UNIVERSIDADE DE ÉVORA

Instituto de Investigação e Formação Avançada

PREDATORY INTERACTIONS AMONG VERTEBRATE TOP PREDATORS

SUPERPREDATION AND INTRAGUILD PREDATION BY LARGE RAPTORS

Rui Nascimento Fazenda Lourenço

Tese orientada por

João Eduardo Rabaça

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Doutoramento em Biologia

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DECLARAÇÃO DO AUTOR

Em conformidade com o Regulamento do Ciclo de Estudos conducente ao Grau de Doutor pela Universidade de Évora (Ordem de Serviço N.º1/2010), esta tese de doutoramento integra um conjunto de quatro trabalhos de investigação, dos quais dois estão já publicados e dois estão submetidos para publicação (todos em revistas com peer-review RiR(ISI)). O autor esclarece que os trabalhos referidos foram realizados em colaboração, e que em todos eles liderou e participou activamente na sua concepção, recolha, análise dos dados e escrita dos artigos. Algumas das normas relativas ao padrão de formatação de cada revista foram retidas nesta tese.

Évora, 01 de Março de 2011

Rui Nascimento Fazenda Lourenço

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Predatory interactions among vertebrate top predators: superpredation and intraguild predation by large raptors

Abstract

This thesis analyses predatory interactions among vertebrate top predadores (intraguild predation and superpredation), using four large raptors as superpredator models: eagle owl, goshawk, golden eagle and Bonelli's eagle. Superpredation in raptors is a widespread phenomenon, that can vary between species, and that is more frequent in human-altered landscapes. Mesopredators are not energetically relevant resources for raptors, and their consumption is related to diet diversification as a result of the decline of staple prey. Competitor and predator removal are additional factors that can cause an increase in superpredation rates. The increase of mesopredators in the diet of raptors is associated to lower breeding success and higher levels of mercury contamination. Predation risk can drive a mesopredator (tawny owl) to reduce its vocal activity in order to be less exposed to its intraguild predator.

Interacções predatórias entre vertebrados predadores de topo: superpredação e predação intraguilda por aves de rapina de grande porte

Resumo

Nesta tese estudaram-se as interacções predatórias entre vertebrados predadores de topo (predação intraguilda e superpredação), utilizando quatro aves de rapina de grande porte como modelos de superpredadores: Bufo-real, Açor, Águia-real, e Águia de Bonelli. A superpredação em aves de rapina é um fenómeno abrangente, que pode variar entre espécies, e mais frequente em paisagens mais humanizadas. Os meso-predadores não são recursos energeticamente relevantes para as aves de rapina, e o seu consumo está associado à diversificação da dieta resultante da diminuição das presas habituais. A eliminação de competidores e potenciais predadores são outros factores que podem aumentar a frequência da superpredação. O aumento da percentagem de meso-predadores na dieta está associado a menor sucesso reprodutor e maiores níveis de acumulação de mercúrio nas aves de rapina. O risco de predação pode levar um meso-predador (Coruja-do-mato) a diminuir a sua actividade vocal de modo a estar menos exposto ao predador intraguilda.

Interacções predatórias entre vertebrados predadores de topo: superpredação e predação intraguilda por aves de rapina de grande porte

Resumo alargado

As interacções predatórias entre vertebrados predadores de topo (predação intraguilda e superpredação) podem potencialmente afectar a estrutura das comunidades através de efeitos ao longo das cadeias tróficas do topo para a base. A designação predação intraguilda aplica-se quando a presa é simultaneamente um competidor do predator. A designação superpredação aplica-se quando o superpredador se alimenta de presas que normalmente estão no topo das cadeias tróficas.

Os objectivos desta tese são: (1) estudar que mesopredadores são mais frequentemente presas de aves de rapina superpredadoras; (2) analisar as causas do aparecimento da superpredação em aves de rapina; (3) investigar a influência da abundância de presas e alterações da paisagem na incidência de predação intraguilda e superpredação em aves de rapina; (4) determinar potenciais efeitos negativos sobre os superpredadores que estão associados ao consumo de presas de níveis tróficos mais elevados; (5) averiguar como o risco de predação intraguilda pode afectar o comportamento de mesopredadores.

Como modelos o estudo incidiu sobre espécies de aves de rapina que são predadores de topo nos ecossistemas europeus: o Bufo-real *Bubo bubo*, o Açor *Accipiter gentilis*, a Águia-real *Aquila chrysaetos*, e a Águia de Bonelli *Aquila fasciata*. Os mesopredadores estudados do ponto de vista comportamental foram: o Milhafre-preto *Milvus migrans*, o Milhafre-real *Milvus milvus*, a Águia-de-asa-redonda *Buteo buteo*, a Águia-calçada *Aquila pennata*, e a Coruja-do-mato *Strix aluco*.

No primeiro artigo científico que faz parte desta tese, foi estudada a dieta das quatro espécies aves de rapina predadores de topo anteriormente referidas: Bufo-real, Açor, Águia-real e Águia de Bonelli. Procedeu-se à compilação de 121 estudos realizados na Europa, que representam um total de 161 456 presas. Neste trabalho verificámos que a superpredação e a predação intraguilda em aves de rapina é um fenómeno abrangente, mas que pode variar consoante a espécie de predador de topo. Os meso-predadores não são por norma recursos energeticamente relevantes para as aves de rapina, e o seu consumo parece associado sobretudo à diversificação da dieta resultante da diminuição da abundância das presas base da dieta. Numa escala europeia, o fenómeno da superpredação está espacialmente aglomerado espelhando a fragmentação e heterogeneidade dos habitats. Nesta escala não foram detectadas tendências espaciais ou temporais da incidência de

superpredação em aves de rapina. Por fim, foi possível concluir que o aumento da percentagem de meso-predadores na dieta está associado ao um menor sucesso reprodutor destas espécies, facto possivelmente relacionado com situações de stress alimentar onde a menor disponibilidade de presas base afecta a capacidade reprodutora dos indivíduos.

No segundo artigo desta tese analisaram-se as hipóteses relativas ao despoletar dos fenómenos de predação intraguilda e superpredação. Duas hipóteses têm sido mais frequentemente sugeridas: (1) o stress alimentar devido à escassez de presas base; e (2) a remoção de competidores. Neste trabalho propomos uma terceira hipótese para o aparecimento destas interacções predatórias: a remoção de predadores. Esta hipótese foi experimentalmente testada num comunidade de aves de rapina no Espaço Natural de Doñana, utilizando um Bufo-real e uma Coruja-do-mato preparados por taxidermia, e observando a resposta de quatro espécies de aves de rapina que são potenciais presas intraguilda: o Milhafre-preto, o Milhafre-real, a Águia-de-asa-redonda, e a Águia-calçada. Estas espécies responderam agressivamente perante um potencial predador intraguilda, o Bufo-real, enquanto a Coruja-da-mato foi ignorada na maioria das sessões experimentais. A resposta agressiva das aves de rapina diurnas é um comportamento defensivo que poderá ter dois intuitos: (1) afastar o predador intraguilda do seu território; ou (2) matar o potencial predador tirando proveito da vantagem de um ataque diurno. Em concordância com o anterior é de esperar que um Bufo-real ao matar estas presas intraguilda, tal como observado na área de estudo, beneficie da remoção de potenciais predadores ou agressores. Em conclusão, a predação intraguilda pode ser uma resposta de um predador intraguilda superior perante presas intraguilda potencialmente perigosas.

No terceiro artigo analisou-se a relação entre a superpredação e os níveis de contaminação por mercúrio nas penas de um predador de topo generalista, o Bufo-real, e das suas principais presas. A concentração de mercúrio nas penas de Bufo-real aumenta com o aumento da percentagem de mesopredadores e diminuição da percentagem de presas herbívoras na sua dieta. Conclui-se assim que a superpredação pode conduzir à acumulação de mercúrio em vertebrados predadores de topo. Apesar dos níveis de contaminação por mercúrio nas populações de Bufo-real estudadas não serem muito elevados, é recomendável a monitorização futura dos efeitos de alterações na composição da dieta deste predador.

No quarto artigo estudou-se o modo como a actividade vocal de uma presa intraguilda, a Coruja-do-mato, é afectada pela presença de um predador intraguilda, o Bufo-real. Observou-se que a actividade vocal da Coruja-do-mato ao anoitecer aumenta com maior luminosidade da lua, uma vez que estas condições facilitam a comunicação visual com indivíduos conspecíficos. A actividade vocal é igualmente mais intensa e começa mais cedo ao anoitecer em situações de maior densidade de vizinhos conspecíficos. No entanto, ao vocalizar mais intensamente a Coruja-do-mato fica mais exposta ao risco de ser detectada pelo Bufo-real. Para avaliar o risco de predação, esta presa intraguilda utiliza as vocalizações de Bufo-real para detectar a presença do predador intraguilda. Como resposta a um maior risco de predação, determinado pela presença e um Bufo-real a cantar, a Coruja-do-mato reduz a sua actividade vocal para a sua localização não ser tão facilmente determinada.

Os estudos realizados no âmbito desta tese permitem traçar várias conclusões gerais sobre as interacções predatórias entre vertebrados predadores de topo com implicações ecologicamente abrangentes. Os fenómenos de superpredação e predação intraguilda em vertebrados predadores de topo e mais particularmente em aves de rapina, eram até há pouco tempo vistos como ocasionais. A primeira conclusão geral é que estas interacções ocorrem na maioria dos ecossistemas onde as aves de rapina de grande porte se encontram no topo das cadeias alimentares. A segunda conclusão é que os fenómenos de superpredação e predação intraguilda nas aves de rapina de grande porte podem ser despoletados pela necessidade de: (1) procurar presas alternativas quando escasseiam as presas base habituais; (2) eliminar competidores com o objectivo de libertar recursos; e (3) eliminar potenciais predadores. É no entanto provável que estes factores actuem conjuntamente no aparecimento destas interacções predatórias. A terceira conclusão aponta para a importância de monitorizar os fenómenos de superpredação e predação intraguilda uma vez que: (1) estas interacções estão associadas à escassez de presas e consequente decréscimo do sucesso reprodutor; e (2) o aumento do consumo de presas de níveis tróficos mais elevados potencia a acumulação de contaminantes persistentes nos predadores de topo. A quarta conclusão diz respeito à importância de avaliar os efeitos comportamentais resultantes do risco de predação em meso-predadores. Muitos mesopredadores são considerados predadores de topo e por isso julga-se não estarem sujeitos aos efeitos da predação. No entanto, mesmo que a frequência de predação seja muito baixa, e não sejam esperados efeitos sobre a densidade, os meso-predadores podem alterar comportamentos de maneira a estarem menos expostos a superpredadores. A redução da actividade vocal é um mecanismo anti-predação utilizado em aves nocturnas de modo a diminuir a sua detecção por superpredadores.

Sabendo que as interacções predatórias entre vertebrados predadores de topo podem afectar a estrutura das comunidades, é importante considerar as suas implicações conservacionistas. O declínio de predadores de topo é responsável pelo desencadear do fenómeno de libertação do meso-predador, já observado em diversos ecossistemas e regiões, e responsável por algumas alterações dramáticas das comunidades onde ocorre. O fenómeno da superpredação pode ser responsável pela promoção da biodiversidade nos ecossistemas em resultado de efeitos do topo para a base da cadeia trófica. No entanto, nalgumas comunidades já profundamente alteradas, o regresso de um superpredador pode levar ao declínio acentuado de espécies sensíveis à superpredação.

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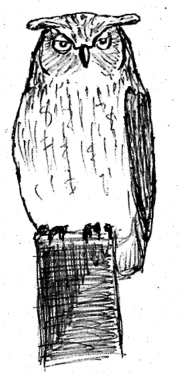

Chapter 1

GENERAL INTRODUCTION

1.1. A framework for lethal interactions among vertebrate top predators

Large vertebrate predators are at the top of both marine and terrestrial food webs. These species are frequently designated as top or apex predators, and generally have none or few species which prey on them. They occupy most ecosystems on earth, from deserts to polar habitats, and many are charismatic species (e.g. large sharks, crocodiles, monitor lizards, large raptors and owls, killer whales, bears, large felids and canids). Their large brains produce elaborate behaviours both as predators and prey, and most species are physically well prepared to injure or kill their prey and competitors.

Interactions among top predators have always interested naturalists and researchers, especially because of the ecological and conservation implications these might have on rare or endangered species and community structure (Schmitz et al. 2000, Heithaus et al. 2008, Sergio et al. 2008). Vertebrate top predators can frequently engage in complex interspecific lethal interactions which have both competitive and predatory components (Polis et al. 1989, Palomares and Caro 1999, Caro and Stoner 2003, Hunter and Caro 2008, Sergio and Hiraldo 2008). Due to this complexity, general theories, models and concepts on interspecific interactions sometimes do not fit interactions among large carnivorous vertebrate species. Scientific literature has some examples where broader meanings have been used so that more complex patterns could be explained by existing concepts.

To study predatory relations in vertebrate top predators it is fundamental to have a clear framework about *interspecific lethal interactions*, that is, interactions between species that end with one of the contenders being killed. Therefore, we exclude all interspecific aggressive interactions aimed at chasing away (defensive agonistic behaviour or mobbing; Pettifor 1990, Garcia and Arroyo 2002, Margalida and Bertran 2005, Mateo and Olea 2007), and not killing a potential predator (and/or a competitor for resources). Scavenging, which can occasionally occur on a dead top predator, is also excluded, although separating scavenging from predation based on the observation of prey remains can sometimes be difficult.

1.1.1. Interspecific killing as an extreme form of interference competition

According with the strict definition gave by Birch (1957) "...competition occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or other in the process". *Interspecific competition* is generally separated in two types, *exploitation competition* and *interference competition* (Birch 1957, Case and Gilpin 1974). In exploitation competition, two species compete for a limited shared resource (e.g. prey, habitat) by its consumption, which eventually ends up in ecological segregation (Case and Gilpin 1974, Schoener 1983). In interference competition a species uses mechanisms (e.g. chemicals, poison, aggression, egg predation, kleptoparasitism) to interfere with a competitor and exclude it from a resource which can be shared or not (Birch 1957, Park 1962, Orians and Willson 1964, Case and Gilpin 1974). Territoriality is perhaps the most common aspect of interspecific interference competition in large vertebrates, and some individuals can defend territories larger than needed from their competitors (Brown 1964, Orians and Willson 1964, Schoener 1968, Brown 1969, Verner 1977, MacLean and Seastedt 1979, Schoener 1983). Another aspect of interspecific interference is kleptoparasitism, a mechanism of encounter interference (Schoener 1983), which is also frequent in large vertebrates (Brockmann and Barnard 1979 and references therein, Jorde and Lingle 1988, Temeles and Wellicome 1992, Creel 2001, Höner et al. 2002, Bertran and Margalida 2004, Siverio et al. 2008).

Interference competition scenarios can be characterized by the fact that: (1) such relationships can be mutual or unilateral, in this last case one species is dominant on a subordinate one (Case and Gilpin 1974, Schoener 1983); (2) larger species are often superior than smaller ones (Persson 1985); (3) interspecific competition tends to be stronger when ecological overlap is greater (Hutchinson 1959, Schoener 1974, Schoener 1983); (4) interference competition has a cost associated with the time and energy used to free up resources by excluding competitors, which is a fixed cost if the species has developed permanent morphological or physiological modifications, or a density-dependent cost if the species has developed behavioural mechanisms (Case and Gilpin 1974); and above all, (5) interference competition should only emerge when it increases fitness (Case and Gilpin 1974).

Scientific literature is full of examples of interspecific interference competition in vertebrates, observed in field and laboratory experiments, but also in observational studies (Carothers 1986, Minot and Perrins 1986, Bolger and Case 1992, Ziv et al. 1993, Kennedy and White 1996, Martin et al. 1996, Marvin 1998, Hansen et al. 1999, Eccard and Ylönen 2002; see also references in Schoener 1983). Although, it has been suggested that competition should be particularly relevant in predators (Hairston et al. 1960, Menge and Sutherland 1976), including birds of prey (Lack 1946), doubts seem to remain about how frequent and important the mechanisms of interspecific interference competition are in ecological systems (Hairston et al. 1960, Schoener 1983, Connell 1983, Sih et al. 1985).

Vertebrate top predators (alone, in pairs, or large social systems) defend large, multi-purpose territories, and their home range size depends mostly on prey abundance (McNab 1963, Schoener 1968, Verner 1977). Most vertebrate top predators are well equipped with teeth, claws, large size or great swiftness, and all these attributes can be effectively employed in interference competition, namely in *interspecific aggression*. These aspects facilitate the engaging in extreme and lethal forms of interspecific interference competition, that is, *interspecific killing*. In agreement, there are many examples of interference interactions in raptors and mammalian carnivores, several of which reaching the killing extreme (e.g. Kostrzewa 1991, Tannerfeldt et al. 2002, Hakkarainen et al. 2004, Vrezec and Tome 2004, Donadio and Buskirk 2006, St-Pierre et al. 2006, Berger and Gese 2007, Martínez et al. 2008, Trewby et al. 2008, Brambilla et al. 2010; reviews in Eaton 1979, Palomares & Caro 1999, Linnel and Strand 2000, Caro and Stoner 2003, Hunter and Caro 2008, Bitetti et al. 2010, Vanak and Gompper 2010). The possible motivations behind interspecific killing among vertebrate top predators are: (1) eliminating competition and free up resources; (2) removing a potential source of mortality; and in both these cases the victim generally should not be consumed; (3) obtaining food, and in this case the victim is consumed; and (4) combinations of the three previous motivations (Eaton 1979, Polis et al. 1989, Palomares and Caro 1999, Sunde et al. 1999, Serrano 2000). However, when interspecific killing as an extreme form of interference competition is followed by consumption of the victim, this interaction should then be more accurately designated as *intraguild predation* (Polis et al. 1989).

1.1.2. Intraguild predation

Intraguild predation (IGP) was first defined by Polis et al. (1989) as a combination of competition and predation, where a species kills and eats another that is a potential competitor. Besides the energetic gain for the intraguild (IG) predator, there is an additional benefit from reducing exploitative and interference competition in two distinct ways: density-mediated effects (direct killing) and trait-mediated effects (predation risk) on the IG prey (Polis and Holt 1992, Creel and Christianson 2008). IGP is also considered to be a special case of omnivory, defined by Pimm and Lawton (1978) in a food web theory context as the feeding by one species on resources at different trophic levels, but with the singularity that the predator and prey share a resource (Polis and Holt 1992). Since the seminal work of Polis et al. (1989), the theoretical background of the intraguild predation concept has largely increased (some relevant references are: Holt and Polis 1997, Křivan 2000, Heithaus 2001a, Mylius et al. 2001, Revilla 2002, Okuyama and Ruyle 2003, Briggs and Borer 2005, Ives et al. 2005, Amarasekare 2006, 2007a, 2007b, 2008, van de Wolfshaar et al. 2006, Vandermeer 2006, Borer et al. 2007, Daugherty et al. 2007, Holt and Huxel 2007, Kimbrell et al. 2007, Takimoto et al. 2007, Okuyama 2008, Drury and Lodge 2009, Aunapuu et al. 2010, Urbani and Ramos-Jiliberto 2010). In addition, many researchers have also invested in testing IGP in a variety of taxonomic groups, both in laboratory and field experiments, but also in observational studies (e.g. Morin 1999, Gerber and Echternacht 2000, Finke and Denno 2005, Katano et al. 2006, Young et al. 2006, Barton and Roth 2008, Salo et al. 2008, Mooney et al. 2010; see also review in Ritchie and Johnson 2009). To give a general panorama of scientific publications referring the intraguild predation concept since Polis et al. (1989), we present in table 1 the number of articles containing both words “intraguild predation” wherever in the text, published in some of the most relevant peer-reviewed scientific journals covering the scope of animal ecology, and also in some publishers.

Table 1. Number of scientific articles containing both words "intraguild predation" wherever in the text, published until October 2010 in some of the most relevant journals and publishers in ecology.

PEER-REVIEWED SCIENTIFIC JOURNAL	No. articles
American Naturalist	46
Animal Behaviour	37
Basic and Applied Ecology	22
Behavioral Ecology	29
Behavioral Ecology and Sociobiology	7
Biological Conservation	25
Biological Control	146
Conservation Biology	12
Ecography	17
Ecological Modelling	35
Ecology	202
Ecology Letters	65
Journal of Animal Ecology	85
Journal of Theoretical Biology	21
Nature	13
Oikos	103
Oecologia	111
Population Ecology	18
Proceedings of the National Academy of Sciences	13
Proceedings of the Royal Society B	22
Theoretical Population Biology	14
Trends in Ecology and Evolution	31
TOTAL	**1074**
PUBLISHER	
BioOne Online Journals	339
Cambridge Journals	98
Chicago Journals	46
Ecological Society of America	254
Elsevier	530
Informa World	20
Royal Society Publishing	41
Springer	573
Wiley-Blackwell	852
TOTAL	**2753**

Intraguild predation is a common and widespread interaction in nature, but its frequency tends to be lower at the highest trophic levels i.e. top carnivores (Polis et al. 1989, Arim and Marquet 2004). Therefore, IGP has been more studied in invertebrates, but also because of the logistic constraints imposed by many field studies focusing on vertebrate species. Intraguild predation is an interspecific lethal interaction with the potential to influence and shape the structure and dynamics of communities (Polis et al. 1989, Arim and Marquet 2004, Ritchie and Johnson 2009). In agreement, studies in vertebrates have shown that this complex trophic interaction can play a crucial role in structuring communities, via the suppression or release of either the mesopredator (intraguild prey) or the shared non-guild prey (Palomares et al. 1995, Crooks and Soulé 1999, Fedriani et al. 2000, Sergio et al. 2003, Baum and Worm 2004, Prugh et al. 2009, but see also Vance-Chalcraft et al. 2007). Furthermore, intraguild predation in vertebrates seems to be most frequent in systems with generalist predators which are larger than their IG prey (Polis et al. 1989, Palomares and Caro 1999, Sergio and Hiraldo 2008).

Intraguild predation in birds of prey has long interested researchers (e.g. Baumgartner 1939, Herrera 1973, Mikkola 1976, Insley and Dugan 1973, Levin et al. 1977, Rudolph 1978, Klem et al. 1985, Real and Mañosa 1990, Rohner and Doyle 1992, Tella and Mañosa 1993, Bosch et al. 2007), but despite this and being a widespread phenomenon in raptor assemblages, it has been frequently overlooked until recently (Sergio and Hiraldo 2008). The emergence of studies of IGP in birds of prey and owls in the last years has shown that this complex interaction also plays a role in shaping raptor assemblages (Hakkarainen and Korpimäki 1996, Gainzarain et al. 2000, 2002, Krüger 2002, Petty et al. 2003, Sergio et al. 2003, 2004, 2007, Hakkarainen et al. 2004, Brambilla et al. 2006, Zuberogoitia et al. 2008).

As in interspecific killing, we can identify different motivations in the intraguild predator: 1) just food acquisition; 2) removing a competitor while obtaining energy; 3) removing a predator while obtaining energy; 4) combinations of the three previous motivations (Polis et al. 1989, Sunde et al. 1999, Serrano 2000).

1.1.3. Assessing guild membership

The concept of intraguild predation (Polis et al. 1989) is intrinsically linked to the concept of guild, first defined by Root (1967) as a group of species exploiting the resources in a similar way, without any reference to the taxonomic position of the organisms involved. By adding that the limits of guild membership should be somewhat arbitrary, Root (1967) induced some of the existing flexibility of the term guild used in the following studies (Simberloff and Dayan 1991). Since then, the most common meaning for guild was that of species sharing the same food resource (Simberloff and Dayan 1991). Most studies attempting to define the structure of vertebrate guilds have only focused on well-defined taxonomic and spatially restricted groups of species; moreover, many of these studies frequently use only food-niche overlap to define trophic guilds, missing other possible shared resources and ways by which species might compete (e.g. Herrera and

Hiraldo 1976, Pianka 1980, Jaksić et al. 1981, Jaksić 1988, Jaksić and Delibes 1987, Marti et al. 1993, Muñoz and Ojeda 1998, Zapata et al. 2007). However, defining a guild structure accurately is a demanding task, which requires detailed information on the biology of many species (Pianka 1980, Mac Nally 1983, Simberloff and Dayan 1991). Despite the existence of several quantitative methods for guild assignment, there is always some ambiguity because the level of clustering is set arbitrarily by the researcher (Jaksić 1988, Simberloff and Dayan 1991, Fedriani and Travaini 2000, Mac Nally et al. 2008). The difficulty in defining guild composition can be illustrated by European vertebrate top predators: although considerably well studied, we could not find a reliable work defining guild membership for these species. In addition, local conditions may introduce variations in guild structure, i.e. the same group of species may or may not compete depending on the ecological scenario in which they are interacting (e.g. Herrera and Hiraldo 1976; Jaksic 1988). Polis et al. (1989) were well aware of the limitations in finding an unequivocal definition of guild, and hence suggested a broader (colloquial) meaning of guild to be used in the intraguild predation concept: a group that includes all taxa in a community using similar resources (food or space) and therefore competing, regardless of differences in resource acquisition tactics and the level of overlap. Not surprisingly, most studies of intraguild predation in vertebrates include few species (generally 2 or 3), for which biological information is good enough to guarantee that strong competition occurs between them (e.g. Fedriani et al. 2000, Sergio et al. 2007, Hass 2009). Consequently, we observed that intraguild predation at a wider community scale has very seldom been analysed.

Therefore, how to name those interactions in which both predator and consumed prey are top order predators but not competitors, that is, they do not belong to the same guild? As an example we could mention the predation of eagle owls *Bubo bubo* on barn owls *Tyto alba* in Portugal (Lourenço 2006), both species are usually considered as top predators, but show almost no overlap in resource use (Herrera and Hiraldo 1976). These type of cases fall out of the scope of the strict definition of intraguild predation, and they are not extreme forms of interference competition as well. This interaction could simply be named predation, but are there any reasons to use another designation?

1.1.4. Defining superpredation

In ecology, the terms *top predator*, *top-order predator*, *alpha predator* and *apex predator* are used as synonyms, to designate species at the top of their food chain (or very near the top), generally above trophic level 3 or 4 (secondary or tertiary consumers), and that are virtually not preyed by any other animal (Fretwell 1987, Estes et al. 2001, Essington et al. 2006, Sergio et al. 2008, Hayward and Somers 2009, Prugh et al. 2009, Ritchie and Johnson 2009). The term superpredator, is also rather common in scientific literature (Smouse 1981, Rinaldi and Muratori 1992, Compagno et al. 1997, De Feo and Rinaldi 1997, Bosh et al. 2007, Berryman and Kindlmann 2008, Davis et al. 2011), being mostly applied with a similar meaning of top predator, and often defined as a predator that eats other predators (Courchamp et al. 1999, Moleón and Gil-

Sánchez 2003, Russel et al. 2009).

Despite intensive search, we could not find any formal definition in ecological context for the term superpredation, seldom used in scientific publications. Southern (1947) used superpredation to address the killing of sparrowhawks *Accipiter nisus* by goshawks *Accipiter gentilis*. Fauth (1990) used superpredation with the meaning of "predators eating other predators" in a freshwater food web involving amphibians and crayfish. Ruiz-Olmo and Marsol (2002) reported the predation of fish eating birds by otters *Lutra lutra* and defined superpredation as "one predator killing competing predators, which may contribute to their regulation and thereby to the conservation or increase in the stock of available prey". Tannerfeldt et al. (2002) used superpredation as synonym of intraguild predation by red fox *Vulpes vulpes* on arctic fox *Alopex lagopus*. Malo et al. (2004) used superpredation referring to wildcats *Felis silvestris* preying on other mammalian carnivore species.

Considering the above mentioned uses of these terms, we suggest a formal definition for superpredation as ***the act performed by top predators of killing and consuming high-order predators (either top predators or meso-predators), independently of sharing or not resources, and thus being competitors or not***. Moreover, these prey species (high-order predators) should belong at least to trophic level 3 (secondary consumers/primary carnivores) or above, and generally should not represent an important part of the diet of the superpredator. It is important to mention that superpredation occurs at the top end of food chains, which means that superpredators might be at trophic level 4 in short food chains and reach up to trophic level 5 or more in long food chains (Post 2002, Essington et al. 2006).

1.1.5. Differences and similarities in the concepts

The three previously mentioned concepts (interspecific killing, intraguild predation, and superpredation) can be used to designate lethal interactions among vertebrate top predators. But, despite some similarities, these concepts do not overlap completely in their meanings, and thus we find particularly useful to stress the differences and nuances between them, aiming a better use of these concepts when studying interactions among vertebrate top predators (fig. 1).

[a] **Consumption of the kill**. The concept of interspecific killing does not specify if the victim was consumed or not, while intraguild predation and superpredation always have implicit the consumption of the victim. Therefore, IGP and superpredation can not be applied when the victim is not consumed. Accordingly, the intraguild predation concept includes all those cases of interspecific killing where consumption occurs.

[b] **Preying on a top predator**. The superpredation concept includes all those cases of intraguild predation involving high-order predators. Nevertheless, the intraguild predation concept includes predation among competitors which are not top predators (e.g. a secondary consumer that eats a primary consumer (herbivore) with which it shares a resource).

[c] **Killing a competitor**. Both intraguild predation and interspecific killing as a form of interference

competition imply that the victim is a competitor, while in superpredation the victim might be a competitor or not. All those cases of superpredation among competitors are also intraguild predation events.

[d] **Interfering with a competitor**. In intraguild predation and interspecific killing with a competitive context the killer is interfering with a competitor, limiting its access to shared resources. This interference mechanism extends to superpredation among competitors, which as previously mentioned might also be designated as intraguild predation among top predators.

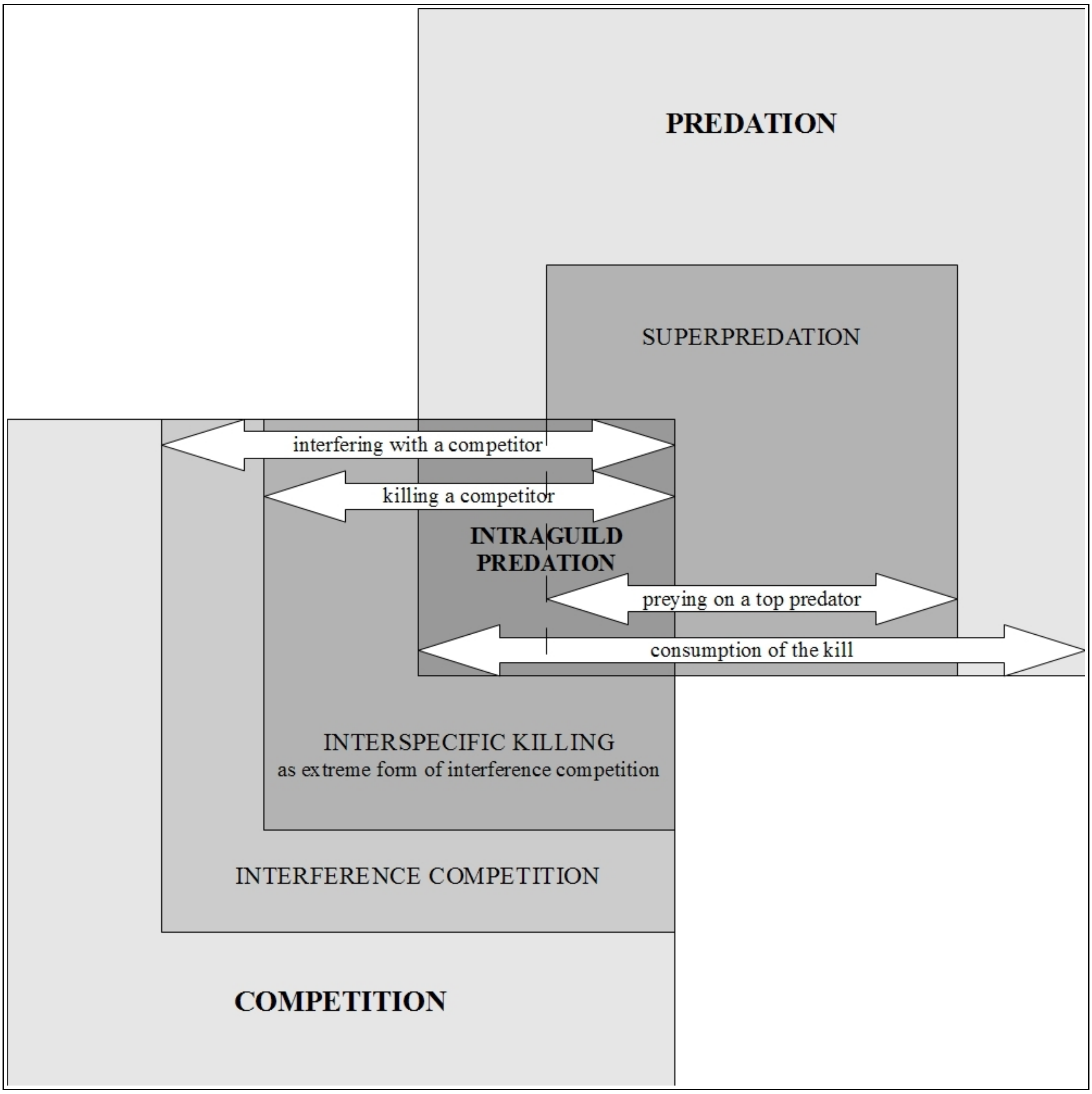

Figure 1. Differences and similarities in lethal interspecific interactions (see text for the explanation of the concepts).

Considering the existence of the terms predation, interspecific killing and intraguild predation, how useful is the superpredation concept in the study of lethal interactions among vertebrate top predators? We gathered the following arguments demonstrating the usefulness of the superpredation concept.

[a] The predation on a top predator causes different effects than the predation on prey from lower trophic levels, therefore superpredation can be employed in the study of these particular effects.

[b] Superpredation can be used in a broader sense than intraguild predation, to include all predatory interactions among top predators (e.g. mammalian carnivores, raptors, sharks and cetaceans), as this approach is common in scientific literature (Palomares and Caro 1999, Heithaus 2001b, Caro and Stoner 2003, Glen and Dickman 2005, Hunter and Caro 2008, Sergio and Hiraldo 2008).

[c] Accurately assigning guild membership can often be very demanding, and choosing the level of clustering can be subjective. Hence, also the boundaries separating predation from intraguild predation can be subjective as well. The superpredation concept does not depend on the guild concept or the need to define overlap in resource use, thus being easier to use, in relation to intraguild predation, when information on competition is difficult to obtain.

[d] Competition between species can show spatial variation, which means that the same two species may compete in some regions and not in others. Hence, the concept of superpredation might be more spatially flexible than the concept of intraguild predation.

[e] Compared with interspecific killing among top predators (e.g. raptors, carnivores), superpredation can be used as a less ambiguous concept concerning the consumption (or not) of the victim.

1.2. Objectives

The broad framework of this thesis is centred on the role of top predators in ecosystem functioning and community structure. In addition, many top predators are also considered key elements in the management of natural areas. The main focus are the predatory interactions of large raptors and owls with other top predators, and the direct and indirect effects resulting from these complex relations. Two concepts in ecology were the basis of this thesis: intraguild predation and superpredation. The main superpredator model species is the eagle owl, and three large diurnal raptors are also studied. Most of the work was centred in Mediterranean habitats, but in chapter 2 it was also extended to the European scale.

This thesis addresses the following specific questions:

1) Which mesopredators represent frequent prey, and what is their energetic role in the trophic ecology of avian superpredators?

2) Why do superpredators kill mesopredators: to obtain food, to remove competitors, to remove predators, or is it a complex interaction of these factors?

3) How do prey abundance and landscape change influence the emergence of intraguild predation and superpredation by large raptors?

4) Does superpredation have negative effects on superpredators associated with increasing the consumption of prey from higher trophic levels?

5) How does intraguild predation risk influence behavioural traits in mesopredators?

Chapter 2 compiles published diet studies to analise the superpredation patterns of four large European raptors, and therefore address questions 1, 2, 3, and 4. **Chapter 3** focus on a specific hypothesis justifying why superpredators kill mesopredators (question 2). In **chapter 4** superpredation is studied as a potential means of mercury biomagnification caused by the increase in the consumption of prey from higher trophic levels (question 4). Finally, **chapter 5** addresses question 5 by studying the behavioural trade-offs of an intraguild prey when exposed to intraguild predation risk.

1.3. Diurnal and nocturnal raptors as model species

1.3.1. Superpredators

This study is focused on four large raptors that are on the top of food webs in European ecosystems: Goshawk *Accipiter gentilis* (Linnaeus, 1758), Golden Eagle *Aquila chrysaetos* (Linnaeus, 1758), Bonelli's Eagle *Aquila fasciata* (Vieillot, 1822), and Eagle Owl *Bubo bubo* (Linnaeus, 1758). These are also emblematic species and of conservation concern, benefiting from having a large amount of studies focusing their trophic ecology and interspecific relations, widely across Europe.

The Goshawk is a large hawk (500 – 2100 g). This diurnal raptor shows a widespread distribution across Europe, having the Mediterranean basin as southern limits and Scandinavia as northern limits (Cramp et al. 1977-94). It is resident throughout most of its European range (Rutz et al. 2006). This species is mainly associated with mature forests, selecting tall trees for nesting (Penteriani 2002). Goshawks are generalist predators that will feed on the most abundant prey, most frequently medium-sized birds (partridges, grouse, waders, pigeons, corvids, thrushes and starlings) and mammals like squirrels, rabbits, hares and dormice (Penteriani 1997, Rutz and Bijlsma 2006, Rutz et al. 2006).

The Golden Eagle is a large powerful eagle (2800 – 6700 g). It occurs in most European countries, although being scarce from France to Poland (Cramp et al. 1977-94). Golden eagles are mostly resident, and breed in remote areas, with low human presence, like mountains and upland forests (Carrete et al. 2000, Pedrini and Sergio 2001, Watson and Whitfield 2002). Nests are built in cliffs or large trees (Cramp et al. 1977-94). The diet of this raptor is mainly composed by medium-sized birds and mammals, such as grouse, ducks, gulls, corvids, foxes, martens, rabbits and hares; but it will often feed on carrion (Delibes et al. 1975, Tjernberg 1981, Marquiss et al. 1985, Johnsen et al. 2007).

The Bonelli's Eagle is a large raptor (1500 – 2500 g), which, in Europe, occurs along the Mediterranean from Portugal to Turkey (Cramp et al. 1977-94). This bird of prey occupies several habitats including woodlands, shrublands and agricultural fields, generally avoiding human presence (Cramp et al. 1977-94). Nests are generally built in cliffs (Ontiveros 1999, Carrete et al. 2002), but in Southern Portugal the species breeds mostly in trees (Palma et al. 2006). Bonelli's Eagle feed mainly on rabbits, pigeons, partridges and corvids (Palma et al. 2006, Moleón et al. 2009).

The Eagle Owl is the largest European owl (1500 – 4200 g), and occurs in most countries (Cramp et al. 1977-94). It occupies several habitats, although mostly associated with areas with rocks, cliffs or mature trees, which are used for nesting (Penteriani et al. 2001, Marchesi et al. 2002, Martínez et al. 2003). Eagle owls have a wide food spectrum going from small prey, such as voles and mice, to medium-sized prey, such as partridges, rabbits and hares (Mysterud and Dunker 1983, Martínez and Zuberogoitia 2001, Penteriani et al. 2002, Lourenço 2006). This owl was the superpredator species used to study the predatory interactions with avian mesopredators more in particular.

1.3.2. Mesopredators

For the study of predatory interactions between the Eagle Owl and avian mesopredators, we considered four diurnal raptor species and one owl species as models: Black Kite *Milvus migrans* (Boddaert, 1783), Red Kite *Milvus milvus* (Linnaeus, 1758), Common Buzzard *Buteo buteo* (Linnaeus, 1758), Booted Eagle *Aquila pennata* (Gmelin, 1788) and Tawny Owl *Strix aluco* Linnaeus, 1758. These mesopredator species were selected because they coexist with eagle owls in our study areas located in Southwestern Iberian Peninsula.

The Black Kite is a medium-sized raptor (800 – 850 g), which occurs in the Iberian Peninsula only during its breeding season (Cramp et al. 1977-94). Black kites are highly generalist in terms of food, eating carrion, insects, fish, waterfowl and rabbits (Veiga and Hiraldo 1990, Viñuela and Veiga 1992). Previous studies have shown that habitat selection and breeding success in this mesopredator can be affected by the presence of eagle owls (Sergio et al. 2003).

The Red Kite is a medium-sized raptor (900 – 1250 g), which occurs during all year in the Iberian Peninsula, however the wintering population is much larger than the breeding one (Cramp et al. 1977-94). Red kites are also generalist predators and their diet is similar to that of black kites (Blanco et al. 1990, Veiga and Hiraldo 1990).

The Common Buzzard is a resident medium-sized raptor (750 – 1000 g), and one of the most common birds of prey in the Iberian Peninsula (Cramp et al. 1977-94). Buzzards show a high ecological plasticity being generalist predators, that can feed on insects, reptiles, small birds, small mammals and rabbits (Bustamante 1985, Mañosa and Cordero 1992, Zuberogoitia et al. 2006). Population density in common buzzards can be affected by the abundance of eagle owls (Sergio et al. 2005).

The Booted Eagle is a medium-sized raptor (700 – 975 g) that occurs in the Iberian Peninsula during the breeding season (Cramp et al. 1977-94). The diet of this diurnal raptor is mainly composed by lizards, small birds, small mammals and rabbits (Veiga 1986, Nevado et al. 1988, García-Dios 2006).

The Tawny Owl is a medium-sized nocturnal raptor (400 – 450 g), and one of the most common owls in Europe, being resident throughout most of its range (Cramp et al. 1977-94). Tawny owls feed mostly on rodents and small birds (López-Gordo 1974, Villarán 2000). Sergio et al. (2007) have demonstrated that eagle owls can affect habitat selection in tawny owls.

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Chapter 2

SUPERPREDATION PATTERNS IN FOUR LARGE EUROPEAN RAPTORS

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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 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 to 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 been seldom 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 less often has the superpredator assumed a central role. Namely, 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. 1977-94).

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: i) the number of individuals consumed for all prey groups; or ii) 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 Ed. 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. (1977-94), MacDonald and Barret (1993), and also the diet studies here included.

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 (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, 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 the 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, 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 heterocedasticity, a common problem when analysing several studies (Gurevitch and Hedges 1999), was present in our data sets, 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 eleven 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).

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 mesopredators 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 in 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.

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.

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 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.

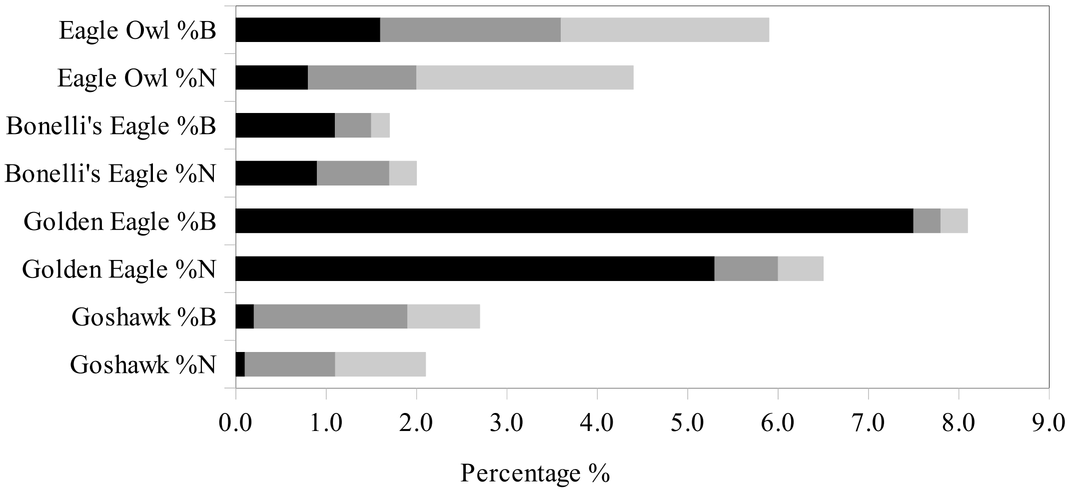

Figure 1. Average numeric percentage (%N), average biomass percentage (%B), of mammalian carnivores (dark), diurnal raptors (grey), and owls (light grey) in the diet of the Goshawk *Accipiter gentilis*, Golden Eagle *Aquila chrysaetos*, Bonelli's Eagle *Aquila fasciata*, and Eagle Owl *Bubo bubo* in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

Objective B: spatio-temporal patterns in superpredation

The LMM showed no evidence of temporal variation in the percentage of mesopredators (β = -0.02, t = -0.92, P = 0.359; see S5 in ESM). Also, we found no longitudinal (β = 0.00, t = 0.11, P = 0.915) or latitudinal spatial trend (β = 0.01, t = 0.23, P = 0.822) in the percentage of mesopredators. The autocovariate had a significant positive effect (β = 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 (β = -0.87, t = -3.99, P = 0.000; see S5 in ESM), rabbits and hares (β = -0.71, t = -3.23, P = 0.002), partridges and grouse (β = -0.63, t = -2.69, P = 0.009), and pigeons and doves (β = -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 (β = 0.08, t = 3.00, P = 0.003) and to more diversified diets (β = 12.79, t = 5.97, P = 0.000). The autocovariate had a positive significant effect (β = 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 as well, 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: $\beta = 0.77$, $t = 3.22$, $P = 0.003$).

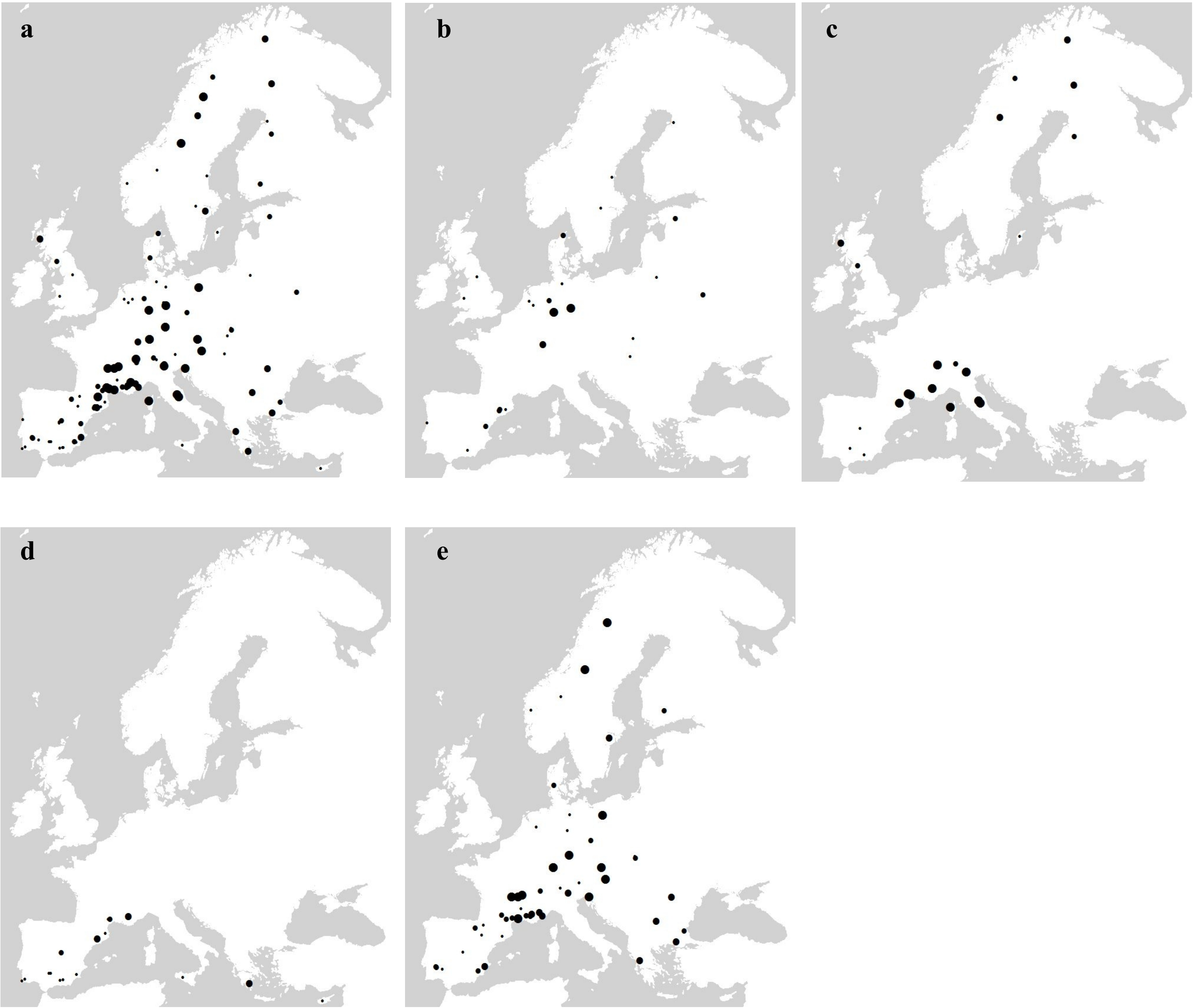

Fig. 2 Mapping of the diet samples with the percentage of mesopredators (*circles* correspond to smaller to larger to four classes of mesopredators percentage: 0.00-2.00. 2.01-3.93, 3.94-6.00, 6.01-21.00%). The value 3.93% was chosen for being the average mesopredators percentage for all the studies (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*.

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 (β = -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 (β = -0.08, t = -1.70, P = 0.10). Areas closer to each other had similar breeding success (autocovariate: β = -0.13, t = -2.12, P = 0.044), but the same effect was not found for population fecundity (β = -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 to predict 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 can not 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, also superpredation 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 predation 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 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: firstly, we could have had a sample size limitation for this particular analysis; secondly, we used diet at a large-scale, and perhaps superpredation trends could have been easier to detect by comparing diet at a territory-scale; thirdly, 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); fourthly, 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 straight-forward 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 relation found between the consumption of mesopredators and top predator's breeding performance, also points out 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 understand more 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 abundances, 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 has 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, allowing 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: firstly, several studies did not present complete lists of prey numbers or frequencies; secondly, sample sizes showed a large variation. Therefore, we strongly suggest that future diet studies should include complete prey lists (namely as on-line only supplementary material), enabling future reviews with larger sample sizes.

Mesopredators might also be consumed by raptors as carrion, and namely 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 on the relations 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 this interaction 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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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.

Raptors (Order Falconiformes)	Goshawk *Accipiter gentilis* (21 studies) F (%)	A (%)	Golden Eagle *Aquila chrysaetos* (18 studies) F (%)	A (%)	Bonelli's Eagle *Aquila fasciata* (16 studies) F (%)	A (%)	Eagle Owl *Bubo bubo* (44 studies) 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.

	Goshawk *Accipiter gentilis* (21 studies)		Golden Eagle *Aquila chrysaetos* (18 studies)		Bonelli's Eagle *Aquila fasciata* (16 studies)		Eagle Owl *Bubo bubo* (44 studies)	
Owls (Order Strigiformes)	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.

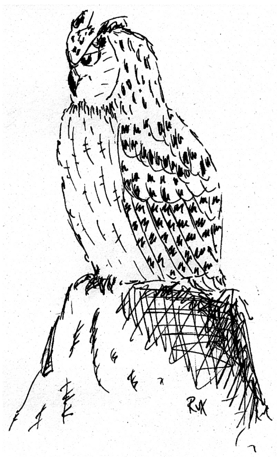
	Value (β)	SE	*df*	*t*-value	*P*-value (*t*)
Intercept	46.630	65.678	35	0.710	0.482
Rabbits	0.007	0.014	35	0.515	0.610
Year	-0.023	0.033	35	-0.706	0.485
Autocovariate	0.780	0.242	35	3.225	0.003
Species (random effect)		SD (intercept)		SD (Residual)	
		0.000		0.582	
Variance function Structure: Power of 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)		SD (Residual)	
		0.585		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)		SD (Residual)	
		0.495		0.298	
Variance function Structure: Power of variance covariate		Formula: fitted values		Parameter estimates: 1.220	



Chapter 3

KILL BEFORE BEING KILLED: AN EXPERIMENTAL APPROACH SUPPORTS THE PREDATOR REMOVAL HYPOTHESIS AS A DETERMINANT OF INTRAGUILD PREDATION IN TOP PREDATORS

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Kill before being killed: an experimental approach supports the predator removal hypothesis as a determinant of intraguild predation in top predators

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Abstract Intraguild predation (IGP) has been explained in terms of competitor-removal, food-stress and predator-removal hypotheses. Only the first two hypotheses have been fairly well studied. To test the predator-removal hypothesis as a main force determining IGP in avian predators, we performed a field experiment to simulate the presence of an IG predator (eagle owl *Bubo bubo* dummy) in the surrounding of the nests of four potential IG prey (black kite *Milvus migrans*, red kite *Milvus milvus*, booted eagle *Aquila pennata* and common buzzard *Buteo buteo*). To discard the possibility that an aggressive reaction towards the eagle owl was not related to the presence of the IG predator, we also presented a stuffed tawny owl *Strix aluco*, which is a potential competitor but cannot be considered an IG predator of the studied diurnal raptors considered in the experiment. While almost always ignoring the tawny owl, raptors chiefly showed an interspecific aggressive behaviour towards their IG predator. Our results supported the predator-removal hypothesis: as IG prey may take advantage of the diurnal inactivity of the IG predator to remove it from their territory, IGP behaviour could be the response of IG predator to the potential danger that IG prey represent for them (mainly when they both share the same home range and show temporal asynchrony in their activity rhythms).

Keywords *Bubo bubo*, interspecific aggression, interspecific competition, mobbing, raptors, superpredation

Introduction

Interspecific interactions among vertebrate top predators are often highly aggressive, ending in the killing and sometimes the eating of one of them (Heithaus 2001; Mikkola 1976; Palomares and Caro 1999; Sergio and Hiraldo 2008). Since these intraguild predation (IGP) events are sometimes symmetrical, a top predator can either be the killer or the victim of another top predator (mutual IGP; Polis et al. 1989). Aggressive interactions among vertebrate apex predators, like IGP or superpredation, have been raising increasingly more interest, mainly due to their potential to shape community structure (Crooks and Soulé 1999; Johnson et al. 2007; Schmitz et al. 2000), but also because these are common and widespread behaviours (Caro and Stoner 2003; Palomares and Caro 1999; Sergio and Hiraldo 2008).

The main reasons proposed to explain the evolution of IGP in vertebrate top predators are: (1) active removal of competitors and free up shared prey (competitor-removal hypothesis); (2) obtaining energy in situations of scarce availability of trophic resources (food-stress hypothesis); and (3) direct elimination of a potential killer threatening the top predator or its offspring (predator-removal hypothesis). Some evidences seem to support these hypotheses: the victim is sometimes not consumed (or is only partially eaten); and predatory interactions among top predators are more common when prey is less abundant (competitor-removal hypothesis: Palomares and Caro 1999; Sunde et al. 1999) or after prey populations crash (food-stress hypothesis: Lourenço et al. in press; Serrano 2000; Tella and Mañosa 1993). However, there are still few empirical evidences supporting these three hypotheses, and to our knowledge the predator-removal hypothesis has never been tested before (only risks of mutual predation have been so far explored; Palomares and Caro 1999). Despite increasing interest for the IGP's ecological and behavioural frameworks, there are still many loose ends in the theoretical reasoning and empirical evidences determining and justifying the emergence of IGP, as researchers have mainly been focused on the study of the consequences of IGP rather than its causes (Linnell and Strand 2000; Palomares and Caro 1999; Sergio and Hiraldo 2008).

By simulating the presence of an IG predator (the eagle owl *Bubo bubo*) near the nest site of four of its IG prey (black kites *Milvus migrans*, red kites *Milvus milvus*, booted eagles *Aquila pennata* and common buzzards *Buteo buteo*), we performed a field experiment to test if the counter-strategy behind the predator-removal hypothesis, kill before being killed, could represent one of the factors engendering IGP. The eagle owl represents a useful biological model for testing IGP hypotheses because: it is a quite well studied superpredator in the context of IGP (Lourenço et al. in press; Sergio et al. 2003, 2007); birds of prey show extremely aggressive responses towards eagle owls (Slagsvold 1982; Zuberogoitia et al. 2008); and both the competitor-removal and food-stress hypotheses have recently shown not to fully explain IGP in this top predator (Lourenço et al. in press). Moreover, eagle owls and diurnal raptors may overlap in space, but show asynchrony in temporal rhythms of activity, which represents a favourable scenario to test the predator-removal hypothesis: eagle owls can easily prey on most diurnal raptors, catching them unaware in the darkness (Mikkola 1976), whereas diurnal raptors attack roosting eagle owls or owlets when they detect them in daylight (authors' observations). Although very few cases of predation by diurnal raptors on eagle owls have been published, and only by golden eagle *Aquila chrysaetos* and white-tailed eagle *Haliaaetus albicilla* (Mikkola 1976), smaller raptors have the potential to kill eagle owls and their mobbing behaviour might displace them. In this case, the risks taken to attack (mobbing or attempt to kill) their larger predator may be compensated by the advantage of a safer environment in which to reproduce (i.e. diurnal raptors increase their fitness by removing a potential predator). Therefore, IGP could be the result of the following counter-strategies: (a) diurnal raptors attack eagle owls to avoid being preyed themselves or their offspring during night; and consequently (b) eagle owls carry out IGP to avoid diurnal fatal attacks and potentially dangerous mobbing behaviours, since all those diurnal raptors breeding close to their regular roost or nesting site may represent, during the day, a menace to the nocturnal predator. That is, kill before being killed, the basic motivation behind the predator-removal hypothesis, should represent a simple and obvious factor engendering IGP in top predators.

Materials and methods

Study Area

The study was performed in Doñana National Park, south-western Spain (37º0'N, 6º30'W), a large wetland located in the estuary of the river Guadalquivir. The area is mainly composed of Mediterranean scrublands scattered with cork oaks *Quercus suber*, stone pines *Pinus pinea* woods, as well as small *Eucalyptus* plantations. This region is favourable to test the predator-removal hypothesis because it holds a dense breeding population of raptors (Sergio et al. 2009; Suárez et al. 2000).

Eagle Owl Diet Data

For a potential IG prey, the risk of trying to kill its IG predator, before it has the opportunity to prey on it, is only justified if a real threat of being preyed exists. A way to demonstrate that a potential IG prey is effectively under predation risk is to evaluate its frequency in the IG predator's diet. For this reason, we analysed pellets and prey remains collected between 2005 and 2009 in eight eagle owl territories in the study area. We determined 1277 prey items using bone and feather identification keys and a reference collection (Laboratory of archaeo-sciences, IGESPAR, Portugal).

Experimental Procedure

A way to corroborate the predator-removal hypothesis is to demonstrate that, if a roosting eagle owl is discovered near an active nest of a diurnal raptor, it will be strongly attacked. If we are able to prove that potential IG prey (diurnal raptors) try to kill their most dangerous IG predator (eagle owls), we will achieve a double result supporting the predator-removal hypothesis for both groups. IG prey and predator perform a “killing race” to avoid nocturnal and diurnal fatal attacks, respectively. We simulated a predator-removal scenario by presenting a stuffed eagle owl dummy in 25 different sites (separated at least 500 m) and closer than 500 m (see below) to occupied nests of at least one of the diurnal raptors (27 black kite, 4 red kite, 11 booted eagle and 3 common buzzard nests), during their breeding period (April-June 2009). All trials were carried out when we observed that at least one of the breeders was near its nest. Because the diurnal raptor species involved in the experiment show light sexual dimorphism for both size and coloration, it was impossible to record the sex of individuals. Each trial lasted 30 minutes, and we categorized individual behaviour into two different response types: (1) passive behaviour - the dummy does not provoke any reaction on the breeder that detected it, or after detecting it, the raptor soared several times above the owl, emitted alarm calls, and/or perched close to it; (2) interspecific aggression - the raptor dived towards the dummy without contact or directly attacked the owl, knocking it down with its talons. In the last case, the trial ended immediately after we observed the attack with contact. To discard the possibility that interspecific aggressive behaviours of diurnal raptors were not related to IG predator presence (e.g. attacks were simply the result of an intruder's presence or a predation act), we performed an equal number of trials with a stuffed tawny owl *Strix aluco* dummy using the exact same procedure. The tawny owl is not an IG predator of the diurnal raptors involved in the experiment, but instead it can be seen as a competitor or a prey (Mikkola 1976; Sunde et al. 2003). In Doñana National Park, tawny owls feed mainly on insects and small mammals, and frequently use raptors' nests to breed, overlapping in diet and habitat niches with the studied diurnal raptors (R. F. Lourenço, unpublished data). In the experiment we always used the same two owl dummies, which were placed on a cork base, approximately one meter above the ground. Both dummies were in typical perched position. Tawny and eagle owl dummies were placed in the exact same visible place, facing the same direction. No playback of the owls' calls was employed since we were simulating the presence of a roosting individual near diurnal raptors' nests. The presentation order of eagle and tawny owl dummies was randomized to avoid a training effect (Penteriani et al. 2007), and visits to the same site were made in consecutive days. During the experiment, we avoided disturbing incubating individuals and remained the minimum time required in each site. We placed the dummies as quickly as possible and then controlled the experiment from a distance and hidden inside a car or bushes. Actually, the experiment did not seem to have any negative effect on the raptors involved, as we did not register any nest or territory abandonments.

Statistical Analysis

In a first approach, we considered for each trial if the owl dummy was attacked by any individual of any of the four diurnal raptor species or ignored by all diurnal raptors that detected the dummy. We then used a 2x2 contingency table (Zar 1999) to check if the responses obtained in the trials were independent of the owl dummy used. In a second approach, we considered the 45 encounters of a different individual of diurnal raptor with the eagle owl dummy and the 35 encounters with the tawny owl dummy, obtained in the 25 trials with each dummy. We then checked the effects of the nominal variables: owl dummy (eagle owl, tawny owl), diurnal raptor (black kite, red kite common buzzard, booted eagle), time of day (8:00-11:00, 11:00-14:00, 16:00-20:00), and dummy's distance to raptor's nest (<100 m, 100-300 m, 300-500 m), on observing a passive or an interspecific aggressive response using a generalized linear mixed model (GLMM) fit by the Laplace approximation (Bolker et al. 2008). We used the site where the trial was done as a random factor. Interactions between explanatory variables were tested, although none of them improved the model's AIC. All statistics were performed in R 2.9.2 statistical software (R Development Core Team 2009) with package lme4 (Bates and Maechler 2009).

Results

The eagle owl diet analysis in Doñana showed that diurnal raptors represented in average 3.7 ± 3.8% of the prey (53 diurnal raptors preyed in all eight territories). The average percentages of the four studied diurnal raptors were: black kite 1.6 ± 2.3% (n = 27); red kite: 0.3 ± 0.7% (n = 3); common buzzard: 0.2 ± 0.3% (n = 3); booted eagle: 0.1 ± 0.3% (n = 2).

During the experiment, the eagle owl dummy was attacked in 16 trials (64%) and ignored in the other 9 trials (36%), whereas the tawny owl dummy was mostly ignored (22 trials; 88%) and attacked in only three trials (12%). The contingency table showed that the responses are significantly different between the owl dummies (Chi-square = 12.22, df = 1, p = 0.0005). In the 16 cases of interspecific aggression towards the eagle owl dummy, we registered 11 direct attacks where the diurnal raptor stroke with its talons the head of eagle owl, pulling head or neck feathers and throwing it down the mount. We consider that such attacks would have caused significant injuries or, more generally, the death of a living eagle owl, i.e. the behaviour reflected an intention to harm and not just trying to scare a potential predator. In the remaining five times, the diurnal raptor dived with talons opened without touching the dummy, more like a mobbing behaviour. From the three interspecific aggressions towards the tawny owl dummy, only one consisted of an attack hitting the head, while the other two where mobbing behaviours similar to those observed with the eagle owl dummy.
The time taken from detection to attack with contact with the eagle owl dummy varied from 32 to 1410 seconds (average ± SE = 667 seconds ± 436 seconds; n = 11). The only attack with contact with the tawny owl dummy took 1147 seconds since its detection.

The owl dummy species was the only significant variable in the GLMM, with diurnal raptors showing a higher frequency of aggressive responses in the presence of the eagle owl dummy (β = -2. 296, SE = 0.72, z = -3.17, P = 0.002). In Figure 1 we show the responses of each diurnal raptor species to the two owl dummies.

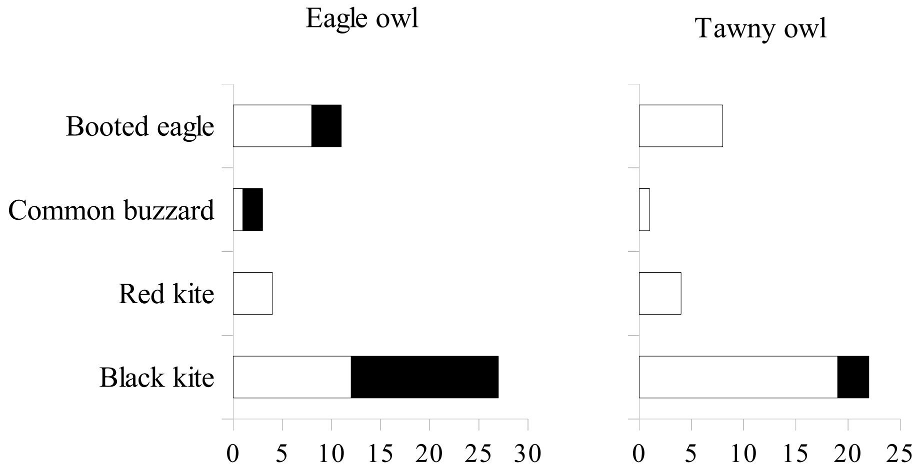

Figure 1. Number of behavioural responses (white: passive behaviour; black: interspecific aggression) obtained for the four species of diurnal raptors when faced with eagle owl (n = 45 interactions; in 25 trials) and tawny owl dummies (n = 35 interactions; in 25 trials).

Discussion

We presented here direct empirical evidence which supports the reduction of predation risk as one of the possible main causes of IGP in vertebrate predators. The diet analysis of eagle owls in Doñana showed that diurnal raptors were frequently consumed, taking into account the known patterns of IGP of eagle owls (Lourenço et al. in press). Therefore, diurnal raptors should easily perceive eagle owls as their potential predators (Sergio et al. 2003). The results of our field experiment showed a high attack frequency (mobbing) and a considerable risk of serious injury or death for a top predator as the eagle owl, when detected during the day by its potential IG prey (i.e. diurnal raptors). This strong interspecific aggressiveness is also well known by researchers using live eagle owls to trap diurnal raptors (Zuberogoitia et al. 2008). Thus, one encounter should perhaps be enough for an eagle owl to perceive large and medium-sized diurnal raptors as very aggressive mobbers and potential predators. Accordingly, we can suggest that: (1) because diurnal raptors may take advantage of the diurnal inactivity of eagle owls to try to remove one of their principal predators, (2) then eagle owls would benefit from removing diurnal raptors because these are potential predators as well, when sharing the same home range. Such a lethal relationship may be exacerbated in high density conditions of the mutual IG predators, like in Doñana National Park, where there might be a lower availability of enemy free space (predators and competitors) and where species share the nesting habitats (in this area eagle owls often breed in nests of diurnal raptors, Penteriani et al. 2008).

In our opinion, the fact that the tawny owl dummy (representing a competitor but not a predator of diurnal raptors) caused very few aggressive responses, compared to the eagle owl dummy, represents a good evidence of this experiment supporting the predator-removal hypothesis. If the aggressive response of IG diurnal raptors was only triggered by the will to remove a competitor, we should have found a similar frequency of attacks on eagle and tawny owl dummies, or perhaps, more attacks to the tawny owl, since it is, supposedly, an easier species to subdue than eagle owls. Thus, the competitor-removal hypothesis seems to fail in explaining the observed aggressive responses of diurnal raptors towards the eagle owl dummy. The IGP attempt of diurnal raptors on eagle owls seems mostly the result of extreme mobbing or brood defence behaviours.

IGP predation in large vertebrates (carnivores and raptors) is usually asymmetrical and size-based, and it has been mainly seen as an extreme form of interference competition (Palomares and Caro 1999; Ritchie and Johnson 2009; Sergio and Hiraldo 2008; Sunde et al. 1999). In this context, the IG predator is granted two main advantages: the removal of a competitor and an energetic input (Polis et al. 1989). The eagle owl is more powerful than the diurnal raptors we considered in this study and, thus, this interaction is prone to be asymmetrical. This is perhaps the most common outcome, as diurnal raptors are frequently preyed by eagle owls, while the opposite is anecdotal (Lourenço et al. in press; Mikkola 1976). But still, as we found in this study, diurnal raptors are very aggressive towards eagle owls, feeding back this interaction into a possible age-structured mutual IGP scenario, even if predatory events would suggest an asymmetrical phenomenon. Although we do not exclude the additional effects of the competitor-removal and food-stress hypotheses, our results represent the first, direct evidence supporting the possibility that IGP by eagle owls on diurnal raptors might be triggered by the predator-removal hypothesis (they identify a potential predator, not a competitor).

The activity rhythms of owls and diurnal raptors show a short overlapping period, and despite strong exploitative competition, their different habits may prevent actual interference competition to be frequent (Carothers and Jaksic 1984; Jaksic 1982; Kronfeld-Schor and Dayan 2003). The competitor-removal hypothesis assumes that the IG predator uses some behavioural mechanism to perceive the IG prey as a competitor (e.g. for food, breeding site, shelter; Serrano 2000). However, the behavioural perception of an exploitative competitor is less probable than the obvious identification of an interference competitor as an enemy (Krüger 2002). Moreover, as we observed in this experiment, interference competition interactions between these species might probably result in killing or predation attempts (see also Krüger 2002), being most likely that diurnal raptors identify eagle owls (and vice-versa) as IG predators rather than as competitors. Also, considering the possibility that a species could be both seen as competitor and predator, then the release from a potential killer should bring more advantages and more immediate to IG prey's individual fitness than eliminating a competitor (Hakkarainen and Korpimäki 1996; Krüger 2002; Sih et al. 1985). Thus the predator-removal could be a stronger behavioural mechanism inducing IGP than competitor-removal.

The need to remove a potential predator does not exclude the possibility that IGP patterns could also be the result of IG prey's capacity to actively avoid those areas where the IG predator can be most frequently found, and therefore where predation risk is higher (Durant 1998; Fedriani et al. 1999; Hakkarainen et al.

2004; Krüger 2002; Sergio et al. 2003, 2007). In fact, this would often be the best option for the "weakest" competitor, the diurnal raptors in our study. It is expected that when the cost of obtaining information about predation risk is low and when the cues used to assess predation risk are reliable (Harvell 1990), IG prey might have the possibility to avoid a direct confrontation with their IG predator, and thus may actively select breeding or hunting areas less frequented by it (Durant 1998, Sergio et al. 2007). But when competition for space is high, direct confrontation with the IG predator could be the only option available. In this case, the predator-removal hypothesis could mainly explain IGP in scenarios of breeding habitat saturation or when the cost of gathering information about predation risk is high and/or the cues used to predict predation risk are not reliable.

We found no differences in the proportion of responses among diurnal raptor species and at different distances from nests, as could be initially expected. This might have resulted from an insufficient sample size, and should be further investigated, as the results can have important consequences in the conservation of the species involved in this complex interaction.

Although our results can be considered as a first direct support to the role played by the removal of a predator in driving IGP, some expectations resulting from the predator-removal hypothesis still need to be explored to improve our understanding of the links between IGP and the predator-removal scenario. Among important points that should be addressed in future studies are: (1) if the degree of IGP is proportional to the abundance of the most aggressive IG prey; (2) if more aggressive IG prey species are more frequently consumed than less aggressive species; and (3) if IG prey species are preferentially removed of the core areas of home ranges (i.e. near active nests and main roost sites). We suggest that the predator-removal hypothesis should also be tested in other interacting pairs of top predator species and in different conditions of density and resource availability. Another related step forward would be to understand if non-guild mobbers, alike IG mobbers, can also be preferential victims for dominant IG predators, as a way to reduce the costs of being mobbed (Pavey and Smyth 1998; Pettifor 1990; Sunde et al. 2003). Finally, we recommend that future studies investigating the causes of IGP in vertebrates, should bear in mind the possibility of mutual IGP scenarios, and besides the competitive and energetic perspectives, the predator-removal behavioural mechanisms should also be included as potential triggers.

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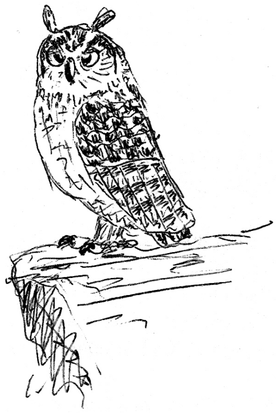

Chapter 4

SUPERPREDATION INCREASES MERCURY LEVEL IN A GENERALIST TOP PREDATOR, THE EAGLE OWL

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Superpredation increases mercury levels in a generalist top predator, the eagle owl

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Abstract Superpredation can increase the length of the food chain and potentially lead to mercury (Hg) bioaccumulation in top predators. We analysed the relationship of Hg concentrations in eagle owls *Bubo bubo* to diet composition and the percentage of mesopredators in the diet. Hg levels were measured in the adult feathers of eagle owls from 33 owl territories in the south-western Iberian Peninsula, and in three trophic levels of their prey: primary consumers, secondary consumers and mesopredators. In addition, we studied 6,181 prey in the eagle owl diet. Hg concentrations increased along the food chain, but the concentrations in eagle owls showed considerable variation. The Hg concentration in eagle owls increased when the percentage of mesopredators in the diet increased and the percentage of primary consumers decreased. Superpredation is often related to food stress, and the associated increase in accumulation of Hg may cause additional negative effects on vertebrate top predators. Hg levels in these eagle owl populations are relatively low, but future monitoring is recommended.

Keywords Bioaccumulation, Biomagnification, *Bubo bubo*, Intraguild predation, Portugal, Spain

Introduction

Owls and raptors occupy upper trophic levels in food webs and are thus more exposed to biomagnification of persistent lipophilic contaminants, including organochlorine pesticides, polychlorinated biphenyls (PCBs) and mercury (Hg). Consequently, there have been major consequences for some raptor species resulting from the bioaccumulation of these chemicals, including low breeding success, increased mortality, and population decline (Newton et al., 1993; Anthony et al., 1999; Frank and Lutz, 1999; Nygård and Gjershaug, 2001).

Mercury is a non-essential trace element with high toxicity to animals. Largely as a consequence of human activities the levels and bioavailability of this heavy metal in the environment have increased in recent decades (Morel et al., 1998; Boening, 2000). Atmospheric transport is a major pathway for Hg, for which the most important anthropogenic sources of entry into ecosystems are waste processing (handling, incineration), industry (e.g. chlor-alkali pulp mills), mining and smelting, and burning of fossil fuels including coal, peat and wood (Carpi, 1997; Morel et al., 1998). Methylmercury (MeHg), which is the most common organic form of Hg in living organisms, has high biomagnification and bioaccumulation capability, and high toxicity (Thompson, 1996; DesGranges et al., 1998; Morel et al., 1998).

Although Hg biomagnification in predatory birds is generally greater in aquatic than terrestrial food webs, some studies have found large accumulations of the contaminant in birds of prey that feed at the top of terrestrial trophic chains (Broo and Odsjö, 1981; Lindberg and Odsjö, 1983; Anthony et al., 1999; Palma et al., 2005). Birds are considered to be sensitive biomonitors of environmental contaminants. This is particularly the case for birds of prey because they: (1) occupy high trophic levels; (2) are long-lived; and (3) many are resident and territorial, indicating local levels of environmental contamination (Becker, 2003; Kenntner et al. 2003).

Intraspecific differences in levels of bioaccumulation are generally associated with spatial or temporal variation of contaminants in the environment (Newton et al., 1993; García-Fernández et al., 1997; Kenntner et al., 2003, Odsjö et al., 2004). However, several studies have shown that for top predators diet composition can also influence the concentration of contaminants (Lindberg and Odsjö, 1983; Elliot et al., 1996; Anthony et al., 1999; Mañosa et al., 2003; Palma et al., 2005). Large raptors often prey on other vertebrate top predators such as mammalian carnivores, diurnal raptors and owls (Lourenço et al., 2011), and this can include acts of superpredation (i.e. predation on other top predators) and intraguild predation (IGP; predation on competitors; sensu Polis et al., 1989). Interactions among apex predators are particularly important because they can markedly influence ecosystem functioning (Polis et al., 1989; Crooks and Soulé, 1999). One of the main causes of increased IGP in raptors is food stress associated with a decline in populations of staple prey (Serrano, 2000; Lourenço et al., 2011), which can be the result of prey cycles, disease and habitat modification (Korpimäki et al., 1990; Penteriani et al., 2002; Moleón et al., 2009). As superpredation or IGP increase a greater proportion of prey will be taken from higher trophic levels, and in these situations a consequence may be an increase in the risk of biomagnification of contaminants.

The eagle owl is a large nocturnal raptor and one of the most common top predators in the Iberian Peninsula. It is a generalist predator that regularly feeds at several trophic levels (Lourenço et al., 2011). The diet of eagle owls in this region is mainly comprised of medium sized mammals including rabbits, hares, hedgehogs and rats, and medium sized birds including partridges, pigeons, jays and magpies (Hiraldo et al., 1975; Martínez and Zuberogoitia, 2001; Lourenço, 2006). As a long-lived superpredator, the eagle owl is prone to bioaccumulation of Hg.

The main aim of the study was to understand the role of superpredation in the biomagnification of local Hg contamination along the food chain. Accordingly, we tested the hypothesis that Hg concentration in a top predator, the eagle owl, is higher in those owl territories where the percentage of other top predators in the eagle owl diet is also higher.

Methods

Study area

Samples were collected in 33 eagle owl territories distributed in four study areas in the south-western Iberian Peninsula (Fig. 1), three in Portugal (area 1, north-eastern Alentejo, 6 territories; area 2, eastern Alentejo, 15 territories; area 3, north-eastern Algarve, 5 territories) and one in Spain (area 4, Sierra Norte, Seville, 7 territories). Area 1 (39°14'N, 7°18'W) is typically mountainous (290–1025 m a.s.l.) and mainly covered by oak woodlands (*Quercus suber*, *Q. rotundifolia*, *Q. pyrenaica*), pine and eucalyptus plantations, and Mediterranean shrubland. Area 2 (38°21'N, 7°21'W) is mainly flat or slightly hilly (74̃300 m a.s.l.), and the dominant habitats are holm oak (*Q. rotundifolia*) and cork oak (*Q. suber*) woodlands, agricultural fields (cereals, olive groves and vineyards), and Mediterranean shrubland. Area 3 (37°28'N, 7°42'W) is hilly (10–570 m a.s.l.), with habitats dominated by Mediterranean shrubland, and holm and cork oak woodlands. Area 4 (37°36'N, 6°02'W) is also hilly (60–200 m a.s.l.), and includes a large dam on the Huelva River. The landscape is dominated by dense Mediterranean shrubland and holm oak woodlands. All the study areas have in common a low human population density.

Sampling procedures

Feather and fur samples

From 2003 to 2007 we visited eagle owl nests and roosting places at the end of the breeding season, and collected moulted adult body feathers. Feathers of avian prey of the eagle owl were collected at feeding perches, where eagle owls pluck the prey before eating, and at nests. The fur of mammalian prey was collected at feeding perches and nests, but also from pellets (when these contained remnants of only one prey). Individual samples were transferred to transparent plastic bags. As Hg accumulation may depend on the trophic level, the 15 prey species sampled were categorised as: a) primary consumers (mainly herbivorous species: rabbit, *Oryctolagus cuniculus*; Iberian hare, *Lepus granatensis*; water vole, *Arvicola sapidus*; red-legged partridge, *Alectoris rufa*; domestic pigeon, *Columba livia domestica*; woodpigeon, *Columba palumbus*); b) secondary consumers (omnivorous and insectivorous species: brown rat, *Rattus norvegicus*; jay, *Garrulus glandarius*; magpie, *Pica pica*; azure-winged magpie, *Cyanopica cooki*; lapwing, *Vanellus vanellus*); and c) mesopredators (strictly carnivorous or insectivorous species: barn owl, *Tyto alba*; little owl, *Athene noctua*; tawny owl, *Strix aluco*; common kestrel; *Falco tinnunculus*).

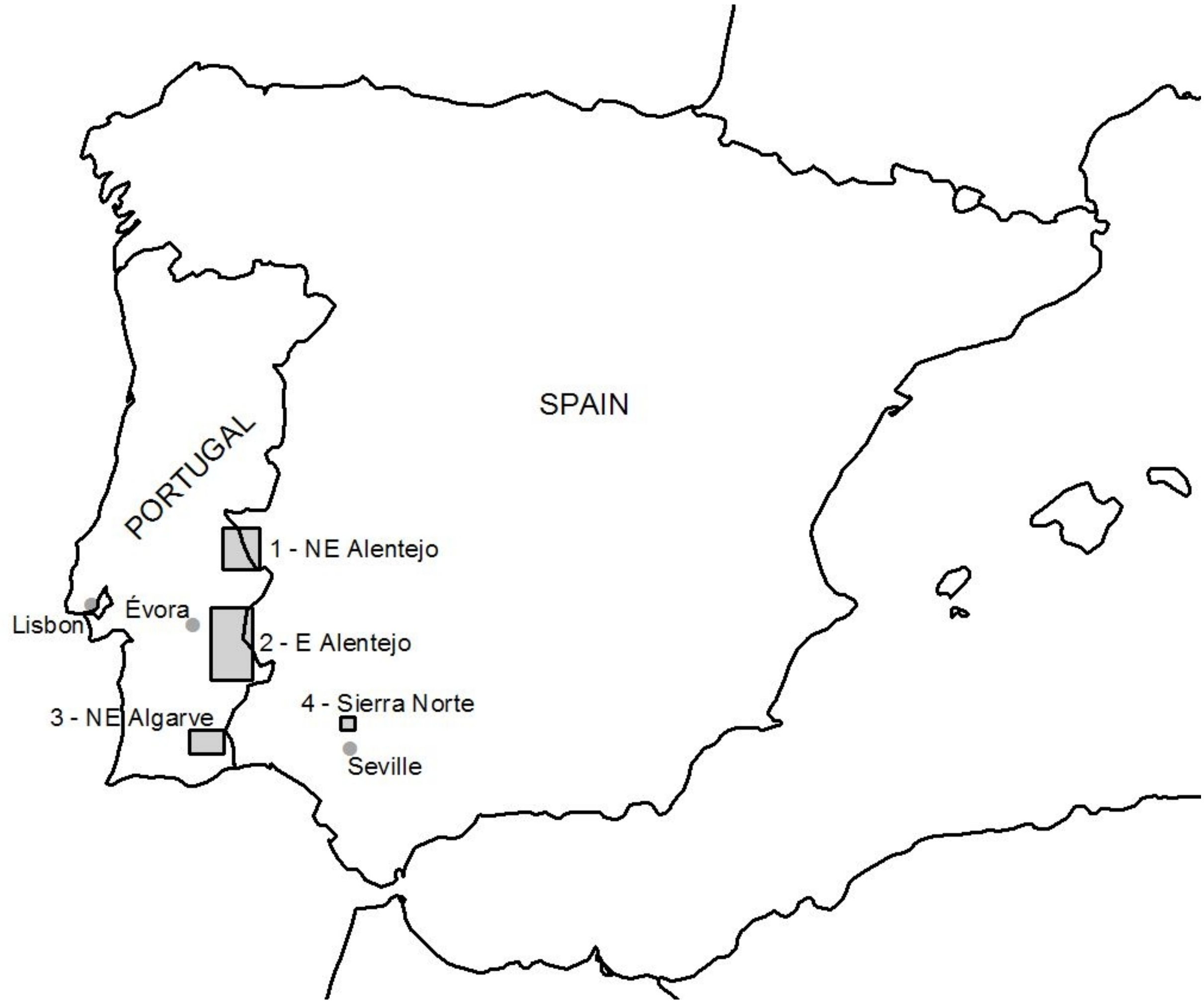

Fig. 1 Location of the four study areas

Diet composition

The diet of eagle owls was assessed by analysing prey remains and pellets collected from nests, roosting and feeding perches during the period 1997˜2010. Prey was identified by comparison of the collected material with a reference collection (Laboratory of Archaeo-sciences, IGESPAR, Portugal), using identification keys for bones and feathers, and the minimum number of individuals in each category was determined. Where possible, prey was identified to species. We calculated the percentage biomass of each prey species from the mean weight of the species obtained from bibliographic references, or used bone measurements to estimate the weight of each individual. We then determined the percentage biomass of each of the three trophic levels considered: primary consumers (lagomorphs, partridges, water vole, pigeons); secondary consumers (hedgehogs *Erinaceus europaeus*, rats, corvids) and mesopredators (mammalian carnivores, raptors and owls, i.e. superpredation).

Mercury analysis

The Hg concentration in feather and fur samples was determined by thermal atomization followed by atomic absorption spectroscopy, using an AMA254 spectrophotometer (Althec, Czech Republic); the procedure was similar to that described by Tavares et al. (2008, 2009). The accuracy of the method was within 10% (95% confidence interval), based on analysis of reference materials including: NIES-5 (human hair from NIES-Japan; certified value 4.4 ± 0.4 mg kg^{-1}), TORT-2 (lobster hepatopancreas from NRCC-IAEA Canada; certified value 0.27 ± 0.06 mg kg^{-1}), and CRM 463 (tuna fish from BCR-Belgium IAEA; certified value 2.85 ± 0.17 mg kg^{-1}). Reproducibility was checked by performing successive measurements on the same sample, which resulted in relative standard deviations in the range of 5%. The stated detection limit (Althec) is 0.01 ng Hg, and 0.1 ng Hg g^{-1} (0.1 ppb) in the case of 0.100 g samples. All Hg concentrations were recorded in mg kg^{-1} on a fresh weight (f.w.) basis.

Statistical analysis

In each territory we collected more than one eagle owl feather, enabling calculation of the mean Hg concentration per territory. We applied a logarithmic transformation to the mean Hg concentration in eagle owl feathers, and an arcsine transformation to all variables representing prey biomass percentage in the eagle owl diet (Quinn and Keough, 2002). We used linear regression models (analysis of variance – Anova – for categorical variables) to: (1) compare superpredation levels across study areas; (2) compare Hg concentrations among study areas and trophic levels; and (3) assess the effects of diet composition (biomass percentage of primary consumers, secondary consumers and mesopredators) and Hg contamination of herbivore prey species on the Hg levels in eagle owls. Comparisons of the mean Hg concentration between trophic levels were performed using a two-tailed *t*-test (Quinn & Keough, 2002). Pearson's correlation was used to relate the percentage superpredation to diet diversity (estimated by Shannon's diversity index, calculated at the Order taxonomic level). The significance level was set to 0.05, and was adjusted using the sequential Bonferroni correction (Rice, 1989) for multiple comparisons. Results are presented as the mean value ± standard deviation. All statistical analyses were performed using R version 2.11.0 software (R Development Core Team, 2010).

Results

Diet and superpredation in eagle owls

Analysis of the eagle owl diet in 33 territories yielded 6181 prey samples. The sample size per territory varied from 61 to 469, with an average of 187 ± 93 prey. The prey groups that contributed the greatest biomass to the eagle owl diet were rabbit (51.2 ± 19.1%), Iberian hare (18.7 ± 12.5%), red-legged partridge (7.5 ± 3.2%), hedgehog (4.4 ± 4.7%), rats (*Rattus* spp.; 3.4 ± 3.9%), pigeons and doves (Columbiformes; 3.2 ± 3.1%), and water vole (1.5 ± 2.1%). The mean biomass percentage of mesopredators (carnivores, raptors and owls) was 2.4 ± 2.2%. The percentage of mesopredators was positively correlated with diet diversity (Pearson's product moment correlation = 0.660, t = 4.891, DF = 31, $P < 0.001$, n = 33). Superpredation levels were significantly different among the four study areas ($F = 5.70$, DF = 3, $P = 0.003$, n = 33). Area 1 had the highest median percentage biomass of mesopredators (Fig. 2).

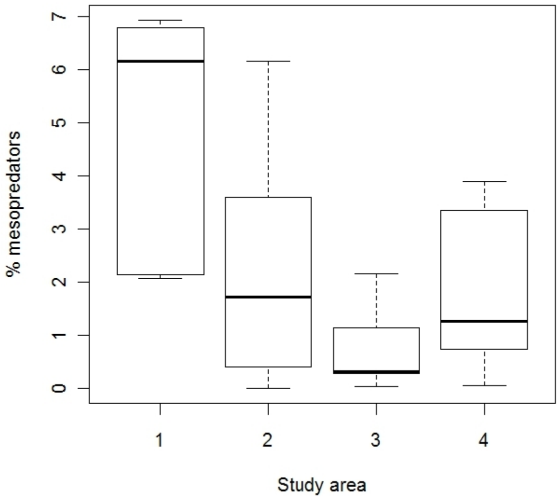

Fig. 2 Percentage of mesopredators (superpredation) in the diet of eagle owls in 33 territories in the four study areas (see text for details). *Box* and *whisker plots* show the median, 25% quartiles and range

Hg levels in eagle owls and their prey

We measured Hg concentrations in 168 samples from eagle owls and 15 prey species. Considerable differences were observed in the mean Hg concentrations among eagle owls, and also between the top predator and some of its prey species (Table 1). Based on the analysis of all study areas combined, the concentrations of Hg increased significantly from the bottom to the top of the food chain ($F = 55.73$, DF = 3, $P < 0.001$, n = 168; Fig. 3). Primary consumers had significantly lower Hg concentrations than secondary consumers (t = -8.13, DF = 34.6, $P < 0.001$). Top predators had significantly higher Hg concentrations than secondary consumers (t = -2.79, DF = 48.2, $P = 0.008$), but there were no significant differences in Hg concentrations between mesopredators and the eagle owl (t = 0.65, DF = 81.7, $P = 0.52$). The concentrations of Hg in eagle owls differed significantly among the four areas ($F = 11.05$, DF = 3, $P < 0.001$, n = 33), with the highest median value observed in area 1 (north-eastern Alentejo; Fig. 4). However, there were no significant differences in the Hg concentrations in primary consumers among areas ($F = 0.19$, DF = 3, $P = 0.90$, n = 53; Fig. 5).

Table 1 Sample size (N), mean, standard deviation (SD) and range of Hg concentrations (mg kg^{-1} wet weight) in feather samples of eagle owls, and feathers and fur of their prey in the south-western Iberian Peninsula (2003-2007)

Species	N	Hg_{Mean}	Hg_{SD}	Hg_{Range}
Eagle owl *Bubo bubo*	61	1.29	2.54	0.03 – 12.80
Barn owl *Tyto alba*	13	1.22	1.11	0.09 – 3.29
Tawny owl *Strix aluco*	3	0.48	0.44	0.18 – 0.98
Little owl *Athene noctua*	15	0.64	0.51	0.10 – 2.27
Jay *Garrulus glandarius*	6	0.43	0.37	0.16 – 1.00
Azure-winged magpie *Cyanopica cooki*	12	0.24	0.20	0.08 – 0.66
Domestic pigeon *Columba livia domestica*	9	0.07	0.06	0.01 – 0.22
Red-legged partridge *Alectoris rufa*	29	0.04	0.03	0.01 – 0.12
Iberian hare *Lepus granatensis*	5	0.14	0.14	0.02 – 0.38
Rabbit *Oryctolagus cuniculus*	8	0.07	0.03	0.02 – 0.11

Mercury values for the remaining species (with one or two samples)

Water vole *Arvicola sapidus* 0.03; Woodpigeon *Columba palumbus* 0.06; Common kestrel *Falco tinnunculus* 0.07; Magpie *Pica pica* 1.19, 0.55; Brown rat *Rattus norvegicus* 0.07; Lapwing *Vanellus vanellus* 1.05

Superpredation and prey contamination effects on mercury levels in eagle owls

The linear regression models showed that Hg concentrations in the eagle owl were negatively correlated with the biomass percentage of primary consumers ($\beta = -1.79$, SE = 0.38, t = -4.683, $P < 0.001$) and positively correlated with the biomass percentage of mesopredators ($\beta = 10.37$, SE = 3.80, t = 2.733, $P = 0.010$). Following sequential Bonferroni correction (reference P level = 0.025; Rice, 1989), the percentage biomass of secondary consumers had no significant effect ($\beta = 3.59$, SE = 1.54, t = 2.335, $P = 0.026$). There was no significant effect of the Hg concentration in primary consumers on the Hg levels in eagle owls ($\beta = 0.18$, SE = 0.35, t = 0.502, $P = 0.622$).

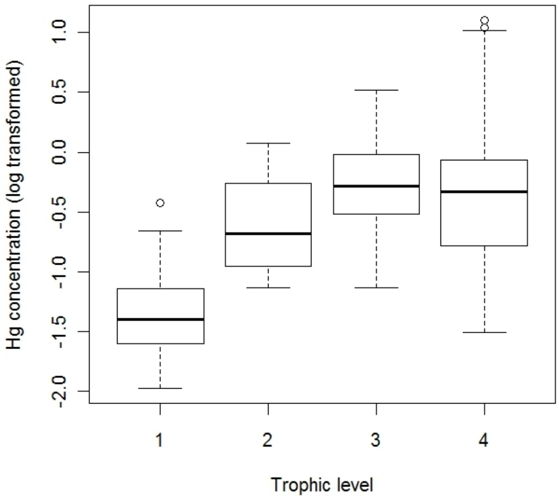

Fig. 3 Hg concentration as a function of trophic level: *1* primary consumers (n = 53); *2* secondary consumers (n = 22); *3* mesopredators (n = 32); *4* top predator (eagle owl, n = 61). *Box* and *whisker plots* show the median, 25% quartiles and range

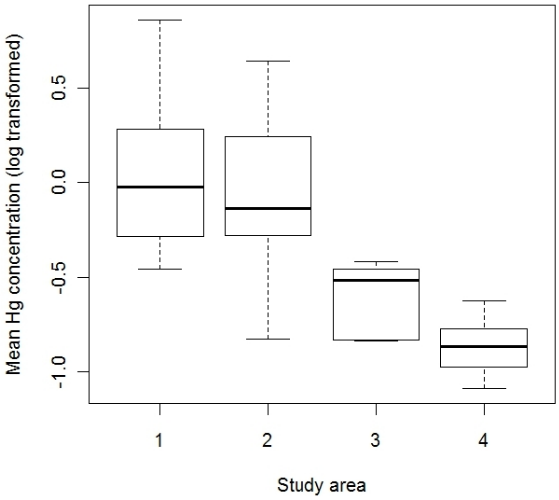

Fig. 4 Mean Hg concentration (mg kg^{-1}) in eagle owls in 33 territories in the four study areas (see names in text). *Box* and *whisker plots* show the median, 25% quartiles and range

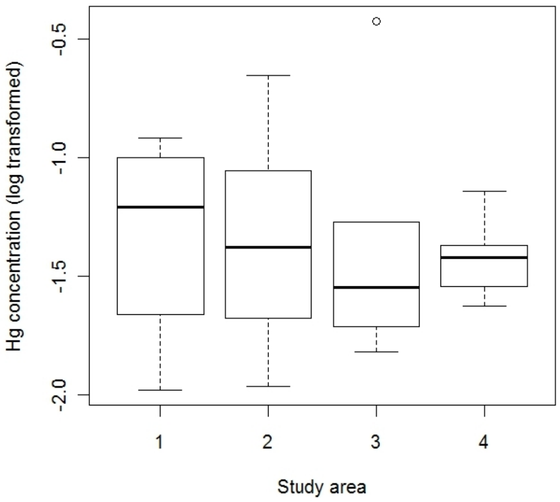

Fig. 5 Hg concentration (mg kg^{-1}) in primary consumers in the four study areas ($n_1 = 8$, $n_2 = 25$, $n_3 = 5$, $n_4 = 15$; see names in text). *Box* and *whisker plots* show the median, 25% quartiles and range

Discussion

The concentration of Hg is biomagnified in the terrestrial food webs of the south-western Iberian Peninsula, where eagle owls are top predators. We found considerable variation in the Hg concentrations in eagle owl feathers, from very low (0.03 mg kg^{-1}) to relatively high (12.80 mg kg^{-1}). However, the Hg concentrations in primary consumers (herbivores) showed little variation and were not related to Hg concentrations found in the top predator. Feathers from eagle owl territories where the percentage of mesopredators was high also had high Hg concentrations, indicating that superpredation is a relevant factor increasing the Hg burden in this top predator. Hence, this study provides further evidence that individual differences in diet can influence Hg concentrations in top predators, particularly through the inclusion of prey species from higher trophic levels, which normally have higher burdens of this contaminant. The optimal prey for eagle owls in Mediterranean ecosystems of the Iberian Peninsula generally consists of medium sized herbivores (rabbits, hares, partridges; Hiraldo et al., 1975), but faced with prey scarcity this generalist predator will diversify its diet to include other predators (Lourenço et al., 2011), thus exposing it to biomagnification and bioaccumulation of Hg. Superpredation and IGP increase the length of terrestrial food chains (which are generally shorter than aquatic ones; Dietz et al., 2000), increasing the potential for biomagnification of contaminants. Increases in superpredation in response to prey scarcity can also occur in other raptor or carnivore species (Palomares and Caro, 1999; Sunde et al., 1999; Lourenço et al., 2011), which is a potential mechanism of biomagnification of Hg and other contaminants in most vertebrate top predators.

Higher concentrations of Hg and other contaminants in the environment are generally associated with areas heavily affected by human activities (Driscoll et al., 2007). The associated changes in habitat characteristics (pollution, fragmentation, disturbance, increased mortality) may be responsible for the decline of herbivore prey populations. Although there is insufficient knowledge of trends in superpredation or IGP levels in raptors (Lourenço et al., 2011), human-caused alteration of habitats can, in a short term, have a strong influence on the diet of apex predators (Marchesi et al., 2002; Penteriani et al., 2005). Consequently, in some areas an increase in the prey burden of Hg, and increased superpredation because of a decline in prey populations, may have an additive effect, resulting in a significant increase in the concentration of contaminants in top predators inhabiting altered and polluted environments.

An increase of superpredation levels in avian top predators seems to be associated with lower breeding performance (Lourenço et al., 2011). As Hg and other contaminants can impair breeding, it is important to establish the role of pollutants that are biomagnified through consumption of prey from higher trophic levels. Low food availability and high contamination levels may have additive effects on breeding performance (Hornfeldt and Nyholm, 1996). Thus, further research is needed to clarify the effects of contaminants on top predators and how superpredation may amplify them.

The few studies analysing Hg concentrations in eagle owls provide limited data for comparative purposes. The mean Hg concentrations in eagle owls in this study are higher than those reported (Ortego et al., 2006) for eagle owls in Toledo (Spain), which is an area with no obvious contamination sources, and where the owl diet consists mainly of rabbits. However, Ortego et al. (2006) only analysed chick feathers, which generally have lower contamination levels (Lindberg and Odsjö, 1983; Monteiro and Furness, 1995). Hg concentrations in eagle owls from four study areas in Sweden (Broo and Odsjö, 1981) were higher than those found in the present study. This is probably related to the use in Sweden of alkyl Hg as a seed-dressing agent in terrestrial habitats, and to a substantial intake of prey from aquatic food chains in coastal habitats (Olsson, 1979; Broo and Odsjö, 1981). These results and those of several studies analysing Hg in feathers of other species (e.g. Lindberg and Odsjö, 1983; Monteiro et al., 1995; Tavares et al., 2008, 2009) suggest that the mean Hg concentration in eagle owls from the south-western Iberian Peninsula is comparatively low, and consequently most individuals might not be negatively affected. Nevertheless, the analysis of 61 eagle owl feathers indicated that 4 territories had a Hg concentration above 4.1 mg kg^{-1} (which is considered to be a high concentration in feathers of raptors; Palma et al., 2005), and in these cases the possibility of sub lethal effects should be further investigated, especially in relation to breeding performance. Detrimental Hg levels in birds are most often associated with high concentrations in the liver and kidney (Thompson 1996), as these are the main organs involved in the metabolism of this contaminant (Scheuhammer 1987). Hg concentrations in feathers represent the blood concentration at the time of feather growth (Thompson et al., 1998), and reflect the Hg concentration in the diet (Lewis and Furness, 1991). However, as transfer of Hg to feathers is a means of excreting mercury, and feathers can contain high concentrations during growth, it is very difficult to relate these values to negative health effects in individuals, although some attempts have made (Burger and Gochfeld, 1997; Wolfe et al., 2009). However, feather analysis remain the best noninvasive method for studying the Hg burden in birds (Monteiro and Furness, 1995), and there is an urgent need to reliably relate Hg concentrations in feathers with health risks to individuals. Study of the impact of long-term exposure to Hg on birds is considered a priority (Seewagen 2010), and such studies should include eagle owls because they are top predators in several terrestrial food webs.

In addition to eagle owls, the barn owl and the little owl are two mesopredators in which relatively high Hg levels (above 2.0 mg kg^{-1}) have been reported. Hence, it is also important to monitor the bioaccumulation of Hg in mesopredator species, which can engage in intraguild predatory interactions in a similar way to top predators.

Eagle owls are sedentary and their home ranges in the south-western Iberian Peninsula are relatively small (Delgado and Penteriani, 2007). Their most common prey species also have small home ranges so Hg concentrations found in this owl may reflect the levels of local environmental contamination, especially when diet composition is accounted for. We found little regional variation in Hg contamination levels in primary consumers, which is consistent with the results reported by Freitas et al. (1999), who detected low concentrations of Hg in lichens in our three study areas in Portugal, although these levels only reflect airborne Hg. Thus, regional differences in Hg concentrations in eagle owls appear to be largely related to diet composition rather than to levels of local contamination. Nevertheless, local contamination sources may have contributed to the highest concentrations we found in eagle owl feathers. In area 1 the two territories that had Hg concentrations above 4.1 mg kg^{-1} are located 4 and 11 km, respectively, from the industrial area of Portalegre, which is the most important local source of Hg. In area 2 the two territories that had Hg levels above 4.1 mg kg^{-1} are located adjacent to the Alqueva dam on the Guadiana River. This dam, which was completed in 2002, has a total flooded area of 250 km^2, and may be mobilizing deposited mineral and atmospheric Hg into food chains (DesGranges et al., 1998; Boening, 2000). Moreover, the Guadiana River basin includes several large cities (e.g. Badajoz), which may result in large inputs of Hg from industry, agriculture and mining, the latter including Almadén, which is the world's largest mining-metallurgical Hg complex.

Raptors and owls are commonly used as bioindicator and biomonitor species in environmental quality assessment, but based on the results of this and other studies (Anthony et al., 1999; Palma et al., 2005) we strongly recommend that diet composition is taken into account in analyses of contamination levels, especially for generalist predators. Thus, there is a need to develop correction factors for diet composition, which can be used in studies using generalist top predators as biomonitors. Alternatively, biomonitoring could be based on more specialist species that have narrow and stable diets, as suggested by Monteiro and Furness (1995).

The emergence of diet changes and increasing superpredation, which are frequently associated with habitat modification, may have detrimental effects on raptors and other top predators by influencing the bioaccumulation of contaminants. The potential consequences for these species, many of which have unfavourable conservation status or are keystone predators, raises the need for long-term national monitoring programs to assess the levels of contamination in top predators (Gjershaug et al., 2008; Walker et al., 2008), including temporal and spatial trends, and their relationships to demographic parameters (breeding success, survival) and diet composition.

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Chapter 5

To call or not to call? Need of conspicuousness under moonlight and predation risk fight for patterns of vocal displays

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To call or not to call? Need of conspicuousness under moonlight and predation risk fight for patterns of vocal displays

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Abstract The brightness of lunar light may represent a double-edged sword for prey species. On the one hand, moonlight increases the conspicuousness of visual signalling in crepuscular and nocturnal species but, on the other hand, it may increase predation risk by visually-oriented predators. The tawny owl *Strix aluco* has a white badge on the throat that is only visible when it is calling, and that seems to be used as a visual signal during vocal displays. In Doñana Protected Area, the tawny owl co-exists alongside its intraguild predator, the eagle owl *Bubo bubo*. The study of vocal behaviour at dusk in 78 tawny owl territories living sympatricly within a population of 19 eagle owls revealed that: 1) tawny owl vocalization rates increased with higher levels of moonlight and 2) decreased when there was an eagle owl calling nearby. Two additional elements contributed towards explaining vocalization patterns at dusk, and these included: 3) probability of calling, calling rate and onset of calling increased with the number of conspecific neighbours; and 4) calling rate was higher during the post-fledging and pair bonding period. These results reveal a trade-off between: 1) the necessity to call more in situations of high breeding density and during optimal moonlight conditions when visual signals associated with vocal displays are more conspicuous; and 2) the need to reduce vocal activity in order to minimize predation risk by a predator that locates its prey by vocalizations. Tawny owls seem to use their intraguild predator's calls as a moment-to-moment cue to assess predation risk, responding with an anti-predator mechanism such as reducing calling rate. This behavioural response may be principally employed by tawny owls when predator-avoidance mechanisms such as distance-sensitive and habitat-mediated measures cannot be effectively used to reduce predation risk.

Keywords: Anti-predator mechanisms, *Bubo bubo*, Eagle owl, Intraguild predation, Predator-avoidance mechanisms, *Strix aluco*, Superpredation, Tawny Owl, Vocal displays

INTRODUCTION

The functions of bird vocalisations have been extensively investigated during the last number of decades (Goodenough et al. 2010) but, despite the vast amount of theoretical and empirical information supporting the different roles of calls and songs, the constraints of singing are still poorly understood, existing the need for further research in this area of avian behavioural ecology (Gil & Gahr 2002).

Most owl species have nocturnal habits, relying principally on sound as an easy and effective way of obtaining information as well as communicating in poor light conditions. In the past, a number of studies have also found the apparently contradictory results that owl species may either increase vocal displays during moonlit nights (Morrell et al. 1991; Clark & Anderson 1997; Takats & Holroyd 1997; Kissling et al. 2010), or call more in the last quarter and new moon phases of the lunar cycle (Ganey 1990). However, recent studies have highlighted that owl communication also relies on visual cues (Penteriani et al. 2006, 2007; Galeotti & Rubolini 2007) and that the conspicuousness of their visual plumage traits (e.g. a white badge on the throat which is only visible during call displays) is increased by the unusual light conditions during dusk (Penteriani & Delgado 2009) or during bright moonlight (Penteriani et al. 2010).

A number of other factors are known to influence the patterns of vocal activity in owls. One of the most obvious is the time of year, with calling rate varying within the breeding cycle (Palmer 1987; Smith et al. 1987; Ganey 1990; Morrell et al. 1991; Clark & Anderson 1997; Sunde & Bølstad 2004; Delgado & Penteriani 2007). Time of day also influences vocal activity, with most owl species being more vocally active during dusk and dawn (Ganey 1990; Clark & Anderson 1997; Penteriani et al. 2002; Hardouin et al. 2008; Delgado & Penteriani 2007). The breeding density of conspecifics is another well known factor influencing vocal activity in owls (Redpath 1995; Penteriani et al. 2002; Penteriani 2003; Sunde & Bølstad 2004). Calling is often stimulated by the calls of conspecifics (Ganey 1990), but the response intensity can be sex-specific and different towards neighbours and strangers (Galeotti & Pavan 1993; Appleby et al. 1999; Hardouin et al. 2006). Many studies have found that weather conditions can influence owl communication. For example, vocal activity is reduced in heavy rain and strong wind (Smith et al. 1987; Takats & Holroyd 1997; Lengagne & Slater 2002; Kissling et al. 2010), as well as by cold temperatures (Clark & Anderson 1997; Takats & Holroyd 1997; Hardouin et al. 2008). Cloud cover, a factor influencing moon luminosity, also seems to have an effect on vocal activity. Great horned owls *Bubo virginianus* and spotted owls *Strix occidentalis* seem to call more during clear sky (Ganey 1990; Morrell et al. 1991), while other studies have shown no effects or contradictory results for other species (Palmer 1987; Clark & Anderson 1997; Swengel & Swengel 1997; Takats & Holroyd 1997).

Finally, because larger owl species can be predators or dominant competitors of smaller owls, predation risk and interference competition have the potential to reduce vocal activity in smaller owls (e.g. Crozier et al. 2006; Zuberogoitia et al. 2008). Conversely, an increased calling rate in response to the calls of a larger owl can be explained by interspecific territoriality or mobbing behaviour (Ganey 1990; Boal & Bibles 2001; Crozier et al. 2005). However, to our knowledge, there have been no attempts to assess the trade-off between the specific needs of the signallers to call in the best conditions and in response to the intraspecific social environment, and the risk to be perceived by an eavesdropping predator. In fact, despite the large amount of studies analysing vocal behaviour of owls , the various factors influencing vocal behaviour are mainly analysed separately (Johnson et al. 1981; Carpenter 1987; Redpath 1994; Takats & Holroyd 1997; Zuberogoitia & Campos 1998; Martínez & Zuberogoitia 2002; Crozier et al. 2005; Kissling et al. 2010). Several studies have focused on census methodology, and therefore disregarded social factors influencing vocal behaviour. In addition, many of these experimental studies have used call playback and imitation to determine the effects of conspecifics and predators on vocalization rates.

In the attempt to fill this research gap, our study focused on the predatory interaction (intraguild predation *sensu* Polis et al. 1989) between two owl species, in a system where the intraguild prey (tawny owl *Strix aluco*) and its intraguild predator (eagle owl *Bubo bubo*) often occur at higher densities in the same areas. This peculiar scenario presents an opportunity to examine both: 1) the conditions promoting the vocal displays of an intraguild prey; and 2) its behavioural response when detecting the presence of its intraguild predator. The tawny owl is a resident and strongly territorial species, aggressively defending its home range from conspecifics (Southern & Lowe 1968; Hirons 1985; Redpath 1994; Sunde & Bølstad 2004). Tawny owls have distinctive vocalizations, and breeding adults recognize the hooting of conspecific neighbours, showing a stronger reaction when faced with stranger males (Galeotti & Pavan 1991, 1993; Galeotti 1998). The eagle owl feeds primarily on small to medium sized mammals and birds, and it can frequently prey on both adult and young tawny owls (Lourenço et al. 2011). The conspicuous calls of adult and young tawny owls are probably an effective way used by eagle owls, a sit-and-wait predator, to detect this intraguild prey (Mougeot & Bretagnolle 2000; Sergio et al. 2007; Penteriani et al. 2008). Intraguild predation risk can strongly influence habitat selection, density, breeding success and behaviour of the IG prey (Hakkarainen & Korpimäki 1996; Cresswell 2008; Sergio & Hiraldo 2008). Tawny owls have shown at least two different mechanisms to avoid and coexist with superior competitors and predators: spatial avoidance; and habitat-mediated avoidance (Korpimäki 1986; Vrezec & Tome 2004; Sergio et al. 2007). However, predation risk may also affect tawny owl vocal behaviour. In particular, we analysed patterns of calling rate at dusk (considered to be an honest signal of male and territory quality in owls; Penteriani 2003; Hardouin et al. 2007, 2008), by specifically testing the trade-off an intraguild prey species has to make when faced with three factors: 1) the potentially stimulating effect of night luminosity (moon phases and cloud cover); 2) the potential inhibiting effect of predation risk associated to the presence of an intraguild predator; and 3) the additional effect of territoriality, expressed in terms of presence and abundance of neighbouring conspecifics, and breeding season.

METHODS

Study area

The study was conducted in Doñana protected area, south-western Spain (37º0'N, 6º30'W), which covers 108 429 ha and includes extensive wetlands in the estuary of the river Guadalquivir. Doñana National Park supports a great diversity of habitat including marshlands, scrublands and woodlands (Fig.1), and this study was undertaken in: Mediterranean scrublands scattered with cork oaks *Quercus suber*; cork oak woodlands (with *Pistacia lentiscus*, *Arbutus unedo*, *Myrtus communis*); stone pine *Pinus pinea* and *Eucalyptus* plantations; and areas of mature riparian vegetation (*Populus* spp., *Fraxinus angustifolia*) alongside large cork oaks, stone pines, and eucalyptus.

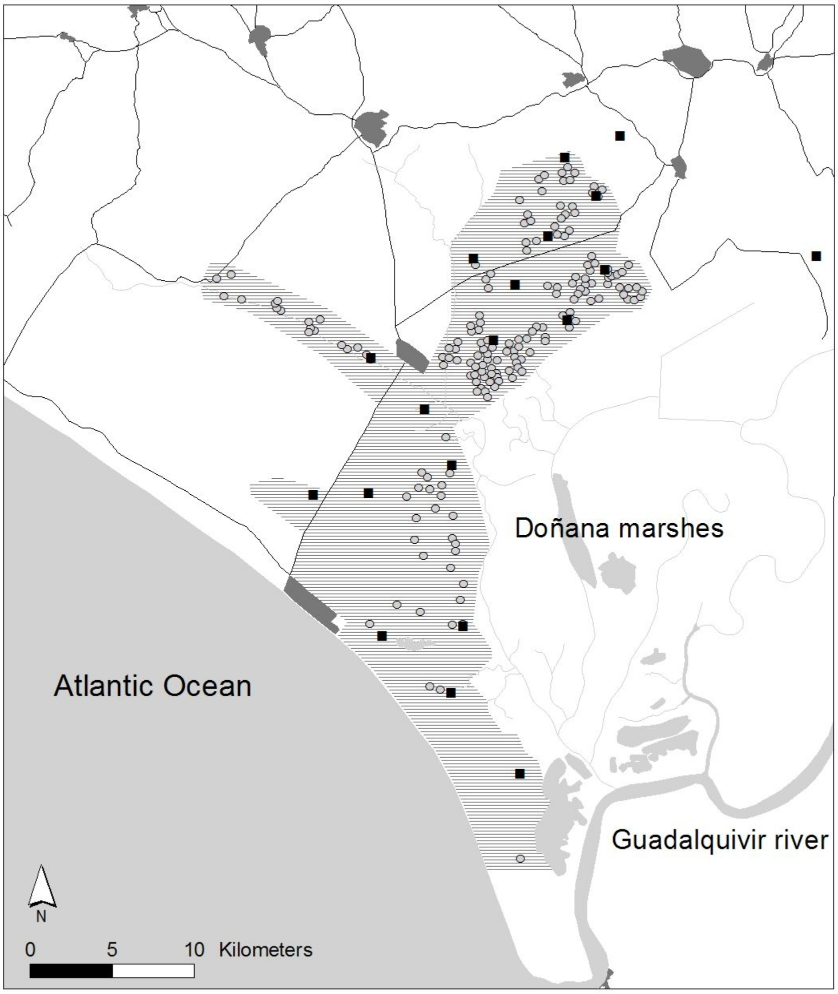

Figure 1. Doñana Protected Area with location of tawny owl territories (white circles) and eagle owl territories (black squares). Area censused for owls is represented by the shaded area. Dark grey polygons represent urban areas and black lines represent main roads.

Tawny owl census and distribution of the eagle owl breeding pairs

From September 2007 to February 2008, we censused tawny owls by visiting 275 censusing stations and listening for spontaneous calls during a three-hour period (one hour before and two hours after sunset), covering a total of 37 780 ha. We registered all owl vocalizations and, where possible, identified individuals and sex. Locations of all vocal contacts were plotted in maps in order to estimate the minimum number of breeding pairs in the study area. From March to May 2008 and 2009, we searched for tawny owl nests in suitable tree cavities and in diurnal raptors' nests (Zuberogoitia & Campos 1998). This census enabled us to identify a minimum of 176 tawny owl territories. Previous to the tawny owl census, and in the context of another research project in Doñana, we located 19 eagle owl breeding sites (average minimum nearest neighbour distance X+SD = 3.7+0.5 km), and this represented the total breeding population of this owl in Doñana during the period of this study (Penteriani et al. 2009).

Characterisation of the vocal activity patterns of tawny owls

From the 176 tawny owl territories detected during the previous census, we selected 78 in order to study the vocal activity of tawny owls. We visited 30 stations from which we controlled these 78 territories. From March to April 2008, and September 2008 to March 2009, we completed 166 listening sessions, visiting each station between four and seven times. Taking account of tawny owl breeding phenology (Cramp 1985; Zuberogoitia et al. 2004; authors unpublished data), we identified three periods: 1) post-fledging dispersal and pair-bonding (September - November); 2) pre-laying and courtship (December - January); and 3) incubation and fledging (February – April). The number of visits during each period was 223, 85, and 100 respectively. No listening sessions were carried out in heavy rain or strong wind. All listening sessions started 30 min before sunset and lasted for 2 hours. We recorded vocalizations (hoots and calls) for all owl breeding pairs. All vocal contacts were mapped to determine the centre of vocal activity for each tawny owl territory. Each listening session was divided in 120 one minute time periods. This allowed us to record the following two response variables: 1) “calling rate”, the number of one-minute periods in which the target breeding pair performed any vocalization; and 2) “onset of calling at dusk”, the number of minutes before or after sunset hour when the first vocalization of the target tawny owl pair was recorded.

Factors influencing vocal activity of tawny owls

The moonlight effect

“Moon phase” accounted for the effect of night time luminosity on vocal behaviour. This parameter was divided into two classes of moon brightness: 1) low luminosity, the period between new moon and waning crescent and waxing crescent; and 2) high luminosity, the remaining period including the full moon. In addition to the moonlight effect, we also recorded “cloud cover” as a two-class categorical variable according to the percentage of clouds in the sky: 0-50 % and 51-100%. As cloud cover can influence moon luminosity, we analysed the interaction between the variables moon phase and cloud cover.

The intraguild predator effect

The possible inhibitory effect of the presence of the eagle owl on the vocal activity of tawny owls was tested using two variables. The first variable represents the distance-effect, calculated as the distance from the centre of activity of a tawny owl territory to the nearest eagle owl nest (“distance to nearest eagle owl”). The second effect is related to the individual ability to obtain direct cues of predation risk (Schmidt 2006). being a binomial variable describing if an eagle owl had hooted or not during the two-hour period at a distance closer than 800 m of the activity centre of the target tawny owl pair (“eagle owl calling”).

Additional factors potentially affecting vocalization patterns

To analyse if the density of conspecifics affects vocal behaviour, we considered the number of activity centres neighbouring tawny owl territories within a buffer of 956 m (i.e. two times the mean nearest neighbour distance: X+SD = 478+320 m, N = 78 breeding pairs) of the activity centre of the target breeding pair (“number of conspecific neighbours”). The three “phenological periods” covered during listening sessions were considered in order to check for seasonal differences in vocal activity. Finally, to account for spatial autocorrelation in tawny owl vocal activity, we calculated an autocovariate term following the recommendations of Augustin et al. (1996) and Dormann et al. (2007). To calculate the autocovariate term we used a distance of 4000 m to search for neighbours, and weights considering the inverse distance.

Statistical analysis

The effects of the explanatory variables on tawny owl vocal activity were tested with linear and generalized mixed models (Pinheiro & Bates 2000; Zuur et al. 2009). After an initial exploratory analysis, the response variable “tawny owl calling rate” revealed an excess of zeros, suggesting the presence of zero-inflated count data (Martin et al. 2005). Additionally, there was an indication of non-independence among some cases due to repeated visits to the same station and tawny owls territories (Pinheiro & Bates 2000). In order to account for these data restrictions, we followed a two-stage protocol in data analysis of calling rate. Firstly, we applied a generalized linear mixed model (GLMM) with a binomial distribution (Zuur et al. 2009) to test the effects of each explanatory variable on the probability of each target tawny owl pair to call or not during the two-hour period. This dataset corresponded to 133 sessions with no vocalizations (classed as zero) and to 275 sessions with vocalizations (classed as one). Secondly, we applied a GLMM with a Poisson distribution (Zuur et al. 2009) to test the effects of explanatory variables on the "tawny owl calling rate". To deal with the problem of zero-inflated count data, we produced ten sub-samples from the initial dataset, by randomly extracting 100 cases with non vocalizations (zeros) in each sub-sample. The number of "zero" cases to be deleted was determine to ensure that the response variable followed a Poisson probability distribution (Zar 1999), avoiding the need to account for a zero-inflation problem. Finally, the effects of the explanatory variables on the response variable "onset of calling at dusk" ($N = 275$) were tested using a linear mixed-effects model (LME; Pinheiro & Bates 2000).

In all models (GLMM's and LME) we considered two random interaction terms: "station" and "target tawny owl territory" (Pinheiro & Bates 2000). The same seven explanatory variables were considered in all models (see details in previous section), in addition to the interaction between "cloud cover" and "moon phase". We also tested other biologically relevant interactions and included them if statistically significant. The variable "distance to nearest eagle owl" was square-root transformed. The parameters in GLMM's were fitted by Laplace approximation and in LME by restricted maximum likelihood (REML). As we were interested in checking all explanatory variables, we followed a hypothesis testing approach by including all fixed effects in the final models, instead of using model selection (Bolker et al. 2008).

Statistical significance was set to $P < 0.05$. All statistical analyses were completed using software R version 2.11.0 (R Development Core Team 2010), with packages spdep (Bivand 2010), lme4 (Bates & Maechler 2010) and nlme (Pinheiro et al. 2009).

RESULTS

Factors influencing tawny owl calling rate at dusk

The generalized linear mixed models obtained for the ten sub-samples showed good coherence. Full results of the ten models are presented as online only supplementary material (sm1). Moon phase had a significant positive effect in all ten models (β range: 0.334 to 0.492; all P values < 0.001), meaning that tawny owl calling rate was higher when moon luminosity was greater. In addition, cloud cover had a significant positive effect on tawny owl calling rate in all models (β range: 0.364 to 0.483; all P values < 0.001). The interaction between moon phase and cloud cover had a significant negative effect in all ten models (β range: -0.319 to -0.392; all P values < 0.001). Tawny owl calling rate was lower in joint conditions of clear skies and reduced moon luminosity. The presence of an eagle owl calling had a significant negative effect on tawny owl calling rate in all ten models (β range: -0.251 to -0.388; all P values < 0.001). The distance to nearest eagle owl had a significant negative effect on tawny owl calling rate in only three out of ten models (β range: -0.004 to -0.012; P range: 0.01, 0.55), meaning that tawny owls were more vocal despite being close to their intraguild predator. The number of conspecific neighbours had a significant positive effect on tawny owl calling rate at dusk in all ten models (β range: 0.124 to 0.197; P range: <0.001 to 0.002). We also found significant differences in calling rate between phenological periods: in nine out of ten models there was a significant difference between calling rate between periods 1 (post-fledging dispersal and pair-bonding) and 2 (pre-laying courtship; β range: -0.079 to -0.209; *P* range: <0.001 to 0.12); and all models showed a significant difference between periods 1 and 3 (incubation and fledging; β range: -0.205 to -0.320; all *P* values <0.001). Therefore, tawny owl calling rate was higher during the period of post-fledging dispersal and pair bonding. Finally, the autocovariate term never had a significant effect in all ten models (β range: 0.007 to 0.057; *P* range: 0.08 to 0.86).

Factors influencing tawny owl probability and onset of calling at dusk

The number of conspecific neighbours was the only significant fixed effect in the binomial GLMM determining the probability of tawny owls calling at dusk (β = 0.140; SE = 0.06, Z = 2.29, *P* = 0.02; Table 1). Thus, individuals at target territories had higher probability of calling when they had more conspecific neighbours. Tawny owls started calling mostly in the first 40 minutes after sunset (58% of all events). LME results (Table 2) showed that a higher number of conspecific neighbours caused tawny owls to start calling earlier at dusk (β = -3.131; SE = 1.08, DF = 45, t = -2.91, *P* = 0.006). Although, there was a significant difference in the onset of calling between phenological periods 1 and 3 (β = -7.904; SE = 3.64, DF = 191, t = -2.17, *P* = 0.03), the combined result including all three periods showed no significant differences ($F_{2,191}$ = 2.85, P = 0.06). The remaining covariates had no significant effect on the onset of calling at dusk (Table 2).

Table 1. Results of the binomial generalized linear mixed model (GLMM) on the probability of tawny owls calling at dusk.

Fixed effects	β	SE	Z	p
Intercept	-0.496	0.76	-0.66	0.51
Distance to nearest eagle owl	-0.016	0.01	-1.84	0.07
Presence of eagle owl calling	-0.063	0.32	-0.20	0.84
Number of conspecific neighbours	0.140	0.06	2.29	0.02
Phenological period (1:2)	0.155	0.29	0.53	0.60
Phenological period (1:3)	0.336	0.28	1.20	0.23
Moon phase (1:2)	-0.030	0.30	-0.10	0.92
Cloud cover (1:2)	-0.120	0.33	-0.37	0.72
Interaction moon phase and cloud cover	-0.124	0.47	-0.27	0.79
Autocovariate	1.906	1.13	1.69	0.09

Random effects	variance	SD
Station	0.000	0.000
Target tawny owl territory	0.024	0.156

Table 2. Results of the linear mixed effects model (LME) on the onset of calling at dusk by tawny owls.

Fixed effects	β	SE	DF	t	p	F_{anova}	p_{anova}
Intercept	55.848	17.84	191	3.13	0.002	165.62	<0.001
Distance to nearest eagle owl	0.108	0.18	45	0.60	0.55	0.23	0.63
Presence of eagle owl calling	3.860	4.69	191	0.82	0.41	1.46	0.23
Number of conspecific neighbours	-3.131	1.08	45	-2.91	0.006	10.40	0.002
Phenological period (1:2)	-1.740	3.83	191	-0.45	0.65	2.85	0.06
Phenological period (1:3)	-7.904	3.64	191	-2.17	0.03		
Moon phase (1:2)	-4.243	4.25	191	-1.00	0.32	1.58	0.21
Cloud cover (1:2)	-1.856	4.32	191	-0.43	0.67	0.66	0.42
Interaction moon phase and cloud cover	-1.623	6.58	191	-0.25	0.81	0.06	0.81
Autocovariate	-0.302	0.39	45	-0.78	0.44	0.58	0.45
Random effects		SD (intercept)			SD (residual)		
Station		9.493					
Target tawny owl territory		5.066			23.800		

DISCUSSION

The interaction of moonlight and predation risk contributes to explain patterns of vocal displays

Our study has highlighted a potential trade-off displayed in the social communication of an intraguild prey species, the tawny owl, when subjected to conflicting constraints: the need to attract a mate through vocal and visual displays in the best conditions to signal its presence; and the risk to be located by its intraguild predator, the eagle owl. Although tawny owl calling rate study increased during high moonlight luminosity increased, the probability of calling and the onset of calling at dusk (when the effect of lunar brightness on the conspicuousness of the visual signal is lower) were not affected by moonlight luminosity. The results of this study also show that predation risk (as measured by the presence of an eagle owl calling) affected the calling rate of tawny owls, but did not affect the probability and the onset of calling at dusk. Therefore, tawny owls do not seem to give up calling completely as a result of having an eagle owl nearby, however they did reduce how often they called, and this could be interpreted as a behavioural mechanism to avoid being located by their intraguild predator and thereby reducing predation risk. The two explanatory variables we considered to study the effects of an IG predator have represent two different behavioural mechanisms. The variable distance to nearest eagle owl represents a potential predator-avoidance mechanism (Hileman & Brodie 1994), but seems to be based on a poorly informative cue of predation risk: assuming that greater proximity represents greater risk. In this case, the level of perceived predation risk is constant along time. In our study, distance to nearest eagle owl was significant in a minority of sub-samples used to analyse its effect on tawny owl calling rate and, accordingly, we do not feel comfortable in reaching any strong conclusions about its effect. The possible increase of tawny owl calling rate with proximity to eagle owl nest could be interpreted as being caused mainly by an overlap in habitat preference by both species. Doñana Protected Area is characterised by a high degree of habitat heterogeneity, and both owl species, like most diurnal raptors and mammalian carnivores, are mainly concentrated in highly productive areas, where prey abundance and breeding success are higher (Veiga & Hiraldo 1990; Viñuela et al. 1994; Ferrer & Donázar 1996; Casado et al. 2008). Consequently, those areas favoured by tawny owls are also preferred by eagle owls. In this case, density of conspecifics is probably the main factor justifying the observed increase of vocal activity in tawny owls with proximity to eagle owl nests (see below). However, this result does show that in our study area, due to habitat heterogeneity, distance-sensitive and habitat-mediated predator avoidance do not seem to be effective mechanisms which tawny owls can use to reduce predation risk by eagle owls (Sergio et al. 2007; Sergio & Hiraldo 2008). So, if tawny owls cannot avoid eagle owls because both species occupy the patches of habitat, has the intraguild prey species developed any alternative behavioural mechanism to reduce predation risk? In this study we used the presence of an eagle owl calling, which was used to understand if reducing vocal activity might serve as an effective anti-predator mechanism in tawny owls (Hileman & Brodie 1994). In fact, detecting an eagle owl calling represents an immediate cue of predation risk, which varies on a moment-to-moment basis (Lima & Dill 1990). When an eagle owl calls, a tawny owl can gauge its predator's location, and thereby temporarily assess the level of predation risk, and adjust its behaviour in agreement to this (Brown et al. 1999; Lima & Bednekoff 1999). In our study, the presence of an eagle owl hooting reduced the calling rate of tawny owls during dusk, which supports the theory that tawny owls can use predator calls as a cue of predation risk and accordingly adapt their calling rate to reduce the risk of being detected by a top predator (Zuberogoitia et al. 2008). Eagle owls generally start calling half an hour before sunset (Delgado & Penteriani 2007), and the same pattern of vocalization was observed in our study area. As tawny owls generally start calling after sunset, they have time to collect information about the presence of an eagle owl in the proximity, evaluate the predation risk and, in agreement with the predation risk allocation hypothesis (Lima & Bednekoff 1999), adjust the intensity of their vocal activity. However, this defence mechanism may not be totally reliable, due to the fact that tawny owls obtain imperfect information, as an eagle owl may still be nearby without announcing its presence by calling (Brown et al. 1999). Thus, tawny owls may need additional cues to employ effective predator-avoidance and anti-predator mechanisms (not tested here), in order to coexist with eagle owls. Still, for tawny owls, reducing the calling rate might contribute to decrease encounter rate and time spent vulnerable to attack (Lima & Dill 1990).

It is worth noting that this is the first time that tawny owl vocalization rates have been shown to increase with brighter lunar light conditions, possibly in a similar way as eagle owls, whose plumage traits associated with vocal displays are enhanced by ambient light (Penteriani & Delgado 2009; Penteriani et al. 2010). Like eagle owls, tawny owls have a white throat patch, which is only exposed when they hoot or ululate (Cramp 1985; see also supplementary material sm2). We suggest that tawny owls may also take advantage of ambient moonlight to maximize their visual communication. In addition to this, by calling preferably in moon lit nights, tawny owls may be able to reduce the chance of being caught unaware by a predator (Woods & Brigham 2008). Cloud cover, like moon luminosity, only affected calling rate and not the onset or probability of calling. This variable has shown opposite effects in different owl species (Ganey 1990; Morrell et al. 1991; Clark & Anderson 1997; Swengel & Swengel 1997; Takats & Holroyd 1997). There are two possible explanations with respect to the effect of cloud cover. Firstly, we cannot disregard a possible bias in the number of days with clouded sky, which would mean that the interaction between moon luminosity and cloud cover was significant as a result of the effect of moon phase interacting with the unbalanced cloud cover. Secondly, cloud cover may create light conditions similar to the crepuscular conditions, which seem to increase white throat patch conspicuousness in owls (Penteriani & Delgado 2009).

Additional effects explaining vocal activity patterns of tawny owl

Vocalizations play a fundamental role in territorial defence, sexual selection and intra-pair communication in owls (Penteriani 2002, 2003; Sunde & Bølstad 2004), and tawny owls are known to defend their territories very aggressively (Hirons 1985; Sunde & Bølstad 2004). In our study, the number of neighbouring conspecifics influenced probability of calling, calling rate and onset of calling at dusk. The fact that the number of conspecific neighbours was the only variable significantly affecting the probability and onset of calling at dusk, suggests that it is the strongest determinant in the observed variations of vocal activity in tawny owls. Therefore, in areas where there is a high density of tawny owls which occur alongside eagle owls, the priority of territorial defence may outweigh the need to reduce vocal behaviour to diminish predation risk, even considering the potential lethal costs of predation. Tawny owls seem to have established a trade-off between the conflicting pressures of territorial functions of vocalizations and the need to reduce predation risk, based on a moment-to-moment cue, which is the ability to detected an eagle owl calling in the proximity. In this situation predation risk represents a cost of reproduction (Magnhagen 1991), however the investment put into vocal advertising should result from the complex interaction between habitat quality, individual quality and conspecific density. In areas with high conspecific density, starting to call earlier at dusk may represent a strategy to reconcile the need to call more in order to secure a territory and mate, and still have time for foraging and other activities (Penteriani 2003).

Taking into account the functions of vocalisations in tawny owls, it is not surprising that phenology influenced calling rate. Tawny owls called more during the period of post-fledging dispersal and pair bonding (September to November), which is in agreement with the results of other studies on this species (Hansen 1952; Cramp 1985; Hirons 1985; Zuberogoitia & Martínez 2000; Sunde & Bølstad 2004).

Future directions

Our study strengthens the established idea that vocal activity in owls is clearly shaped by various factors impacting on individual fitness. We believe that this work presents new opportunities which will contribute towards our understanding of vocalization patterns in nocturnal birds. Some of these factors will stimulate, while others will inhibit vocal activity, and the observed vocalization patterns in nocturnal birds should result from a complex series of trade-offs. The behavioural response of tawny owls to reduce predation risk may be costly to other components of fitness, such as those related to reproductive fitness (i.e. territory defence and mate attraction). We need to understand what are the direct and indirect consequences for tawny owls by vocalizing less. In tawny owls, a number of behavioural mechanisms have been identified which may reduce predation risk (Vrezec & Tome 2004; Sergio et al. 2007; this study) however, is there a cost dependent hierarchy in behaviours which tawny owls employ to reduce predation risk? It is possible that an intraguild predator species first employs anti-predator mechanisms to survive encounters, resulting in a minimal cost to fitness. If these behavioural mechanisms do not effectively minimise predation risk (e.g. a predator which is too efficient), a range of more costly predator-avoidance mechanisms may be employed, such as avoiding habitats associated with a high predation risk or even avoiding proximity to predators independent of habitats (Hileman & Brodie 1994; Hakkarainen et al. 2001). We strongly suggest that any future studies should integrate both intra- and inter-specific behavioural interactions when analysing vocal activity in nocturnal birds.

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ELECTRONIC SUPPLEMENTARY MATERIAL

To call or not to call? Need of conspicuousness under moonlight and predation risk fight for patterns of vocal displays

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Supplementary material (sm1)

Results of the GLMM performed on ten sub-samples with 100 randomly extracted zeros

Sub-sample	Fixed effects	Estimate β	SE	*Z*	*P*
1	Intercept	1.199	0.33	3.66	<0.001
2		1.256	0.33	3.83	<0.001
3		0.986	0.33	3.00	0.003
4		1.220	0.27	4.45	<0.001
5		1.251	0.27	4.69	<0.001
6		1.155	0.27	4.26	<0.001
7		1.295	0.26	4.96	<0.001
8		1.349	0.28	4.86	<0.001
9		1.271	0.28	4.62	<0.001
10		1.238	0.29	4.29	<0.001
1	Distance to nearest eagle owl	-0.007	0.01	-1.17	0.24
2		-0.007	0.01	-1.21	0.23
3		-0.004	0.01	-0.60	0.55
4		-0.011	0.00	-2.23	0.03
5		-0.012	0.00	-2.44	0.01
6		-0.009	0.00	-1.77	0.08
7		-0.010	0.00	-2.19	0.03
8		-0.010	0.01	-1.91	0.06
9		-0.008	0.00	-1.57	0.12
10		-0.008	0.01	-1.52	0.13
1	Presence of eagle owl calling	-0.366	0.07	-5.59	<0.001
2		-0.330	0.07	-5.04	<0.001
3		-0.316	0.07	-4.80	<0.001
4		-0.358	0.07	-5.50	<0.001
5		-0.330	0.07	-5.05	<0.001
6		-0.251	0.06	-3.89	<0.001
7		-0.388	0.06	-6.02	<0.001
8		-0.256	0.07	-3.90	<0.001
9		-0.313	0.06	-4.83	<0.001
10		-0.296	0.06	-4.59	<0.001
1	Number of conspecific neighbours	0.197	0.05	4.31	<0.001
2		0.182	0.05	3.87	<0.001
3		0.194	0.05	4.29	<0.001
4		0.144	0.04	3.60	<0.001
5		0.161	0.04	4.13	<0.001
6		0.124	0.04	3.12	0.002
7		0.138	0.04	3.60	<0.001
8		0.156	0.04	3.88	<0.001
9		0.145	0.04	3.59	<0.001
10		0.157	0.04	3.73	<0.001
1	Phenological period (1:2)	-0.144	0.05	-2.85	0.004
2		-0175	0.05	-3.42	<0.001
3		-0.119	0.05	-2.33	0.02
4		-0.177	0.05	-3.50	<0.001
5		-0.208	0.05	-4.09	<0.001
6		-0.209	0.05	-4.14	<0.001
7		-0.158	0.05	-3.12	0.002
8		-0.079	0.05	-1.55	0.12
9		-0.200	0.05	-3.99	<0.001
10		-0.127	0.05	-2.51	0.01
1	Phenological period (1:3)	-0.275	0.05	-5.49	<0.001
2		-0.231	0.05	-4.55	<0.001
3		-0.205	0.05	-4.07	<0.001
4		-0.320	0.05	-6.37	<0.001
5		-0.275	0.05	-5.41	<0.001
6		-0.238	0.05	-4.73	<0.001
7		-0.307	0.05	-6.11	<0.001
8		-0.297	0.05	-5.85	<0.001
9		-0.281	0.05	-5.53	<0.001
10		-0.253	0.05	-4.99	<0.001

1	Moon phase (0:1)	0.334	0.06	5.41	<0.001
2		0.393	0.06	6.41	<0.001
3		0.398	0.06	6.51	<0.001
4		0.386	0.06	6.25	<0.001
5		0.492	0.06	8.05	<0.001
6		0.401	0.06	6.55	<0.001
7		0.444	0.06	7.36	<0.001
8		0.418	0.06	6.85	<0.001
9		0.398	0.06	6.56	<0.001
10		0.428	0.06	7.04	<0.001
1	Cloud cover (1:2)	0.483	0.06	8.11	<0.001
2		0.377	0.06	6.24	<0.001
3		0.456	0.06	7.60	<0.001
4		0.380	0.06	6.43	<0.001
5		0.398	0.06	6.07	<0.001
6		0.420	0.06	6.95	<0.001
7		0.408	0.06	6.87	<0.001
8		0.398	0.06	6.64	<0.001
9		0.370	0.06	6.16	<0.001
10		0.364	0.06	6.11	<0.001
1	Interaction moon phase and cloud cover	-0.384	0.09	-3.37	<0.001
2		-0.322	0.09	-3.70	<0.001
3		-0.387	0.09	-4.53	<0.001
4		-0.341	0.09	-4.00	<0.001
5		-0.392	0.09	-4.57	<0.001
6		-0.319	0.09	-3.69	<0.001
7		-0.391	0.07	-4.54	<0.001
8		-0.386	0.09	-4.42	<0.001
9		-0.378	0.09	-4.40	<0.001
10		-0.336	0.09	-3.88	<0.001
1	Autocovariate	0.007	0.04	0.18	0.86
2		0.007	0.04	0.18	0.86
3		0.009	0.04	0.23	0.82
4		0.057	0.03	1.76	0.08
5		0.039	0.03	1.24	0.22
6		0.057	0.03	1.78	0.08
7		0.045	0.03	1.47	0.14
8		0.020	0.03	0.62	0.54
9		0.034	0.03	1.08	0.28
10		0.024	0.03	0.71	0.48
	Random effects	Variance		SD	
1	Station	0.098		0.314	
2		0.069		0.262	
3		0.106		0.326	
4		0.000		0.000	
5		0.000		0.000	
6		0.001		0.030	
7		0.000		0.000	
8		0.023		0.153	
9		0.010		0.098	
10		0.019		0.137	
1	Target tawny owl territory	0.233		0.482	
2		0.292		0.540	
3		0.222		0.472	
4		0.302		0.550	
5		0.283		0.532	
6		0.292		0.541	
7		0.270		0.520	
8		0.248		0.498	
9		0.276		0.526	
10		0.291		0.539	

Supplementary material (sm2)

Tawny owls exhibit a white throat badge when they call, that may serve as a means of visual communication during vocal displays (Photos: Romilly Hambling).

Chapter 6

GENERAL DISCUSSION

6.1. The frequency and incidence of predatory interactions among vertebrate top predators

In the last four decades, field research has frequently brought to light episodes of predatory interactions among vertebrate top predators, which were reported mostly because of their unusual character (e.g. Herrera 1973, Insley and Dugan 1973, Mikkola 1976, Klem et al. 1985, Real and Mañosa 1990, Rohner and Doyle 1992, Tella and Mañosa 1993, Bosch et al. 2007, Sørensen et al. 2008). Accordingly, there was a general impression that predation among top predators were in fact occasional events. However, more or less in the last ten years, several articles have contributed to reverse this idea, showing that predatory interactions among vertebrate top predators are widespread, meaning that most of these species are exposed to predation, most frequently by a larger species or by social predators (Palomares and Caro 1999, Heithaus 2001, Caro and Stoner 2003, Hunter and Caro 2008, Sergio and Hiraldo 2008). Yet, most of these works do not quantify how frequently a top predator will prey on another top predator.

In chapter 2 "**Superpredation patterns in four large European raptors**" we have studied the diet of four large raptors which are at the top of food webs in many European ecosystems. This study represents the first published large-scale approach to the quantification of superpredation in vertebrate top predators. We concluded that, from the studied raptors, the Golden Eagle *Aquila chrysaetos* had the highest average percentage of mesopredators in its diet (6.6% of the prey), which represented 8.0% of the biomass consumed by this species. Mammalian carnivores were the group of mesopredators mostly captured by golden eagles (5.3%). On the other side, owls were mainly victims of the nocturnal superpredator, the Eagle Owl *Bubo bubo*, a fact most probably related to both predator and prey having nocturnal activity rhythms. The Bonelli's Eagle *Aquila fasciata* and the Goshawk *Accipiter gentilis* showed lower percentages of mesopredators in the diet, still the values were close to 2% of the prey captured.

To help analysing these results in a wider raptor community context, we have compiled the percentage of mesopredators in the diet of other large European raptors, that may as well act as superpredators (Table 1). It is possible to confirm that the four raptors selected in chapter 2 showed higher average percentage of mesopredators than other large European raptors, such as the Spanish Imperial Eagle *Aquila adalberti*, White-tailed Eagle *Haliaeetus albicilla*, Ural Owl *Strix uralensis*, or Great Grey Owl *Strix nebulosa*. Although variable, all these eight raptors regularly engage in superpredatory interactions. Hence, it is possible to conclude that wherever large raptors occur, there will be a certain degree of effect on the populations of mesopredators caused by predatory events.

Table 1. Percentage of mesopredators in the diet of four large European diurnal raptors and owls, in addition the species studied in chapter 2.

Region and reference	Sample size	Mammalian carnivores	Diurnal raptors	Owls	Meso predators
Spanish Imperial Eagle *Aquila adalberti*					
Doñana, Spain (Delibes 1978)	479	0.0	0.2	0.4	0.6
Sierra Morena, Spain (Delibes 1978)	171	0.0	0.6	0.0	0.6
Spain (Sánchez et al. 2008)	1161	0.3	0.5	0.3	1.0
White-tailed Eagle *Haliaeetus albicilla*					
Scotland (Watson et al. 1992)	804	0.9	0.4	0.2	1.5
Finland (Sulkava et al. 1997)	3152	0.6	0.2	0.1	0.9
Netherlands (van Rijn et al. 2010)	213	0.0	0.0	0.0	0.0
Ural Owl *Strix uralensis*					
Finland (Korpimäki and Sulkava 1987)	6022	0.6	0.0	0.2	0.8
Belarus (Tishechkin 1997)	613	0.2	0.0	0.0	0.2
Great Grey Owl *Strix nebulosa*					
Belarus (Tishechkin 1997)	454	0.2	0.0	0.0	0.2

In **chapter 2** we also found that superpredation episodes occurred in almost all diet studies of the four raptors. Therefore, we can conclude that superpredation and intraguild predation by raptors are spatially widespread phenomena across Europe. This same idea has been mentioned in studies reviewing intraguild predation, considering the large number of studies reporting these complex species interactions (Arim and Marquet 2004, Sergio and Hiraldo 2008).

We also found that superpredation rates are highly variable across Europe, with higher percentages of mesopredators being most frequently associated with ecosystems where human influence is larger (Central Europe mainly). This fact suggests that human-caused habitat changes can alter animal communities, modifying predation dynamics in vertebrate top predators.

We could not find evidence of a temporal variation in superpredation rates at the continental-scale, as could be expected having into account the increasing human pressure on ecosystems in the last decades. Nevertheless, because diet composition is known to change along short and long-time periods at a regional scale (Férnandez 1993, Toyne 1998, Nielsen and Drachmann 1999, Martínez and Zuberogoitia 2001, Moleón et al. 2009), future research should look for variations in superpredation rates in long-term diet data on a local scale.

6.2. Why do large raptors engage in superpredation and intraguild predation?

Vertebrate predator species, such as mammalian carnivores, diurnal raptors and owls, are not expected to represent staple prey for large raptors. This is mainly because: (1) the abundance of top predator species is generally low when compared to the abundance of species from lower trophic levels, thus the effort (time and energy) spent to search for them is higher; (2) top predators are frequently fast and agile species, which may be harder to catch; and (3) top predators are generally dangerous prey because of their large size, but above all, they are well equipped to attack (e.g. claws, large teeth), and these same tools can also be very effective in defence.

In agreement with the above mentioned, in **chapter 2** we found that the biomass that large raptors obtained through superpredation events was relatively low (between 1.8 and 8.0%), meaning that mesopredators were occasional prey species that just complemented the food intake of basic ones (e.g. rabbits, hares, rats, pigeons, partridges). Moreover, we also found that superpredation was associated with lower breeding performance, suggesting that mesopredators generally do not seem to represent profitable prey items.

Considering all this facts, what justifies the effort taken by top predators to engage in superpredation acts? Several hypotheses have been suggested and analysed, which may, separately or jointly, contribute to the emergence of predatory interactions among top predators.

The **food-stress hypothesis** is possibly the most studied and accepted reason for vertebrate top predators to engage in superpredation acts. The rationale behind this hypothesis is simple: (1) the diet of a top predator is generally composed by prey species which are not top predators; (2) normally, these prey species are abundant enough to sustain a stable population of the top predator; (3) when there is a decline of one or several of the staple prey species, the top predator enters in a food-stress situation; (4) facing this, top predators must diversify their diet to cope with the lack of their usual prey; (5) then, the top predator may have more frequent predatory encounters with other top predators; or (6) may actively search for top predators as alternative prey. Thus, due to food-stress situations, those predator species that the superpredator would normally not invest time and energy trying to catch, turn into food resources that are necessary for survival. This hypothesis first appeared when researchers related superpredation events with observed declines of staple prey in the field (Rohner and Doyle 1992, Tella and Mañosa 1993, Sunde et al. 1999, Serrano 2000). In **chapter 2** we presented the first study, covering a broad area, which supports the food-stress hypothesis by showing that superpredation increases when the percentage of staple prey in the diet declines, and sometimes diet diversity increases simultaneously.

The **competitor-removal hypothesis** stands on the idea that intraguild predation facilitates the deliberate elimination of competitors, with additional energetic benefit (Polis et al. 1989, Palomares and Caro 1999, Sergio and Hiraldo 2008). In this case it is assumed that the intraguild predator identifies a species as competitor and deliberately preys on it. Here, intraguild predation is ultimately an extreme form of interspecific interference competition where killing occurs, and the victim is totally or partially consumed.

The fact that intraguild prey are more frequently partially consumed than non-guild prey has been considered evidence supporting this hypothesis (Sunde et al. 1999). According to this hypothesis, the frequency of intraguild interactions should be higher in areas where the abundance of the staple prey is less abundant, because intraguild predators have a greater need to eliminate competitors (Palomares and Caro 1999, Sunde et al. 1999). However, as shown in **chapter 2** and also observed by Serrano (2000), predatory interactions among vertebrate top predators are often not among competitors (cases of superpredation but not of intraguild predation). Hence, a way to separate food-stress and competitor-removal hypotheses is to analyse if the predation is mainly focused on competitors or if it is evenly distributed across mesopredator species (either competitors or not). Still, there is a lack of studies clearly addressing the competitor-removal hypothesis and testing it.

The motivation behind the **predator-removal hypothesis** is the deliberate elimination of a potential predator or a very aggressive mobber, which can represent a serious threat to the individual or its brood. This issue has very seldom been raised as a mechanism justifying predatory interactions among vertebrate top predators (Eaton 1979, Palomares and Caro 1999). The manuscript in chapter 3 "**Kill before being killed: an experimental approach supports the predator-removal hypothesis as a determinant of intraguild predation in top predators**" constitutes the first formal presentation of the predator-removal hypothesis. Predator-removal reasoning happens in situations of potential symmetrical intraguild predation (Polis et al. 1989), which can occur when an intraguild prey species can, even if seldom, kill its intraguild predator or its young. The predator-removal hypothesis can then also be considered as a defensive counter-strategy, which we designated as the "kill before being killed" behaviour. Consequently, potential predators of very aggressive mobbers might be preferential targets of intraguild predation by large raptors. The experiment carried out in **chapter 3** supports this hypothesis, showing that the eagle owl is frequently a target of aggressive mobbing by diurnal raptors, which can often reach killing attempt. This can be enough for the eagle owl to perceive these raptor species as potential predators and consequently, take advantage of nocturnal hunting conditions to remove them. Research on this subject is still in an emergent state and further work is required to elucidate how this behaviour occurs.

As a conclusion, I would suggest the possibility that more than one motivation may be behind raptors engaging in predatory interactions with other vertebrate top predators, and so future experiments should consider these entangled behaviours.

6.3. Signals and consequences of predatory interactions for the superpredator

As previously exposed in **chapter 2** and **section 6.2**, raptors might engage in superpredation acts when under food stress situations (see also Tella and Mañosa 1993, Serrano 2000). Also, some studies have found that, when food availability is scarce, breeding success in raptor species might also decrease (Tjernberg 1983, Fernández 1993, Steenhof et al. 1997, Martínez and Calvo 2001, Martínez and Zuberogoitia 2001, Penteriani et al. 2002, Nyström et al. 2006, Whitfield et al. 2009). Accordingly, a correlation between increases in superpredation and decreases in breeding success would be expected to occur. However, no previous analyses on the subject had been conducted until now. In **chapter 2**, we show that there is a negative association between the percentage of mesopredators in the diet and breeding performance: raptors that show high superpredation rates, generally have low breeding success. So, despite the possible effort of a top predator to increase superpredation as a way to compensate situations of food stress, negative effects on breeding performance might still persist. Therefore, the increase in superpredation rate can be interpreted as an alarm signal for decreasing breeding performance, which is consequence of a decrease in prey availability. Thus, long-term diet studies, in which superpredation rates can be monitored, have the potential to represent useful tools for conservation.

The increase in superpredation rates causes a larger consumption of biomass from prey at higher trophic levels (mesopredators). Generally, carnivorous species (mesopredators) have higher concentrations of persistent contaminants then herbivorous species, caused by a biomagnification process. So, as trophic chain length increases due to the predatory interactions among top predators, so does the concentration of persistent contaminants in superpredators. As a result, those large raptor individuals that engage in superpredatory interactions might have higher concentrations of widespread pollutants such as mercury (Hg), highly toxic in its organic form (Hylander and Goodsite 2006).

In chapter 4 “**Superpredation increases mercury levels in a generalist top predator, the eagle owl**” we analysed the bioaccumulation of mercury in the eagle owl. We found that the inclusion of more mesopredators in the diet of this superpredator was associated with larger Hg concentrations. Therefore, mercury bioaccumulation can be an additional negative effect to top predators under food stress.

In conclusion, habitat degradation caused by human activities might negatively affect the breeding success and the survival of vertebrate top predators, because of food-stress situations, and the consequent increase in bioaccumulation of persistent contaminants due to predatory interactions among top predators.

6.4. How do predatory interactions influence raptors (IG prey) which are under predation risk

Predation is a central feature of ecological communities, one of the most complex systems researchers have tried to understand. Most ecological theory has viewed predator-prey interactions in terms of consumption, where predators reduce prey population densities through direct consumption, that is, a **density-mediated effect** (also known as numerical or lethal effect; Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008). However, predators can also affect prey population density by inducing phenotypic changes associated with predation risk, that can be developmental, morphological, physiological, or behavioural (Lima and Dill 1990, Werner and Peacor 2003, Luttbeg and Kerby 2005). The costs of these defensive strategies are **trait-mediated effects** (also known as behavioural, non-lethal, or sub-lethal effects), and include reduced energy income (changes in foraging effort), energetic investment in defensive structures, lower mating success, increased vulnerability to other predators, or emigration (Abrams 1984, Preisser et al. 2005, Creel and Christianson 2008). The study of trait-mediated effects associated with intimidation by a predator has been considered within the sub-discipline of **ecology of fear** as part of game theory between predator and prey (Brown et al. 1999, Ripple and Beschta 2004).

Trait-mediated effects are a very common feature of predator-prey interactions (Lima and Dill 1990, Werner and Peacor 2003, Schmitz et al. 2004, Cresswell 2008), and these can often exceed the effects of direct consumption (Abrams 1984, Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008).

Trait values depend on allocation decisions, so the allocation of time to one trait (e.g. vigilance) due to predation pressure, often comes at the cost of reducing time to another (e.g. feeding rate), meaning that trade-offs exist (Werner and Peacor 2003, Lima and Bednekoff 1999). Quantitative expression of a defensive trait might enhance an aspect of performance while decreasing another. In chapter 5 "**To call or not to call? Need of conspicuousness under moonlight and predation risk fight for patterns of vocal displays**", the study of the vocal behaviour of tawny owls *Strix aluco* showed that this species can reduce its vocal activity in order to reduce the risk of intraguild predation by the eagle owl. In turn, the trait-mediated direct effect may lead to a decrease in territory defence and mate attraction abilities in tawny owls that have eagle owls as neighbours. So, tawny owls are faced with a trade-off when it comes to allocating time to vocal activities.

Since large vertebrate predators are behaviourally plastic and sophisticate (Brown et al. 1999), trait-mediated effects resulting from predatory interactions among them may be potentially relevant to their life-history (e.g. survival, breeding performance), distribution and use of space. Scientific literature has several examples of trait-mediated effects resulting from predatory relations involving large predators (mammalian carnivores, birds of prey), some of which we will discuss next.

6.4.1. Trait-mediated effects resulting from behavioural mechanisms to deal with predation risk

6.4.1.1. Cues of predation risk

The anti-predatory response of a prey is necessarily dependent on the cues it can assess to infer the risk of predation. Vertebrates may use a large variety of direct (auditory, olfactory, or visual) and indirect cues (e.g. habitat, moonlight). For example, Brown and colleagues (1988) demonstrated that rodents can use both direct (owl presence) and indirect cues (illumination) to assess predatory risk, and accordingly reduce their foraging activity. Gerbils also use visual (owl in flight) and auditory direct cues (owl hunger calls) to adjust their activity in order to reduce predatory risk (Abramsky et al. 1996). Hedgehogs *Erinaceus europaeus* use badger *Meles meles* faeces as a direct cue to assess the risk of encountering this potential intraguild predator (Ward et al. 1997). Cheetahs use a direct auditory cue (playback of the roar of lions, an intraguild predator) and respond by moving away from the call and reducing their hunting activity (Durant 2000). White-footed mice *Peromyscus leucopus* use a combination of direct (owl calls) and indirect cues (moonlight) to assess predation risk and reduce their activity in space only if detect owl calls during a full moon (Schmidt 2006). In an intraguild predation scenario, foxes *Vulpes vulpes* use direct cues (e.g. scats) to assess predation risk by wolves *Canis lupus* and moonlight as an indirect cue of risk of predation by hyenas *Hyaena hyaena* (Mukherjee et al. 2009).

The study of cues used to assess the risk of intraguild predation is still insufficient, especially in raptors. In **chapter 5**, we found that tawny owls can use the vocalizations of their intraguild predator, the eagle owl, as a direct cue of predation risk.

Cues can be more or less reliable, which can have a strong influence on the behaviour displayed to reduce predation risk. Prey with perfect information, will know exactly where the predator is, which means that they know if the predator is present in the patch or not, and exactly when it arrives, thus can instantly take on the optimal level of anti-predatory response (Brown et al. 1999). On the other side, the prey may know the number of predators and probability of being within the patch but be ignorant of predator whereabouts (Brown et al. 1999). In these cases, the prey will retain the same level of anti-predatory response regardless of whether the predator is present in the patch or not, meaning that the prey will be over-vigilant when the predator is absent and under-vigilant when it is present (Sih 1984, Abrams 1994). A third possibility is having to deal with imperfect information, meaning that the prey are uncertain of the whereabouts of the predators but are able to estimate the encounter rate with predators based on cues (Brown et al. 1999). In these situations, the prey adjust their background level of apprehension when they obtain information regarding the possible presence of predators.

In conclusion, depending on the cues available to assess predatory risk, mesopredators should use those behavioural mechanisms that best reduce the probability of an encounter with a superpredator.

6.4.1.2. Predator avoidance behaviour

Predator avoidance behaviours represent a category of mechanisms aimed at enhancing the survivorship of a species by reducing the probability of occupying the foraging habitat of potential predators (Brodie et al. 1991, Hileman and Brodie 1994). It has been suggested that top predators can avoid superpredators in three ways: (1) spatial avoidance (distance-sensitive avoidance) – the top predator selects areas at a safe distance from the superpredator, taking advantage of superpredator-free sites (predation refugia; Kostrzewa 1991, Palomares et al. 1996, Durant 1998, Sergio et al. 2003, 2007); (2) habitat-mediated avoidance (risk-sensitive habitat selection) – the top predator avoids habitats with higher risk of encountering the superpredator (Fedriani et al. 2000, Sergio et al. 2007, Sergio and Hiraldo 2008); (3) temporal segregation – the top predator alters its activity patterns in order to avoid the superpredator (Fedriani et al. 1999).

The evolution of mechanisms of predator avoidance by top predators that face intraguild predation risk is fairly well documented, suggesting that these behaviours may be frequent. The mechanism of spatial avoidance is common in vertebrate top predators, including raptors. For example, common buzzards *Buteo buteo* and honey buzzards *Pernis apivorus* avoid the proximity of goshawk nests (Kostrzewa 1991). The probability that common buzzards occupy the same territory the next year is smaller when exposed to predation risk by goshawks in the previous breeding season (Hakkarainen et al. 2004). Tengmalm's owl *Aegolius funereus* increase nest-hole shift and breeding dispersal distances when more exposed to predation risk by mustelids (Sonerud 1985, Hakkarainen et al. 2001); and avoid the vicinity of Ural owl nests (Hakkarainen and Korpimäki 1996). The return rate of merlins *Falco columbarius* to breeding sites in the next season was lower when subjected to nest predation in the previous season (Wiklund 1996). Black kites select predation-refugia to avoid nesting in close to eagle owls (Sergio et al. 2003). Spatial avoidance of superpredators (e.g. golden eagle, eagle owl) has also been well documented in peregrine falcons *Falco peregrinus* (Gainzarain et al. 2000, Sergio et al. 2004, Martínez et al. 2008). In the Alps, the scops owl *Otus scops* avoids proximity to tawny owls (Sergio et al. 2009). All these examples show how important it is to consider the possible spatial avoidance effects caused by predatory interactions when studying habitat selection in raptors. Sergio and colleagues (2007) presented a case of shift between distance-sensitive avoidance and habitat-mediated avoidance in tawny owls exposed to predation by eagle owls.

In **chapter 5**, we saw that sometimes the intraguild prey cannot avoid sharing space with the intraguild predator, and that under this scenario they may need to use anti-predator behaviours to reduce predation risk, as discussed next.

6.4.1.3. Anti-predator behaviour

Anti-predator behaviours are mechanisms used by prey to reduce the probability of successful predation when they share the habitat with predators aware of their presence (Brodie et al. 1991, Hileman and Brodie 1994). Anti-predator behaviours represent alternatives to predator-avoidance mechanisms, and facilitate the coexistence of the predator and prey in the same habitat. Anti-predator mechanisms may be broadly separated into pre-attack and post-attack mechanisms (Hileman and Brodie 1994). For a prey, avoiding a predator attack is frequently consequence of reducing its detectability, and this can include short-term behaviours like immobility, crypsis, fleeing and hiding (Hileman and Brodie 1994, Sergio and Hiraldo 2008).

In **chapter 5**, we have seen that tawny owls can use an anti-predator behaviour to avoid predation by eagle owls. Tawny owls reduce their vocal activity when they have information on the presence of an eagle owl by detecting the calls of the intraguild predator. By doing this, tawny owls can reduce the risk of being detected despite occupying the same microhabitat. This behaviour revealed a trade-off between the need to call (for territory defence and mate attraction purposes) and the risk of predation by a predator that can use vocalizations to detect its intraguild prey.

There are a few studies illustrating anti-predator mechanisms in birds of prey used in an intraguild predation or superpredation context. Fleeing is perhaps one of the simplest anti-predator behaviours, and common buzzards use this behaviour when faced with goshawk dummies (Krüger 2002). Little owls *Athene noctua*, besides fleeing for shelter, can alternatively stay quiet and silent when they detect the presence of barn owls *Tyto alba*, their potential predator (Zuberogoitia et al. 2008). Spotted owls *Strix occidentalis* suppress their calling behaviour when detect the presence of barred owls *Strix varia* (Crozier et al. 2006).

In conclusion, as trait-mediated effects might complicate the empirical assessment of predatory interactions among top predators, it is not safe to assume that consumption rates are a good measure of the top predator's impact on intraguild prey (Abrams 1993, Preisser et al. 2005). Despite low consumption rates, trait-mediated effects may be strong, and thus predatory interactions among top predators may have far more importance in determining community structure than previously supposed by consumption rates alone (Werner and Peacor 2003, Preisser et al. 2005, Creel and Christianson 2008, Cresswell 2008).

6.5. Concluding remarks: conservation implications of predatory interactions among vertebrate top predators

It is well established that humans have persecuted apex predators for millennia, often leading to their regional extinction (Woodroffe 2000, Prugh et al 2009). Typical examples of persecuted species in Europe are wolves *Canis lupus*, brown bears *Ursus arctos*, lynxes *Lynx lynx* and *L. pardinus*, golden eagles *Aquila chrysaetos*, or eagle owls *Bubo bubo*, and, in the last centuries, this persecution has caused severe range reduction of these top predators (Mikkola 1983, Delibes 1990, Boitani 1992, Mech 1995, Breitenmoser 1998, Whitfield et al. 2004, McLellan et al. 2008). There are many reasons why people have tried to eradicate top predators, but recently, perhaps the most important motivation is that they compete with us for food (Graham et al. 2005). This conflict with human populations happens mostly because these large vertebrates prey on game species and domestic livestock (Villafuerte et al. 1998, Thirgood et al. 2000, Kenward et al. 2001, Baker et al. 2008, Park et al. 2008). In marine ecosystems vertebrate top predators have also been persecuted (e.g. sharks, dolphins, killer whales, seals), but these mostly for being food resources or as fisheries bycatch (Baum et al. 2003, Myers and Worm 2003, Heithaus et al. 2008). For centuries, persecution of top predators has been supported by governments (Breitenmoser 1998, Berger 2006), and despite many countries have banned these practices, mostly due to pressure from international conservation laws, top predators are still illegally persecuted (Villafuerte et al. 1998, Pedrini and Sergio 2001, Whitfield et al. 2003, Smart et al. 2010).

Traditionally, in many studies of community structure, top predators have just been seen as species that eat herbivores. However, their role in food webs can be far more complex than this, as most apex predators are omnivorous, extending across multiple trophic levels (Ritchie and Johnson 2009, see also chapter 2). Such complexity has frequently confounded researchers when attempting to anticipate how populations or communities will respond to human interventions (Polis and Strong 1996). As previously mentioned in this thesis, predatory interactions among vertebrate top predators can be rather common, and hence the effects of the decline of top predators on mesopredators should be thoroughly accounted in a conservation perspective.

6.5.1. Mesopredator release

Mainly in the past 20 years, research focusing on the worldwide decline of vertebrate top predators has demonstrated that, frequently, an undesired increase in mesopredators follows a local crash of a top predator (Prugh et al. 2009, Ritchie and Johnson 2009). These mesopredator outbreaks were first named by Soulé and colleagues (1988) as the **mesopredator release effect**. Prugh and colleagues (2009) defined mesopredator release more broadly as “the expansion in density or distribution, or the change in behaviour of a middle-rank predator, resulting from a decline in the density or distribution of an apex predator”. Therefore, the mesopredator release is essentially the result from a change in a predatory interaction among top predators (superpredation and intraguild predation). Mesopredator release can most frequently be read as a signal of ecosystem imbalance, but besides affected by top-down effects (e.g. apex predator decline due to persecution) it can also be influenced by bottom-up effects, like the availability of food resources and variations in habitat structure (Litvaitis and Villafuerte 1996, Elmhagen and Rushton 2007, Ritchie and Johnson 2009). The ability of apex predators to suppress populations of mesopredators is a well known ecological process, supported by many published studies (e.g. Boveng et al. 1998, Sergio et al. 2003, Helldin et al. 2006, Berger and Gese 2007, Sergio et al. 2007, Johnson and VanDerVal 2009). Human influence on ecosystems, and the decline in top predator species are both global processes, and accordingly, researchers have found that the mesopredator release is a widespread phenomenon, occurring in most continents and a wide variety of systems (Heithaus et al. 2008, Prugh et al. 2009, Ritchie and Johnson 2009).

The mesopredator release effect has been mostly documented in mammalian carnivores. A classic example is that of Soulé and colleagues (1988, see also Crooks and Soulé 1999), where the absence of coyotes *Canis latrans* caused the release of several native and exotic mesopredator species, which in turn caused local extinction of some bird species. Australia is the stage of a continent-wide mesopredator release example, as the decline of dingoes *Canis lupus dingo* has favoured the increase of non-native mesopredators, with catastrophic consequences for the native marsupials (Johnson et al. 2007). In Sweden, the decline of wolves and Eurasian lynx has favoured the increase of red fox *Vulpes vulpes* (Elmhagen and Rushton 2007). Similarly, the decline of the Iberian lynx *Lynx pardinus* in Doñana seems to have caused an increase in the population size of smaller carnivores (Palomares et al. 1996).

Some examples of mesopredator release involve the disruption of the native community by introduced species, which often creates conservation dilemmas about the removal of alien top and mesopredators (Courchamp et al. 1999, Roemer et al. 2002, Rayner et al. 2007). But the potential mesopredator release in native species also has to be accounted when defining conservation actions: it is the case of sea turtle nest protection, where removing raccoons *Procyon lotor* to decrease egg mortality triggers the release of a mesopredator which is also an egg predator, and increases total predation pressure (Barton and Roth 2008).

Our understanding of the effects of mesopredator release is strongly biased towards mammalian carnivores (Ritchie and Johnson 2009), but there are also some examples in marine vertebrates (Myers et al. 2007, Baum and Worm 2009, Ferretti et al. 2010). To our knowledge, mesopredator release caused by the decline of large raptors has seldom be studied, existing mainly empirical evidence of smaller raptors being more abundant where large raptors are scarce (e.g. Gainzarain et al. 2000, 2002, Petty et al. 2003, Sergio et al. 2003, 2007, Martínez et al. 2008). An exception is the three level guild study of Chakarov and Krüger (2010) who found that the recolonization by a superpredator, the eagle owl, caused the decrease of goshawk density, which in turn released buzzards from predation risk by the goshawk.

Concluding, top predators generally play an important role in controlling mesopredator populations, thus it is fundamental to study predatory interactions among large vertebrate predators as a way to foresee mesopredator releases and be able to best react before conservation needs. The effects of these predatory interactions will be best understood within a broad food web context (Holt and Huxel 2007).

6.5.2. Do top predators promote biodiversity?

The idea that keystone predators could regulate biodiversity was first introduced by Paine (1966), and since then, researchers have seen that vertebrate top predators can promote species richness or are associated with it, although their surrogate efficacy as seldom been tested (Sergio et al. 2005, Sergio et al. 2006, Ale and Whelan 2008, Sergio et al. 2008). The use of top predators as conservation tools is not unanimous among researchers (Kerr 1997, Andelman and Fagan 2000, Linnell et al. 2000, Cabeza et al. 2008, Kéry et al. 2008, Roth and Weber 2008; see also Sergio et al. 2008). Still, top predators have frequently been used as keystone, umbrella, sentinel, flagship, and indicator species (Simberloff 1998, Caro and O'Doherty 1999, Sergio et al. 2008), in part because of the respect and admiration they inspire, which attracts the attention of the general public.

Predatory interactions among top predators (superpredation and intraguild predation) are mechanisms by which these species can promote biodiversity via resource facilitation and top-down trophic cascades (Sergio et al. 2007, Sergio et al. 2008). In this thesis we have seen that large birds of prey have a strong potential to influence mesopredator populations, which can cascade to lower trophic levels and determine community structure and diversity. If on the one side the loss of top predators is known to lead to biodiversity loss, often compromising ecosystem functioning (Berger et al. 2001, Estes et al. 2001, Terborgh et al. 2001), on the other side, there are a few examples where the top predator is affecting a mesopredator species of conservation concern, like African wild dogs *Lycaon pictus* (Creel and Creel 1996), cheetahs *Acinonyx jubatus* (Durant 1998, 2000), or black kites *Milvus migrans* (Sergio et al. 2003), sometimes resulting in biodiversity loss, as the case of the predation of killer whales on sea otters (Estes et al. 1998). Therefore, conservation science needs to watch carefully how predatory interactions among top predators are entangled with our conservation goals. The most important step is perhaps to develop long-term monitoring programs of apex and mesopredator populations, if possible integrated in a food web context. Management of apex predators might be employed as a conservation tool (Ritchie and Johnson 2009). And, although the effort to preserve and restore top predator populations may be costly, it can generate ecosystem services such as greater ecosystem resilience and mesopredator control by top predators. Nevertheless, we still need more rigorous cost-benefit analyses accounting for the ecosystem services of vertebrate top predators (Prugh et al. 2009). But the conservation of top predators in human-modified landscapes requires improved habitat management and educational programs to teach populations to live along with top predators (Linnel et al. 2001).

All we believe to know about the outputs of predatory interactions among top predators might suddenly change when dealing with different communities or ecosystems. It is crucial to increase our knowledge on these subject since beyond typical predator-prey interactions there is much more than meets the eye.

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