor species (Newton 1979), and decrease in food availability is a well-documented cause (Fernández 1993; Steenhof et al. 1997; Martínez and Calvo 2001; Pedrini and Sergio 2002; Nyström et al. 2006).

Our results show that, despite a possible increase in superpredation as an effort to compensate situations of food stress, there are still some associated negative effects on breeding performance for the top predator. Therefore, the increase in superpredation can work as an alarm signal for decreasing breeding performance, probably associated with a decrease in prey availability. Thus, long-term studies on superpredation trends have the potential to represent a useful tool in conservation studies. This fact has another particular implication for apex predators, because it denotes that mesopredators do not seem to be profitable enough to ensure the fitness of individuals, being no good alternative to their usual main prey. Superpredation triggered by food stress does not seem to be part of the solution for the lack of main prey in large raptors, but on the contrary, it can be part of a problem for those mesopredator populations in less favourable situations. So, in those cases where evidence is gathered for food-stress superpredation, priority actions might be needed to recover the main prey populations of large raptors.

Final remarks

The concept of IGP has gathered a strong theoretical framework in the last decades (Polis et al. 1989; Holt and Polis 1997; Ives et al. 2005; Holt and Huxel 2007; Daugherty et al. 2007; Kimbrell et al. 2007; Amarasekare 2008). This theoretical basis can be useful to understand superpredation events and interspecific killing among predators. However, most observational and experimental studies have been carried out with invertebrates and freshwater vertebrates (e.g., Morin 1999; Amarasekare 2007; Borer et al. 2007; Vance-Chalcraft et al. 2007; Janssen et al. 2007). Only more recently has IGP and superpredation in raptors been focused on, though mostly based on observational studies, because experimental studies with this group face many ethical and logistic restrictions. Consequently, many theoretical expectations of IGP have never been checked in vertebrate predators. A premise for further studies is the existence of a large amount of information about interactions in vertebrate predators, namely predatory relations. Future analyses could benefit if there were more, well-distributed diet studies, so as to better deal with all the expected heterogeneity in a large area like Europe (Donázar et al. 1989). We found two main obstacles in the dietary literature of raptors: first, several studies did not present complete lists of prey numbers or frequencies, and second, sample sizes showed a large variation. Therefore, we strongly suggest that future diet studies should include complete prey lists (as on-line-only supplementary material), presenting future reviewers with larger sample sizes.

Mesopredators might also be consumed by raptors as carrion; thus, Golden Eagles regularly scavenge on dead animals (Marquiss et al. 1985; Pedrini and Sergio 2001; Seguin et al. 2001). As a consequence, some of the recorded mesopredators might have been consumed as carrion and not actually killed. In these cases, by studying diet only, we might have overestimated superpredation and consequently its potential effects on mesopredators. Therefore, in future studies and whenever possible, there should be a separation of predation and scavenging, because they have different implications for the mesopredator.

To better understand the causes behind predatory interactions among vertebrate apex predators, future studies should focus on long-term analyses with large sample sizes, relating superpredation to diet changes and abundance of mesopredators and main prey, and combined with experimental and observational studies testing some proposed hypotheses (competitor removal, predator removal, food-stress and opportunism). It would also be worthwhile putting some effort into the relationships between superpredation, diet diversity and breeding performance, mediated by the role of the availability of main prey. Finally, overlooked information can be obtained by studies assessing the effects of superpredation and IGP on both the mesopredator population dynamics and the community structure (e.g., diversity, complexity, spatial heterogeneity), as these interactions might be triggering unnoticed top-down effects.

The study of IGP and superpredation in vertebrate predators is just now starting to unravel potentially strong interactions that are essential to understand the dynamics of vertebrate communities, and to ecological management. Landscape heterogeneity is an aspect to consider when studying these phenomena, being necessary to find the adequate scale. Furthermore, as vertebrates show behaviourally complex responses to predation risk (Palomares and Caro 1999; Sergio and Hiraldo 2008), it is particularly challenging to study these complex interactions. As a combination of competition and predation, IGP can contribute to high species diversity (Menge and Sutherland 1976), and trophic cascades and resource facilitation are two ways by which top predators can promote biodiversity (Sergio et al. 2008). But, when the mesopredator is a threatened species (e.g., Real and Mañosa 1990), then superpredation can mean an additional and demanding problem. Conservation biology urgently needs more clues about the positive and negative effects of superpredation and IGP in vertebrate top predators.

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SUPERPREDATION PATTERNS IN FOUR LARGE EUROPEAN RAPTORS

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ELECTRONIC SUPPLEMENTARY MATERIAL

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S2. Explanatory variables used for data analysis

List of all the explanatory variables used in the Linear Mixed-effects Models (LMM). The LMM are identified by same number used to designate the objectives of the study.

Variable name	LMM	Description
Superpredator	All	Nominal, random factor. The four raptors: Goshawk *Accipiter gentilis*, Golden Eagle *Aquila chrysaetos*, Bonelli's Eagle *Aquila fasciata*, Eagle Owl *Bubo bubo*
Central year	B	Continuous. The central year of the period to which the diet sample concerns
Biomes	B	Nominal. Classification of the world ecoregions and biomes according to WWF (www.worldwildlife.org//science/ecoregions/): (1) Mediterranean forests, woodlands, and scrub; (2) Temperate broadleaf and mixed forests; (3) Temperate coniferous forests; (4) Boreal forests/Taiga; (5) Tundra
Grouped biomes	B	Nominal. Grouped biomes from the previous variable: (a) biome 1; (b) biome 2; (c) biomes 3, 4, 5
Longitude coordinate	B	Continuous. Longitude coordinate of the central location of the study area
Latitude coordinate	B	Continuous. Latitude coordinate of the central location of the study area
Squared longitude	B	Continuous. Squared value of the longitude coordinate
Squared latitude	B	Continuous. Squared value of the longitude coordinate
Longitude × latitude	B	Continuous. Longitude value multiplied by the latitude value
Autocovariate meso-predators (all Europe)	B, C	Continuous. Autocovariate calculated for the all percentages of IG prey
Autocovariate meso-predators (SW Europe)	C	Continuous. Autocovariate calculated for the percentages of IG prey in the studies in SW Europe
Autocovariate breeding success	D	Continuous. Autocovariate calculated for the values of breeding success
Autocovariate population fecundity	D	Continuous. Autocovariate calculated for the values of population fecundity
Mammals	C	Continuous. Percentage of prey of the Class Mammalia
Insectivora (hedgehogs, moles and shrews)	C	Binomial. Presence/absence of prey of the Order Insectivora (0-1)
Artiodactyla (deers and wildboar)	C	Binomial. Presence/absence of prey of the Order Artiodactyla
Rodentia (rats, voles and mice)	C	Continuous. Square root of the percentage of prey of the Order Rodentia (rodents)
Lagomorpha (rabbits and hares)	C	Continuous. Square root of the percentage of prey of the Order Lagomorpha (lagomorphs)
Rabbits	C	Continuous. Percentage of rabbits *Oryctolagus cuniculus* in all prey
Birds	C	Continuous. Percentage of prey of the Class Aves
Galliformes (partridges and pheasants)	C	Continuous. Percentage of prey of the Order Galliformes
Columbiformes (pigeons and doves)	C	Continuous. Percentage of prey of the Order Columbiformes
Passeriformes (passerines)	C	Continuous. Percentage of prey of the Order Passeriformes
Reptiles	C	Binomial. Presence/absence of prey of the Class Reptilia (0-1)
Diet diversity	C	Continuous. Shannon diversity index at the Order level
Mesopredators	D	Continuous. Percentage of prey of the classes Carnivora, Falconiformes, Strigiformes

S3. Main prey of the Goshawk Accipiter gentilis, Golden Eagle Aquila chrysaetos, Bonelli's Eagle Aquila fasciata, and Eagle Owl Bubo bubo in Europe.

Average percentage of main prey groups and meso-predators in the diet four raptors and diet diversity (Shannon Diversity Index). Average values are shown with standard deviation and in brackets the number of diet samples used for calculation.

	Goshawk *Accipiter gentilis*	Golden Eagle *Aquila chrysaetos*	Bonelli's Eagle *Aquila fasciata*	Eagle Owl *Bubo bubo*
MAMMALS	16.8 ± 15.3 (27)	59.3 ± 17.7 (23)	41.4 ± 14.3 (16)	65.1 ± 18.0 (54)
Insectivora	0.4 ± 1.1 (24)	2.3 ± 9.1 (21)	0.1 ± 0.4 (16)	5.7 ± 6.2 (51)
Carnivora	0.1 ± 0.2 (26)	5.3 ± 5.1 (23)	0.9 ± 1.3 (16)	0.8 ± 1.1 (54)
Artiodactyla	0.0 ± 0.0 (25)	9.3 ± 9.3 (23)	0.6 ± 2.1 (16)	0.0 ± 0.1 (51)
Rodentia	8.3 ± 10.6 (25)	10.3 ± 16.0 (21)	8.4 ± 9.3 (16)	44.3 ± 23.8 (51)
Lagomorpha	7.6 ± 8.6 (25)	32.8 ± 19.9 (23)	31.4 ± 17.7 (16)	14.0 ± 17.1 (54)
BIRDS	82.2 ± 16.3 (28)	35.2 ± 18.6 (23)	51.8 ± 16.7 (16)	26.9 ± 17.9 (54)
Falconiformes	1.0 ± 1.4 (25)	0.7 ± 1.0 (21)	0.8 ± 2.6 (16)	1.2 ± 1.6 (47)
Galliformes	11.9 ± 11.3 (25)	21.5 ± 18.8 (23)	17.4 ± 12.6 (16)	3.9 ± 4.1 (54)
Columbiformes	27.5 ± 18.1 (25)	1.0 ± 1.3 (23)	17.2 ± 13.4 (16)	3.8 ± 7.8 (54)
Strigiformes	1.0 ± 0.9 (26)	0.5 ± 0.6 (23)	0.3 ± 0.8 (16)	2.4 ± 2.7 (51)
Passeriformes	31.1 ± 15.6 (25)	6.7 ± 5.2 (21)	9.8 ± 7.0 (16)	7.5 ± 5.6 (51)
REPTILES	0.8 ± 1.8 (26)	5.4 ± 7.1 (23)	5.6 ± 4.4 (16)	0.2 ± 0.4 (54)
AMPHIBIANS	0.2 ± 1.2 (26)	0.1 ± 0.6 (21)	0.1 ± 0.2 (16)	4.2 ± 9.2 (54)
MESOPREDATORS	2.1 ± 2.0 (25)	6.6 ± 5.6 (21)	2.0 ± 1.6 (16)	4.3 ± 3.8 (54)
DIET DIVERSITY SDI	0.65 ± 0.10 (23)	0.66 ± 0.10 (21)	0.67 ± 0.12 (16)	0.66 ± 0.19 (48)

S4. Mesopredators as prey of the Goshawk *Accipiter gentilis*, Golden Eagle *Aquila chrysaetos*, Bonelli's Eagle *Aquila fasciata*, and Eagle Owl *Bubo bubo*

	Goshawk *Accipiter gentilis* (21 studies)		Golden Eagle *Aquila chrysaetos* (18 studies)		Bonelli's Eagle *Aquila fasciata* (16 studies)		Eagle Owl *Bubo bubo* (44 studies)	
Carnivores (Order Carnivora)	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)
Dog *Canis familiaris*			16.7	0.5			2.3	0.1
Red fox *Vulpes vulpes*			100	2.1	12.5	0.2	45.5	0.3
Wild cat *Felis silvestris*			11.1	0.8	6.3	0.1		
Cat *Felis catus*	14.3	0.5	44.4	0.8	12.5	0.4	20.5	0.1
Otter *Lutra lutra*			11.1	0.1				
Stone marten *Martes foina*			16.7	0.8	12.5	0.8	6.8	0.1
European pine marten *Martes martes*			44.4	1.8			2.3	0.0
Eurasian Badger *Meles meles*			22.2	1.9			2.3	0.0
European polecat *Mustela putorius*	4.8	0.1	5.6	1.2			6.8	0.4
Least weasel *Mustela nivalis*	14.3	0.1	27.8	1.7	18.8	2.3	38.6	0.5
European mink *Mustela lutreola*							2.3	0.1
Ermine *Mustela erminea*	19.0	0.1	22.2	0.5			22.7	1.2
American mink *Neovison vison*			33.3	0.8	6.3	3.4	2.3	0.0
Genet *Genetta genetta*			5.6	1.2			2.3	0.0
Raccoon dog *Nyctereutes procyonoides*			5.6	0.1				

Note: F – frequency of occurrence in the studies. A – average percentage in the diet calculated from the studies reporting the prey species.

	Goshawk *Accipiter gentilis* (21 studies)		Golden Eagle *Aquila chrysaetos* (18 studies)		Bonelli's Eagle *Aquila fasciata* (16 studies)		Eagle Owl *Bubo bubo* (44 studies)	
Raptors (Order Falconiformes)	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)
Honey buzzard *Pernis apivorus*	19.0	0.1	5.6	0.0			13.6	0.3
Black-shouldered kite *Elanus caeruleus*							2.3	0.1
Black kite *Milvus migrans*							11.4	0.4
Red kite *Milvus milvus*	4.8	0.1					4.5	0.1
Short-toed eagle *Circaetus gallicus*							2.3	0.0
Marsh harrier *Circus aeruginosus*							4.5	0.1
Montagu's harrier *Circus pygargus*	4.8	0.1					11.4	0.1
Hen harrier *Circus cyaneus*	4.8	0.2	5.6	0.2				
Goshawk *Accipiter gentilis*	42.9	0.2	16.7	0.1	6.3	0.1	27.3	0.1
Sparrowhawk *Accipiter nisus*	61.9	0.5	5.6	0.3	18.8	0.6	40.9	0.3
Common buzzard *Buteo buteo*	42.9	0.3	33.3	0.2	12.5	0.5	56.8	0.7
Rough-legged buzzard *Buteo lagopus*			11.1	0.1			9.1	0.4
Lesser kestrel *Falco naumanni*					6.3	0.6		
Common kestrel *Falco tinnunculus*	42.9	0.3	44.4	0.6	62.5	0.8	59.1	0.7
Hobby *Falco subbuteo*	4.8	0.0					9.1	0.1
Merlin *Falco columbarius*	4.8	0.0	5.6	0.4			4.5	0.1
Gyr falcon *Falco rusticolus*							4.5	0.1
Red-footed falcon *Falco vespertinus*							2.3	0.2
Peregrine falcon *Falco peregrinus*			11.1	0.0	6.3	0.1	13.6	0.3

Note: F – frequency of occurrence in the studies. A – average percentage in the diet calculated from the studies reporting the prey species.

Owls (Order Strigiformes)	Goshawk *Accipiter gentilis* (21 studies)		Golden Eagle *Aquila chrysaetos* (18 studies)		Bonelli's Eagle *Aquila fasciata* (16 studies)		Eagle Owl *Bubo bubo* (44 studies)	
	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)	F (%)	A (%)
Barn owl *Tyto alba*	9.5	0.2	11.1	0.2			43.2	0.6
Scops owl *Otus scops*							18.2	0.4
Eagle owl *Bubo bubo*			5.6	1.2	6.3	0.1	18.2	0.2
Little owl *Athene noctua*	28.6	0.4			18.8	1.0	45.5	0.7
Tawny owl *Strix aluco*	42.9	0.6	11.1	0.6	18.8	0.7	54.5	1.0
Ural owl *Strix uralensis*	9.5	0.2	16.7	0.1			4.5	0.2
Great grey owl *Strix nebulosa*			16.7	0.1				
Long-eared owl *Asio otus*	42.9	0.6	27.8	0.4	6.3	0.2	61.4	0.9
Short-eared owl *Asio flammeus*	9.5	0.0	33.3	0.5			13.6	0.5
Tengmalm's owl *Aegolius funereus*	9.5	0.4	11.1	0.0			20.5	0.5
Hawk owl *Surnia ulula*			16.7	0.2			6.8	0.7
Pigmy owl *Glaucidium passerinum*	9.5	0.2	5.6	0.0			2.3	0.1
Snowy owl *Nyctea scandiaca*							2.3	0.0

Note: F – frequency of occurrence in the studies. A – average percentage in the diet calculated from the studies reporting the prey species.

S5. Complete results of the Linear Mixed-effects Models

Results of the Linear Mixed-effects Model used in objetive B – spatio-temporal patterns in super-predation.

	Value (β)	SE	*df*	*t*-value	*P*-value (*t*)
Intercept	30.830	33.274	108	0.93	0.356
Coordinate X	0.003	0.028	108	0.11	0.915
Coordinate Y	0.008	0.037	108	0.23	0.822
Autocovariate	0.746	0.183	108	4.07	0.000
Central year	-0.015	0.017	108	-0.92	0.359
Species (random effect)		SD (intercept)		SD (Residual)	
		0.767		0.889	
Variance function					
Structure: Exponential of variance covariate		Formula: fitted values		Parameter estimates: 0.32	

Results of the Linear Mixed-effects model used in objective C – effect of prey.

	Value (β)	SE	*df*	*t*-value	*P*-value (*t*)
Intercept	-0.448	1.762	93	-0.254	0.800
Mammals	0.079	0.026	63	3.002	0.003
Hedgehogs, shrews (0,1)	-0.570	0.436	93	-1.308	0.194
Deers and wild boar (0,1)	0.239	0.562	93	0.425	0.671
Rodents	-0.866	0.217	93	-3.992	0.000
Rabbits and hares	-0.712	0.220	93	-3.231	0.002
Partridges and grouses	-0.629	0.234	93	-2.685	0.009
Pigeons and doves	-0.799	0.254	93	-3.144	0.002
Passerines	0.021	0.310	93	0.067	0.947
Reptiles (0,1)	-0.615	0.485	93	-1.267	0.208
Diet diversity	12.790	2.142	93	5.972	0.000
Autocovariate	0.315	0.119	93	2.654	0.009
Species (random effect)		SD (intercept)		SD (Residual)	
		0.000		0.950	
Variance function					
Structure: Exponential of variance covariate		Formula: fitted values		Parameter estimates: 0.254	

Results of the Linear Mixed-effects model used in objective C – Rabbits and super-predation in SW Europe.

	Value (β)	SE	*df*	*t*-value	*P*-value (*t*)
Intercept	46.630	65.678	35	0.710	0.482
Rabbits	0.007	0.014	35	0.515	0.610
Year	-0.023	0.033	35	-0.706	0.485
Autocovariate	0.780	0.242	35	3.225	0.003
Species (random effect)		SD (intercept) 0.000		SD (Residual) 0.582	
Variance function Structure: Power of variance covariate		Formula: fitted values		Parameter estimates: 1.536	

Results of the Linear Mixed-effects model used in objective D – Breeding success and IGP.

	Value (β)	SE	*df*	*t*-value	*P*-value (*t*)
Intercept	2.089	0.312	24	6.701	0.000
IG prey	-0.090	0.038	24	-2.377	0.026
Autocovariate	-0.123	0.061	24	-2.121	0.044
Species (random effect)		SD (intercept) 0.585		SD (Residual) 0.056	
Variance function Structure: Power of variance covariate		Formula: fitted values		Parameter estimates: 2.693	

Results of the Linear Mixed-effects model used in objective D – Population fecundity and IGP

	Value (β)	SE	*df*	*t*-value	*P*-value (*t*)
Intercept	1.410	0.317	26	4.454	0.000
IG prey	-0.081	0.048	26	-1.680	0.101
Autocovariate	-0.008	0.141	26	-0.058	0.954
Species (random effect)		SD (intercept) 0.495		SD (Residual) 0.298	
Variance function Structure: Power of variance covariate		Formula: fitted values		Parameter estimates: 1.220	