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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