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Why do top predators engage in superpredation? From an empirical scenario to a theoretical framework

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Lethal interactions can shape ecosystem structure, and consequently understanding their causes is ecologically relevant. To improve both empirical and theoretical knowledge on superpredation (i.e. predation on high-order predators), we studied an eagle owl population, including its main prey and mesopredators, and then we crossed these results with existing theories to provide a reasoning framework. We fitted our field data into four main causes explaining lethal interactions: food stress, opportunistic superpredation, removal of a competitor, and removal of a potential threat. Empirically, superpredation seemed to be mostly determined by the combination of the food-stress and opportunistic-superpredation hypotheses, which highlights the complexity of the factors triggering superpredation. Therefore, besides being a response to lower food availability, superpredation may also represent an effective mechanism to remove potential predators and/or competitors, either intentionally or not. Our theoretical framework focused on the decision-making process in superpredation, considering four inter-related stages: encountering; attacking; and capturing a mesopredator; as well as consuming a mesopredator once killed. Superpredation almost certainly results from a complex process of decision-making, accounting for costs and benefits assessed moment-to-moment and for each mesopredator individual. It is time to build bridges between theoretical and empirical studies to further understand the mechanisms driving complex interactions among top predators and mesopredators.

Keywords: competitive killing, decision-making, food stress, injury risk, intraguild predation, mesopredators, optimal diet, superpredation, top predators

Synthesis

Lethal interactions among predators can shape ecosystems and animal communities. To improve both empirical and theoretical knowledge on the causes of superpredation, we studied an eagle owl population, its main prey and mesopredators. We considered four main causes: food stress, opportunism, competitor removal, and removal of potential threats. Empirically, superpredation seemed to be mostly determined by a combination of food-stress and opportunism. Our theoretical framework focused on the decision-making process, considering four inter-related stages: encountering, attacking, capturing, and consuming a mesopredator. Superpredation should result from a complex process of decision-making for each mesopredator individual, accounting for costs and benefits assessed moment-to-moment.

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Introduction

Top predators, from small invertebrates to large vertebrates, often kill other predators of similar or smaller size, which are not their usual and most profitable prey (Palomares and Caro 1999, Heithaus 2001, Arim and Marquet 2004, Sergio and Hiraldo 2008). Many of these predatory interactions fit into two general concepts: intraguild predation, when predator and prey are competitors (Polis et al. 1989); and superpredation, when the prey is also a high-order predator in the ecosystem but an unusual food resource for the top predator, regardless of whether it is a competitor (Lourenço et al. 2014). The control exerted by top predators on mesopredator populations through these lethal interactions is a widespread phenomenon, both taxonomically and geographically (Polis et al. 1989, Arim and Marquet 2004, Heithaus et al. 2008, Ritchie and Johnson 2009). Consequently, the decline of top predators can trigger trophic cascades capable of altering ecosystem functioning and biodiversity (Crooks and Soulé 1999, Baum and Worm 2009, Ritchie and Johnson 2009). On the other hand, an increase of top predators may cause unexpected effects on mesopredators and shared prey, which may have unfavourable status and/or are targeted by conservation and management efforts (Linnell and Strand 2000, Ritchie and Johnson 2009, Chakarov and Krüger 2010). Therefore, determining the causes of lethal interactions among top predators is crucial to our understanding of ecosystem functioning.

The consequences of lethal interactions among top predators have been well-examined (Linnell and Strand 2000, Sergio and Hiraldo 2008, Ritchie and Johnson 2009). However, the causes of lethal interactions are still poorly understood, which is possibly linked to the great difficulty in assessing the frequency in which top predators engage in these interactions. Four main causes have been proposed to explain lethal interactions: 1) food stress, 2) opportunistic superpredation, 3) removal of a competitor, and 4) removal of a potential threat (Polis et al. 1989, Palomares and Caro 1999, Sergio and Hiraldo 2008, Ritchie and Johnson 2009, Lourenço et al. 2014, Hoy et al. 2017; Table 1). These different causes can have different implications for mesopredators and influence trophic cascades, i.e. by varying in their potential to generate mesopredator suppression/release phenomena and indirect effects at lower trophic levels (Mueller et al. 2016, Terraube and Bretagnolle 2018). The food-stress hypothesis has been the most frequently cited explanation: top predators will include a higher proportion of mesopredators in their diet when facing a decrease in main-prey availability (Korpimäki and Norrdahl 1989, Tella and Mañosa 1993, Serrano 2000, Rutz and Bijlsma 2006, Lourenço et al. 2011a, Hoy et al. 2017). The opportunistic-superpredation hypothesis is applicable when a top predator includes mesopredators in its diet, only driven by chance, and mostly because of its superiority, without being under food stress (Lourenço et al. 2014, Hoy et al. 2017). The competitor-removal hypothesis has been suggested since killing a competitor may free up resources for a top predator (Polis et al. 1989, Palomares and Caro 1999, Sunde et al. 1999, Helldin et al. 2006). Finally, the predator-removal hypothesis takes into account the advantage obtained from eliminating a mesopredator that can represent a potential threat to the individual and/or its offspring (Palomares and Caro 1999, Lourenço et al. 2011b). When mesopredators are regularly killed but not often included in the diet, the most plausible explanations are the competitor- and predator-removal hypotheses, whereas these two premises should be a less important cause when mesopredators are frequently consumed (Sunde et al. 1999, Lourenço et al. 2014). The main issue is that, often, two or more determinants may be driving lethal interactions among top predators. When specifically trying to determine the causes behind superpredation, given that the mesopredator is consumed, one can discard the competitor- or predator-removal hypothesis as the main single explanation. Instead, one should focus on the food-stress or opportunistic-superpredation hypotheses, or perhaps on combinations of several causes (Polis et al. 1989, Lourenço et al. 2014; Table 1; Supplementary material Appendix 1 Fig. A1).

A practical approach to unravelling the causes of lethal interactions among top predators involves analysing the relationships between the percentage of superpredation in individuals' diet and the abundance of both main prey and mesopredators in nature (Lourenço et al. 2011a, 2014, Hoy et al. 2017). In addition, to determine the competitive degree of the interaction, it is important to compare the frequency of superpredation on mesopredators that compete with the top predator and the frequency of superpredation on mesopredators that do not compete or pose a serious threat (Sunde et al. 1999, Serrano 2000, Lourenço et al. 2014, Morosinotto et al. 2017).

To improve our understanding of the causes of superpredation, we present here a theoretical framework that crosses empirical results with the known theory on optimal diet (Emlen 1966, Schoener 1971, Pulliam 1974, Charnov 1976, Sih and Christensen 2001), lethal interactions among top predators (Polis et al. 1989, Lourenço et al. 2014), and foraging on dangerous prey (Mukherjee and Heithaus 2013). With such an aim, we first studied the above-mentioned relationships using extensive information on the diet of a top predator, the eagle owl *Bubo bubo*, and on the abundance of the main prey and mesopredators within this predator's home range. Empirically, we want to find the main determinants of superpredation in a common superpredator. Second, we developed a general theoretical framework of the decision-making process to attack a mesopredator as this is of vital importance to further understand the causes of superpredation.

Methods

Eagle owl investigation and diet study

Out of the potential candidates among vertebrate top predators in which to study the determinants of superpredation, the eagle owl is an ideal species for the following reasons: 1) it regularly engages in lethal interactions with other

Table 1. Hypotheses proposed as causes of lethal interactions among top predators.

	Single causes			Combination of causes		
	Food stress	Competitor/predator removal	Opportunistic superpredation	Food stress+opportunistic superpredation	Food stress + competitor/ predator removal	Competitor/predator removal + opportunistic superpredation
Synopsis	superpredator is under food stress because the main prey is scarce	superpredator actively removes competitors, predators, or aggressors to obtain a benefit	superpredator is not under food stress, it just takes advantage of its superiority to kill and eat mesopredators	predator is under food stress and takes advantage of its superiority to eat mesopredators	predator is under food stress while simultaneously actively removing competitors/ predators to obtain a benefit	predator is actively removing competitors/predators to obtain a benefit; and although not under food stress it will eat mesopredators it kills
Active search for alternative food	yes	no	no	yes	yes	no
Active search for mesopredators	no	yes (to kill but not to eat)	no	no	yes	yes
Victim consumption	always	no; occasionally; or only partly consumed	always	yes	yes	yes
Expected relationships						
Between mesopredator consumption and main prey abundance	correlated	uncorrelated	uncorrelated or just slightly correlated	correlated	correlated	uncorrelated or just slightly correlated
Between mesopredator consumption and abundance	not strongly correlated	correlated	correlated	correlated	correlated	correlated
Notes	greater need to prey on dangerous mesopredators with increasing food stress, but other alternative prey should be preferred	mesopredators which are dangerous or strong competitors should be frequent victims	dangerous mesopredators should be avoided (to minimize risks to the superpredator)	inclusion of mesopredators in proportion to their abundance, but avoiding larger and more dangerous species	predation of mesopredators in proportion to their abundance, including large-bodied competitors*	predation of mesopredators in proportion to their abundance, including large-bodied competitors

* This combination may be difficult to separate from the combination of the three drivers acting together (not described in this table).

predators (Lourenço et al. 2011a); 2) its diet is easy to study (using pellets and prey remains), providing large sample sizes per breeding site and accurate identification of prey species (Lourenço et al. 2015a); 3) it has a generalist diet, taking advantage of the most profitable prey and responding to changes in its main prey abundance (Korpimäki et al. 1990, Lourenço et al. 2011a, Tobajas et al. 2016); 4) it has a relatively small home range enabling a reliable estimate of prey and mesopredator abundance within its potential hunting area (Campioni et al. 2013, Lourenço et al. 2015a); 5) it occupies many ecosystems across its geographically widespread distribution (the whole Palearctic region); and 6) it plays a similar ecological role to its con-generic species of similar size occurring in almost all parts of the world (e.g. great horned owl *Bubo virginianus*, Magellanic horned owl *B. magellanicus*, rock eagle owl *B. bengalensis*, Cape eagle owl *B. capensis*).

This study was conducted in the southwestern Iberian Peninsula, throughout four regions – Alentejo and Algarve in Portugal, and Seville and Huelva in Spain. Eagle owls were investigated from 2000 to 2012 (more details in Lourenço 2006, Campioni et al. 2012, 2013). Eagle owls occur in similar landscape typologies and habitats in the four regions: mostly agro-pastoral woodlands of varying density, and Mediterranean scrublands mainly managed for small-game hunting (Lourenço 2006, Campioni et al. 2012, 2013). The four regions are among the most suitable for eagle owls, showing medium to high population density (Lourenço et al. 2015a, b).

We determined superpredation levels in 65 eagle owl nest sites by collecting prey remains and pellets in both nests and perches. The number of years in which each nest site was visited varied between one and seven (mean ± SD = 3.0 ± 1.3 years). Visits were carried out mostly at the end of the breeding season or thereafter, between April and September. Thus, diet samples were mostly comprised of prey captured during the eagle owl breeding period (December – July). Although we have dietary data from 2000 to 2012, most samples (89%) were collected between 2004 and 2010. We identified 12 726 prey (mean sample size per nest site ± SD = 195.8 ± 114.7 prey; range: 47–522 prey; Supplementary material Appendix 1 Table A1) using identification keys for bones and feathers and an osteological reference collection (Laboratory of Archaeosciences, IGESPAR, Portugal). We estimated the minimum number of individuals combining pellets and prey remains (Marchesi et al. 2002, Lourenço 2006). Superpredation was calculated for each nest site as the percentage of prey individuals belonging to two avian mesopredator groups (diurnal raptors – Accipitriformes, Falconiformes; and owls – Strigiformes) from the total prey sample. Mammalian carnivores were excluded because their percentage in the diet of eagle owls is generally very low (Lourenço et al. 2011a). Moreover, determining carnivore abundance with sufficient accuracy is extremely difficult, which could also result in biased estimations and less reliable analyses. We estimated diet diversity calculating the Shannon diversity index using prey numeric percentage at the taxonomic level of the order (Lourenço et al. 2015a).

Main prey and mesopredator abundance

Rabbits *Oryctolagus cuniculus* are the main prey of eagle owls in the study area (Lourenço 2006, Lourenço et al. 2015a), representing between 8% and 82% of the prey items found in the diet (mean ± SD = 39.7 ± 18.4; Supplementary material Appendix 1 Table A1, Fig. A2). The relative rabbit abundance in each eagle owl nest site was determined using counts of rabbit faecal pellets (latrine counts; Beja et al. 2007), carried out from the beginning of March to the beginning of May, during 2009 and 2010. We walked transects with a total length between 1000 and 2600 m (mean ± SD = 2019 ± 333 m) in each home range, recording the number of latrines found within 4 m on both sides of transects. Transects were located in habitats suitable for rabbits within a radius of 2.5 km from the eagle owl nest. This radius was chosen taking into account our previous radio-tracking data in order to encompass the home range of most eagle owls in the study area (Campioni et al. 2012, 2013). To obtain comparable indices of main prey abundance, in each nest site we calculated the number of latrines per km of transect.

To estimate mesopredator abundance, we considered the number of potentially occupied breeding sites of diurnal raptors and owls reported as prey of eagle owls in Lourenço et al. (2011a), within a 2.5 km radius centered on the eagle owl nest. The estimated total number of mesopredator breeding sites resulted from the accumulation of information collected between 2007 and 2010, obtained from: 1) 2-h diurnal point counts (range: 2–5 point counts per eagle owl nest site) and 2-h nocturnal listening sessions (range: 2–6 sessions per eagle owl nest site); 2) active searches for raptor and owl nests (range: 1–3 visits per eagle owl nest site); and 3) occasional records made during eagle owl monitoring. Mesopredator censuses were performed between March and June, and focused only on breeding raptor species. Wintering raptors were not considered in estimates of mesopredator abundance, mainly because they were not detected as prey in our eagle owl diet data. The estimated value of mesopredator abundance for each eagle owl nest site corresponded to the total number of occupied breeding sites of all mesopredator species pooled for the whole censusing period (2007–2010). To reduce potential bias, for each eagle owl nest site, we concentrated the mesopredator censuses in the same breeding season, using information from other years mostly as complementary.

Specific traits may cause each particular mesopredator species to have a different potential for being victim of superpredation (Palomares and Caro 1999, Donadio and Buskirk 2006). Therefore, we determined the body mass ratio between the eagle owl and each mesopredator by dividing the eagle owl body mass by the mesopredator body mass. We used weight information for the Iberian Peninsula, and, for sexual-dimorphic species, we calculated the mean value for males and females. Then, for the whole study area, we calculated the position of each mesopredator species in the predation rank by ranking species in descending order of their mean percentage in eagle owl diet (i.e. the first species is the most frequently captured mesopredator). We ranked species by abundance (using the mean number of breeding sites of each mesopredator species near eagle owl nests) and body mass ratio, and then calculated a rank of potential as prey by summing these two ranks. If the predation rank was below the potential as prey rank, the mesopredator was apparently more frequently captured than its potential interest as prey, whereas, if the predation rank was above the potential as prey rank, the mesopredator was apparently being less frequently captured than its potential interest as prey.

Data analysis

In each nest site we had diet samples from several years. Therefore, to consider data altogether, we first checked if there was large inter-annual variation in prey proportions. We selected 23 nest sites from which we had large samples (n > 30 prey) for two or more years. Then, we used linear mixed models and an information-theoretic approach (Burnham and Anderson 2002) to assess the effect of year and ordinal sequence of sampling on the percentage of rabbits, the percentage of mesopredators, and diet diversity (Supplementary material Appendix 1 Table A2). Since we found no effect of year or sampling sequence in this sub-sample, we pooled the diet data from all available years for each eagle owl nest site, and then extracted our response variable, i.e. superpredation. We decided to pool the data because the consumption of mesopredators is not a common event in the diet of eagle owls (Lourenço et al. 2011a), thus it is cautious to use a large sample to obtain a more robust estimation of the average superpredation frequency.

Main prey abundance (i.e. rabbits) and mesopredator abundance were the explanatory variables considered in the analysis. We screened our data to detect outliers, and checked data distribution and collinearity between explanatory variables. We designed a set of competing models, considering either the single effect of main prey or mesopredator abundance, and also combinations of both effects as determinants of the level of superpredation. These models could then be compared to the theoretical expectations of the causes of superpredation. We used an information-theoretic approach to select the model (i.e. hypothesis) that best fitted our data (multi-model inference; Burnham and Anderson 2002). Since the explanatory variables showed non-linear (main prey abundance) or roughly linear (mesopredator abundance) relationships with the response variable, we alternatively built additive and linear models. We used additive models with an integrated smoothness estimation by a quadratically penalized likelihood type approach (Faraway 2006, Wood 2006). Models used a Gaussian distribution (identity link function), and smooth terms (thin plate regression splines) were represented using penalized regression splines with GCV (generalized cross validation) as the smoothing parameter estimation method (Wood 2006). We defined a set of seven competing models illustrating the determinants of superpredation (Table 2), i.e. superpredation is (M1) mostly a function of a non-linear relationship with main prey abundance; (M2) mostly a function of a non-linear relationship with mesopredator abundance; (M3) mostly a function of a linear relationship with mesopredator abundance; (M4) a function of a non-linear relationship with both main prey and mesopredator abundance; (M5) a function of a non-linear relationship with main prey abundance and a linear relationship with mesopredator abundance; (M6) a function of a non-linear relationship with interacting main prey and mesopredator abundance. Finally, we also included the null model (M0) to provide inferential information. Models were fitted one by one and ordered according to their AICc values (second-order Akaike information criterion, used to correct for small sample size). For each model we determined the degrees of freedom, log-likelihood value, AICc difference (ΔAICc), Akaike weight (w_i, probability of each model given the data and set of models), and evidence ratio (Burnham et al. 2011).

We found no spatial dependence in model residuals after analysing bicolour residual xy-plots (bubble plots) and assessing statistical significance of Moran's I in model residuals using spatial correlograms. We used model diagnostic plots to validate model results (Faraway 2006). All analyses were performed using the software R ver. 3.3.0 (<www.r-project.org>) with the packages gmcv (Wood 2006), gplots

Table 2. Multi-model inference procedure for the set of models, showing that superpredation is mostly a function of a non-linear relationship with both main prey and mesopredator abundance. Models are ordered according to AICc value (second order Akaike information criterion). In the models, 's' signifies that the variable has a smooth term associated. df – degrees of freedom; logLik – loglikelihood value; w_i – Akaike weight; R^2 – explained deviance.

Model	df	logLik	AICc	ΔAICc	w_i	R^2
M4: s(rabbit abundance) + s(mesopredator abundance)	8.81	–141.45	303.65	0.00	0.94	61.1%
M6: s(rabbit abundance, mesopredator abundance)	8.67	–145.00	310.38	6.73	0.03	56.6%
M5: s(rabbit abundance) + mesopredator abundance	6.40	–148.26	310.95	7.30	0.02	52.1%
M2: s(mesopredator abundance)	5.09	–152.92	317.06	13.41	0.00	44.7%
M3: mesopredator abundance	3	–157.01	320.41	16.76	0.00	37.3%
M1: s(rabbit abundance)	5.29	–160.75	333.2	29.55	0.00	29.6%
M0: null model	2	–172.16	348.52	44.87	0.00	---*

* Negative value below –0.001

(Warnes et al. 2014), ncf (Bjornstad 2013), MuMIn (Barton 2014), sp, spdep (Bivand et al. 2013).

Building a conceptual framework for the decision-making process in superpredation

We developed a theoretical framework for disentangling the causes of superpredation, which has the potential for a broad application to the study of interactions among predators. This theoretical framework takes into account the costs and benefits of superpredation, crossing the known theory on optimal diet (Emlen 1966, Schoener 1971, Pulliam 1974, Charnov 1976, Sih and Christensen 2001), lethal interactions among top predators (Polis et al. 1989, Lourenço et al. 2014), and foraging on dangerous prey (Mukherjee and Heithaus 2013). We followed the predator–prey interaction stages suggested by Sih and Christensen (2001) to describe the decision-making process in superpredation. Our framework assumes that: 1) mesopredators are not usual prey of superpredators; 2) mesopredators are less profitable than common prey (and thus less preferred when available); 3) mesopredators are more dangerous to kill than common prey or may require different and more costly hunting techniques; and 4) superpredation should have a short-term positive effect on the fitness of superpredators.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.k114944> (Lourenço et al. 2018).

Results

Empirical results on the causes of superpredation in the eagle owl

The model including both non-linear relationships of superpredation with main prey and mesopredator abundance (M4) was best supported by our data, with a probability (w_i) of 0.94 of being the actual best model from our set of competing models (Table 2, Supplementary material Appendix 1 Table A3). Considering the evidence ratio, the empirical support for model 4 was 31 times that of the second best model (M6). Superpredation decreased with increasing abundance of the main prey (rabbits; Fig. 1a), with a threshold around a main prey abundance value of 10 rabbit latrines km^{-1}, above which superpredation seemed to stabilize at a low level (mesopredators representing ca 2% of the prey). Furthermore, superpredation increased with increasing mesopredator abundance (Fig. 1b), with a more pronounced relationship above an estimated abundance of 9 owl/raptor breeding sites within 2.5 km of an eagle owl nest site. Moreover, according to our best model, superpredation reached its highest level in breeding sites where simultaneously main prey abundance was the lowest and mesopredator abundance was the highest (Fig. 1c). Taking into account the observed threshold in main prey abundance (10 rabbit latrines km^{-1}; Fig. 1a), the relationship between superpredation levels and mesopredator abundance was stronger in eagle owl breeding sites with lower main prey abundance (Fig. 2).

Interestingly, the most frequently preyed upon mesopredator species shared some characteristics (Table 3): 1) the first three are nocturnal species (little, barn, and tawny owls), being active at the same time as eagle owl; 2) three out of the first four were the most abundant species within eagle owl nest sites; and 3) their size is relatively small in relation to the predator. Mesopredators such as the barn owl *Tyto alba*, black kite *Milvus migrans*, red kite *M. milvus*, and the long-eared owl *Asio otus* seemed to be predated more than what would be expected by their potential as prey (Fig. 3). Conversely, the Eurasian kestrel *Falco tinnunculus*, black-shouldered kite *Elanus caeruleus*, common buzzard *Buteo buteo*, and the sparrowhawk *Accipiter nisus* seemed to have been captured less frequently than what their potential as prey would suggest.

A theoretical framework for the decision-making process in superpredation

Following the predator–prey interaction stages by Sih and Christensen (2001), we consider that the superpredation frequency (S_i) for a mesopredator species i is determined by four inter-related stages: 1) the probability of encountering a mesopredator (E_i), 2) the probability of attacking the detected mesopredator (A_i), 3) the probability of capturing it after initiating an attack (C_i), and 4) the probability of consuming the mesopredator once killed (P_i). All stages are both species- and individual-specific, and therefore the overall superpredation frequency (S_t), for a given time interval t, should be the summation of the product of encounter probability (E_i), attack probability (A_i), capture probability (C_i), and consumption probability (P_i) for each mesopredator species i (or intraspecific group, e.g. juveniles, adults, males, females):

$$S_t = \sum_{i=1}^{n} (E_i \times A_i \times C_i \times P_i) \tag{1}$$

While the decision-making process behind the attack probability (A_i) is of crucial importance to understanding the determinants of superpredation, the other three stages may also influence superpredation levels. Thus, we will further analyse Eq. 1.

Encounter probability

Mesopredator encounter probability (E_i, i.e. the likelihood that a superpredator will detect a mesopredator species during a given time t) may be influenced by three major components: 1) landscape structure; 2) mesopredator density; and 3) mesopredator behaviour. Landscape structure is related to differences in the detectability of mesopredators according to habitat and the availability of refugia (Sergio et al. 2007, Sergio and Hiraldo 2008, Morosinotto et al. 2017). The relevance of the mesopredator density in the hunting range of

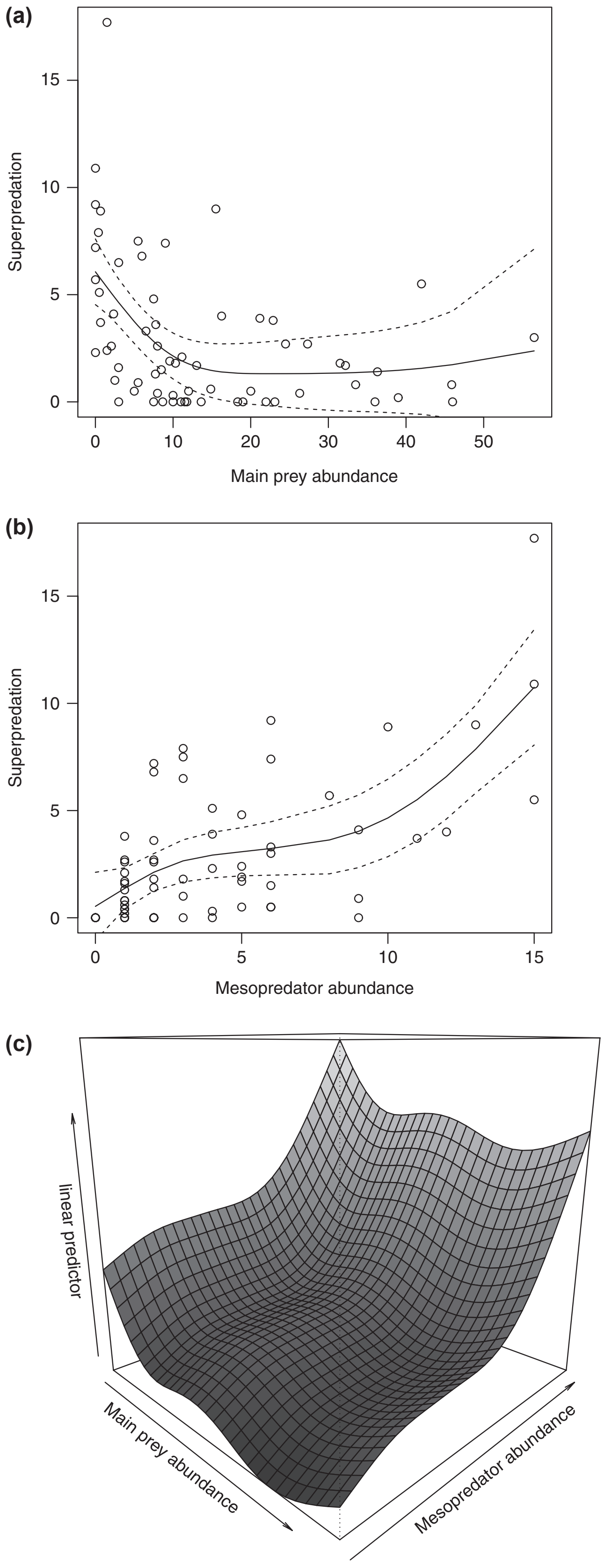

Figure 1. (a) Plot of the GAM (with 95% confidence intervals) showing that superpredation (percentage of mesopredators in the

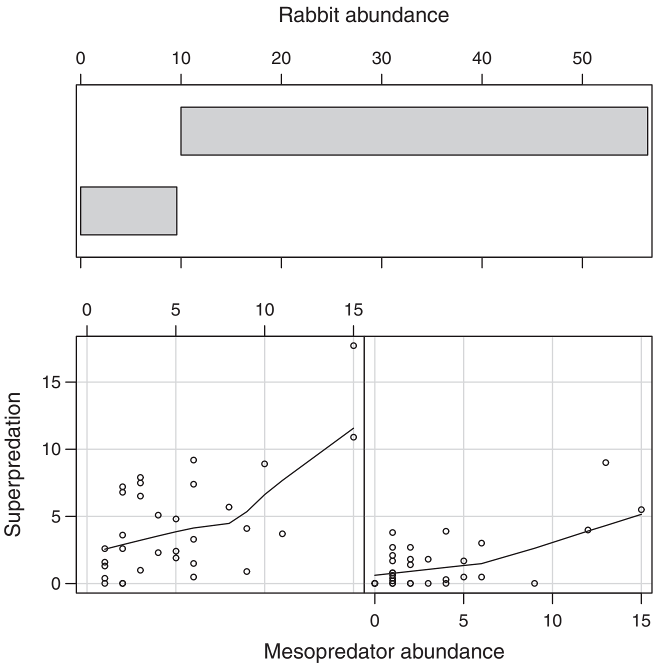

Figure 2. Relationships between superpredation (percentage of mesopredators in the diet) and mesopredator abundance (n of mesopredator breeding sites within 2.5 km of an eagle owl nest site) under low (below 10 rabbit latrines km^{-1}; left-hand panel) and high (above 10 rabbit latrines km^{-1}; right-hand panel) rabbit abundance. The continuous line represents a smooth curve fitted by LOESS (local polynomial regression).

the superpredator for the observed superpredation frequency is quite straightforward (Lourenço et al. 2011a, Dröge et al. 2017). The third component, mesopredator behaviour, can be crucial for encounter probability, namely the overlap in activity rhythms. Also, individuals calling more frequently, such as males or fledglings, or when they exhibit more exposed behaviours (e.g. during displays) may be more easily detected by superpredators (Hakkarainen and Korpimäki 1996, Lourenço et al. 2013, Hoy et al. 2015). These three components also represent what is commonly referred as prey availability, which in superpredation concerns only mesopredator species.

Figure 1. Continued

diet) decreased with increasing main prey abundance (rabbit abundance index – n latrines km^{-1}). Superpredation seems to stabilize at low levels above a threshold of 10 rabbit latrines km^{-1}. (b) Plot of the GAM (with 95% confidence intervals) showing that superpredation (percentage of mesopredators in the diet) increases with increasing mesopredator abundance (n of mesopredator breeding sites within 2.5 km of an eagle owl nest site). (c) 3D plot of the GAM. The linear predictor corresponds to superpredation (i.e. percentage of mesopredators in eagle owl diet), which reaches the highest levels where main prey abundance (rabbit abundance index – n latrines km^{-1}) was the lowest and mesopredator abundance (n of mesopredator breeding sites within 2.5 km of an eagle owl nest site) was the highest.

Table 3. Ranking of the mesopredators coexisting with eagle owls and victims of superpredation according to: 1) mean percentage in the diet; 2) mean abundance; 3) predator/prey body mass ratio; and 4) potential as prey (sum of the abundance rank and body mass ratio rank of each prey species). Species were ordered by decreasing predation rank.

Potential prey species	Predation rank (mean percentage in the diet of eagle owls)	Abundance rank (mean number of breeding sites near eagle owl nests)	Body mass ratio rank (predator/prey body mass ratio)	Potential as prey rank (sum of abundance and body mass ratio ranks)
Little owl *Athene noctua*	1 (0.95)	1 (0.88)	3 (11.1)	1 (4)
Barn owl *Tyto alba*	2 (0.54)	7 (0.22)	9 (6.3)	5 (16)
Tawny owl *Strix aluco*	3 (0.53)	2 (0.66)	10 (4.0)	3 (12)
Eurasian kestrel *Falco tinnunculus*	4 (0.23)	4 (0.45)	5 (9.1)	2 (9)
Black kite *Milvus migrans*	5 (0.20)	6 (0.31)	11 (2.4)	8 (17)
Long-eared owl *Asio otus*	6 (0.11)	16 (0.03)	7 (6.6)	14 (23)
Black-shouldered kite *Elanus caeruleus*	7 (0.09)	9 (0.14)	6 (7.7)	4 (15)
Common buzzard *Buteo buteo*	8 (0.08)	3 (0.57)	13 (2.2)	5 (16)
Red kite *Milvus milvus*	9 (0.04)	12 (0.05)	14 (1.8)	15 (26)
Lesser kestrel *Falco naumanni*	10 (0.03)	17 (0.02)	2 (12.5)	9 (19)
Booted eagle *Hieraaetus pennatus*	10 (0.03)	8 (0.17)	11 (2.4)	9 (19)
Scops owl *Otus scops*	12 (0.01)	18 (0.00)	1 (20.4)	9 (19)
Montagu's harrier *Circus pygargus*	12 (0.01)	11 (0.06)	8 (6.5)	9 (19)
Sparrowhawk *Accipiter nisus*	14 (0.00)	12 (0.05)	4 (9.5)	5 (16)
Goshawk *Accipiter gentilis*	14 (0.00)	12 (0.05)	15 (1.7)	17 (27)
Short-toed eagle *Circaetus gallicus*	14 (0.00)	5 (0.34)	16 (1.2)	13 (21)
Bonelli's eagle *Aquila fasciata*	14 (0.00)	9 (0.14)	17 (1.0)	15 (26)
Spanish imperial eagle *Aquila adalberti*	14 (0.00)	12 (0.05)	18 (0.7)	18 (30)

Attack probability

The attack probability (A_i, i.e. the likelihood that a superpredator will attack a detected mesopredator species) results from several decision-making processes made for each individual mesopredator at a particular moment. Consequently, decisions should be influenced by specific traits of each mesopredator individual and the current internal condition of the superpredator. The decision to attack a mesopredator should result from a tradeoff between the costs and benefits of that action, as explored in optimal diet theory. The most classical views of optimal diet theory identified the costs of pursuit, handling and eating the prey (*Es* – energy spent to capture and eat the prey; MacArthur and Pianka 1966, Emlen 1966, Schoener 1971, Charnov 1976). Later, Brown (1988) introduced the missing opportunity costs (*MOC*). And, more recently, Berger-Tal et al. (2009) and Mukherjee and Heithaus (2013) suggested that when dealing with dangerous prey (and many mesopredators fit this description), a predator should stop hunting a given prey *i* when the harvest rate (H_i) equals the sum of the metabolic cost of capturing, handling and eating the prey (Es_i), the cost of risk of injury (RI_i), and the missed opportunity cost (*MOC*).

On the other hand, the benefits for a superpredator of capturing a mesopredator should be the metabolic benefit obtained (*Eg*, energy gain; Emlen 1966, Schoener 1971), and the benefit to fitness of eliminating a competitor or potential predator (*BF*; Polis et al. 1989, Lourenço et al. 2014). Thus, the attack probability for a specific mesopredator *i* (A_i) may be expressed as a function of (a) the metabolic benefit of eating the mesopredator (energy gain, Eg_i), (b) the perceived benefit to individual fitness of eliminating a predator and/or competitor (BF_i), (c) the metabolic cost of capturing, handling and eating the mesopredator (energy spent, Es_i), (d) the

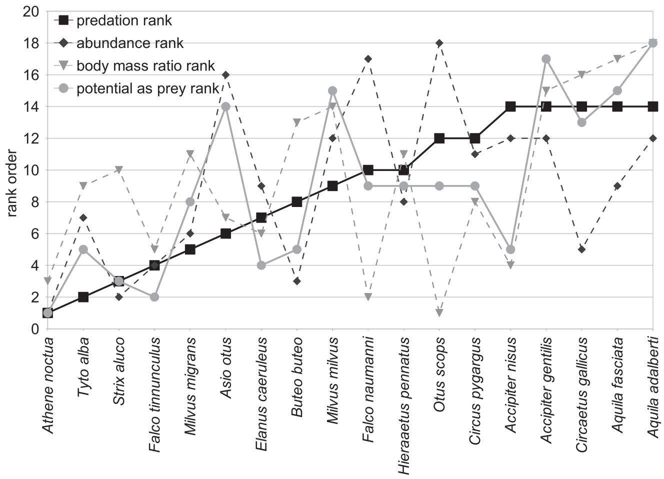

Figure 3. Rank order of predation frequency, abundance, body mass ratio (mesopredator/superpredator), and potential as prey (sum of the abundance rank and body mass rank). When the predation rank (black line) is below the potential as prey rank (red line), the mesopredator is apparently being more frequently captured than its potential interest as prey (e.g. the barn owl *Tyto alba*, black-kite *Milvus migrans*, long-eared owl *Asio otus*, and the red kite *Milvus milvus*). In contrast, when the predation rank is above the potential as prey rank, the mesopredator is apparently being less frequently captured than its potential interest as prey (e.g. the Eurasian kestrel *Falco tinnunculus*, black-winged kite *Elanus caeruleus*, and the common buzzard *Buteo buteo*).

perceived risk of injury (RI_i), and (e) the missed opportunity cost (MOC):

$$A_i = f\left(Eg_i + BF_i - Es_i - RI_i - MOC\right) \qquad (2)$$

The metabolic benefit of eating a mesopredator (Eg) should depend mostly on 1) its body-mass (i.e. potential caloric content), and 2) the energetic state of the superpredator. Under food stress situations, less profitable prey species (i.e. those which are smaller-sized, require more energy to capture, or can be more dangerous) may represent a greater energetic value to fitness (Emlen 1966, Charnov 1976, Mukherjee and Heithaus 2013).

The perceived benefit from eliminating a predator and/or competitor (BF) is a particular characteristic of superpredation and intraguild predation interactions. It will result mostly from individual experience in associating a specific mesopredator with a strong competitor or a serious threat (Lourenço et al. 2011b).

The metabolic cost of capturing and handling a mesopredator (Es_i) will depend mostly on 1) the health condition of the superpredator, and 2) mesopredator vulnerability. A superpredator in good health, or with superior physical traits among conspecifics (e.g. larger body size, faster, more agile) may spend less energy in capturing and killing a mesopredator (MacNulty et al. 2009a, b). Additionally, each mesopredator individual will have different vulnerability to predation. Clearly, species-specific characteristics determine vulnerability, as a faster and more agile mesopredator species may require more energy to capture. Furthermore, within a mesopredator species, substandard individuals (e.g. sick, weak, old, young) should require less energy to be captured and subdued, which has already been found to be of paramount importance in the study of predator–prey relationships (Penteriani et al. 2008, Hoy et al. 2015).

The perceived risk of injury (RI_i) should depend mostly on 1) the mesopredator's traits, 2) the superpredator's health condition; and 3) the superpredator's individual experience and personality. Traits like mesopredator size, weaponry and behaviour are crucial for the superpredator to assess the risk of injury before engaging in a capture attempt (Cooper and Stankowich 2010). Different mesopredators may require specific hunting techniques, with different levels of associated risk of injury. Eagle owls, for example, take advantage of poor light conditions to surprise diurnal raptors and thus reduce the risk associated with killing them (Lourenço et al. 2011b). In addition, a superpredator with physical limitations may be less willing to take risks, because its condition may cause it to be more prone to injuries. Finally, daring (i.e. the willingness to incur risk of injury, Mukherjee and Heithaus 2013) may be part of the personality (individuals may be more or less daring), and it could also be influenced by experience (more experienced individuals may be more daring).

The missed opportunity costs (MOC) represents the alternative activities that the superpredator foregoes while attempting to capture a mesopredator, which includes, for example, hunting other prey, defending the territory from conspecifics, searching for a mate and strengthening their bond, protecting its young, and resting (Brown 1988, Mukherjee and Heithaus 2013).

As both costs and benefits of superpredation may be influenced by the internal state of the superpredator, it means that the probability of attacking a mesopredator should be a state-dependent decision. Notwithstanding, the condition of the superpredator may have an opposite effect, i.e. a poorer condition, such as food-stress-associated malnutrition, could increase both costs and benefits of superpredation, as it can be more physically demanding to catch a mesopredator, but at the same time more important for survival.

Capture probability

Capture probability (C_i) does not correspond to a decision process, and thus it is less relevant to understanding the determinants of superpredation. Capture success should be influenced mostly by 1) the mesopredator's specific and individual traits, 2) the individual characteristics and internal state of the superpredator, and 3) landscape characteristics. Mesopredator traits include species-specific (e.g. size, speed, agility, defensive mechanisms and behaviour) and intra-specific individual characteristics (e.g. size, age, health condition). Similarly, inter- and intra-individual variation in the characteristics of each superpredator should influence capture success, including size, sex, age, experience, personality and health condition. Finally, capture success may depend on the habitat in which the attempt is carried out. For example, since many mesopredators show greater agility and manoeuvrability than superpredators, in habitats like young forests or dense scrublands, large superpredators may have more difficulty in capturing them.

Consumption probability

Consumption probability (P_i) is also relevant to understand the determinants of superpredation, namely because a kill should most likely be consumed if the superpredator is under food stress, whereas kill consumption should be less likely if the main driver is exclusively predator/competitor removal (Palomares and Caro 1999, Sunde et al. 1999). Therefore, consumption probability should be influenced mostly by 1) the nutritional condition of the superpredator, and 2) mesopredator characteristics, specifically if it is perceived as a predator/competitor, and its palatability to the superpredator.

Discussion

We showed empirically that the relationship between consumed mesopredators and the abundances of both main prey and mesopredators may prove useful to understand the causes of superpredation. Indeed, superpredation levels increased with the decreasing abundance of main prey, indicating that food stress should be a relevant determinant. This is in fact the most frequently suggested cause of superpredation reported in birds of prey and mammalian carnivores (Korpimäki and Norrdahl 1989, Palomares and Caro 1999, Sunde et al. 1999, Serrano 2000, Rutz and Bijlsma 2006, Lourenço et al. 2011a, Hoy et al. 2017). This relationship is consistent with the well-established prediction of optimal diet theory, i.e. a predator increases its diet diversity when the abundance of its main prey decreases (Sih and Christensen 2001). In our case study this leads to the inclusion of mesopredators in the diet as alternative prey. Furthermore, the observed relationship between superpredation and main prey abundance suggests the existence of a threshold in food abundance above which superpredation should be less frequent. This may be a useful indicator of potential food stress states, especially when no profitable alternative prey is available.

Additionally, we also showed that superpredation levels increased with greater mesopredator abundance, even when the main prey abundance was apparently high. This suggests that, besides being a response to lower food availability, superpredation may also represent an effective mechanism to remove potential predators and/or competitors, either intentionally or not (Polis et al. 1989, Lourenço et al. 2014). Therefore, even if there is no food limitation, a superpredator may still regularly engage in predatory interactions with mesopredators. The question remains, however, whether superpredation results mostly from opportunism, or intentional predator/competitor removal?

The answer may arise from three main elements: 1) which mesopredator species are being captured, 2) what is their frequency in the diet, and 3) what is their availability. Nonetheless, arriving at the answer requires considerable effort in order to obtain a large sample size of the superpredator's diet and accurate estimates of abundance of mesopredator species (which take into account not only territorial adults but also juveniles, i.e. the whole population). Our results, despite some limitations, provide a good indication that superpredation seems to occur mostly on small-sized and common mesopredators, which normally do not represent a serious threat to the superpredator nor strong competitors. Moreover, the most frequently eaten mesopredators were nocturnal (i.e. have daily habits similar to that of the superpredator), which suggests their capture falls under the hypothesis of opportunism carried out by a superpredator with obvious superiority. Another potentially relevant hint regarding the determinants of superpredation is the frequency of consumption of the victim. In our study, despite the fact that we were focusing on diet data, we never detected any non-consumed (or only partially consumed) mesopredator carcasses during the extensive investigation. However, we are fully aware of the low probability of detecting a freshly killed mesopredator owing to its relatively low frequency. Also, it is more likely that a killed but not consumed carcass is left farther from the nest site and feeding perches, or consumed by scavengers.

Considering all the above mentioned, we suggest that, on average in our population, superpredation does not seem to have a single determinant, but rather it may result from a combination of food stress and opportunism. Although we cannot discard the possibility that competitor/predator removal also played a role, this potential triggering factor does not seem to be as prominent a cause as are food stress and opportunism. However, we have been discussing the determinants behind the pattern resulting from the overall superpredation, and thus it is possible that the motivations may be specific for each mesopredator species, especially if these have a large size range, and consequently different costs, benefits, and risks associated to killing and consuming them.

Crossing empirical results with a theoretical framework for superpredation

We verified that our field data on the eagle owl as model species may give insight into establishing direct relationships between empirical results and theoretical expectations on the determinants of superpredation. Most of our empirical measurements contribute to more than one step of the decision-making process, and thus to several parameters of the theoretical framework. The two most evident cross-cutting parameters are: 1) the mesopredator's specific and individual traits, and 2) the superpredator's individual traits and internal condition.

Regarding the contributions to understand mesopredator encounter probability (E_i) our empirical results suggest mesopredator density in the hunting range of the superpredator may sometimes have an effect on superpredation. Moreover, our data highlights the relevance of mesopredator behaviour, as nocturnal mesopredators were more frequently captured than diurnal mesopredators by the eagle owl, apparently due to a greater overlap in activity rhythms (Petty et al. 2003, Lourenço et al. 2011a).

The parameters contributing to assess attack probability (A_i) assume particular relevance to understanding the determinants of superpredation, although their correspondence with empirical data is challenging. Mesopredator's traits are of prime importance since they influence parameters such as energy gain (Eg_i), energy spent (Es_i), and risk of injury (Ri_i). In our case study, eagle owls seemed to kill smaller-sized mesopredators species more often, which should require less energy and less risk to subdue. The benefit to fitness of eliminating a competitor or potential predator (BF_i) represents the most distinctive parameter in our theoretical framework for superpredation, when compared to the classical formulations for predation (optimal foraging theory). However, this parameter is difficult to assess empirically because it should be based mostly on the superpredator's individual experience with mesopredators. This previous experience may also depend on the superpredator species, as for example, very often, eagle owls are aggressively mobbed by other diurnal and nocturnal raptors, which may contribute to eagle owls creating a negative association with these species (Lourenço et al. 2011b).

Conclusions

Our ability to understand, predict and minimize the detrimental effects of superpredation on mesopredators (and also top predators) can be greatly enhanced if we have extensive knowledge of the determinants of this interaction. Although it may prove to be a very challenging goal, our study on the largest nocturnal avian top predator in Europe and the theoretical framework developed around it suggest that superpredation can be investigated and modelled by integrating information on the abundance of the main prey (but also of alternative prey), abundance and characteristics of mesopredators, as well as the behaviour and internal state of the top predator. Superpredation is almost certainly the product of a complex process of decision-making, which takes into account costs and benefits assessed moment-to-moment and for each mesopredator individual. It may well now be time to build bridges between theoretical expectations and analysis of extensive data sets in order to fine-tune our understanding of the mechanisms driving complex interactions among top predators and mesopredators.

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Supplementary material (available online as Appendix oik-05118 at <www.oikosjournal.org/appendix/oik-05118>). Appendix 1.