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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

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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 (74–300 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

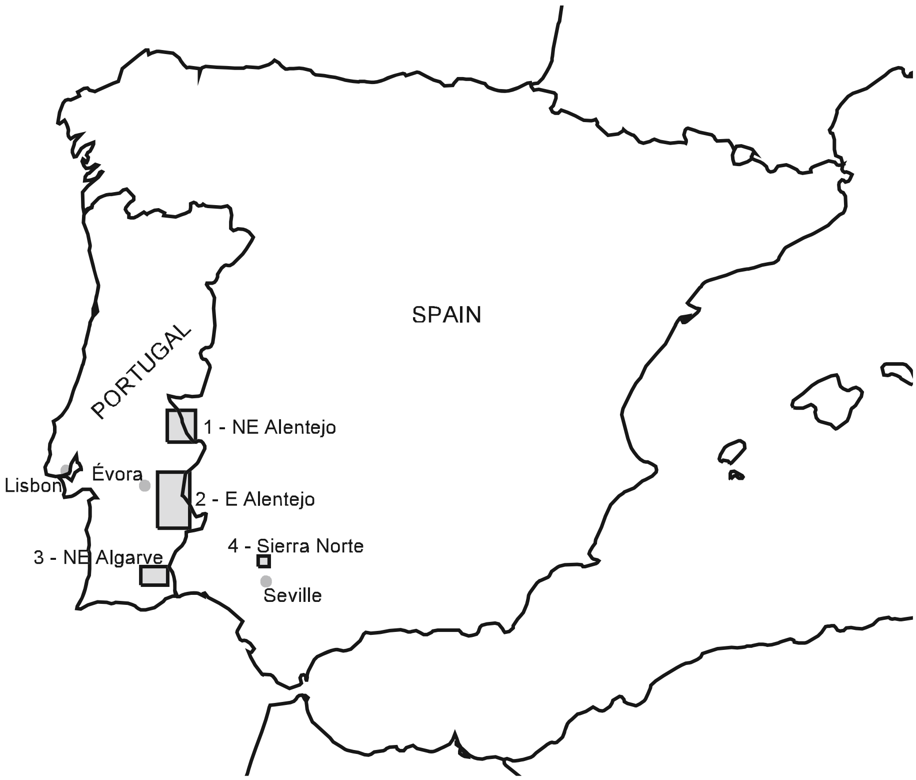

Fig. 1 Location of the four study areas

(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*).

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 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 and 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).

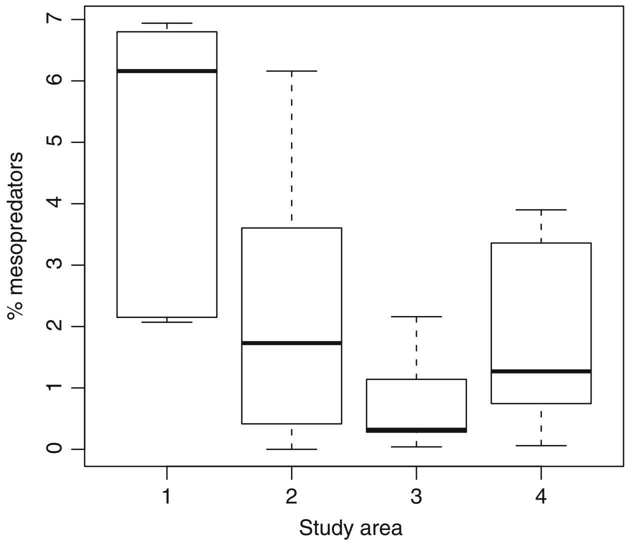

Fig. 2 Percentage of mesopredators (superpredation) in the diet of eagle owls in 33 territories in the four study areas (see text for details). *Box* and *whisker plots* show the median, 25% quartiles and range

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

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).

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

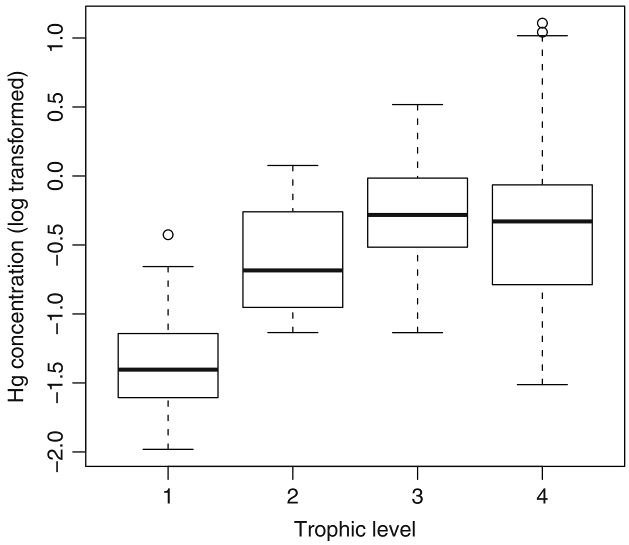

Fig. 3 Hg concentration as a function of trophic level: *1* primary consumers ($n = 53$); *2* secondary consumers ($n = 22$); *3* mesopredators ($n = 32$); *4* top predator (eagle owl, $n = 61$). *Box* and *whisker plots* show the median, 25% quartiles and range

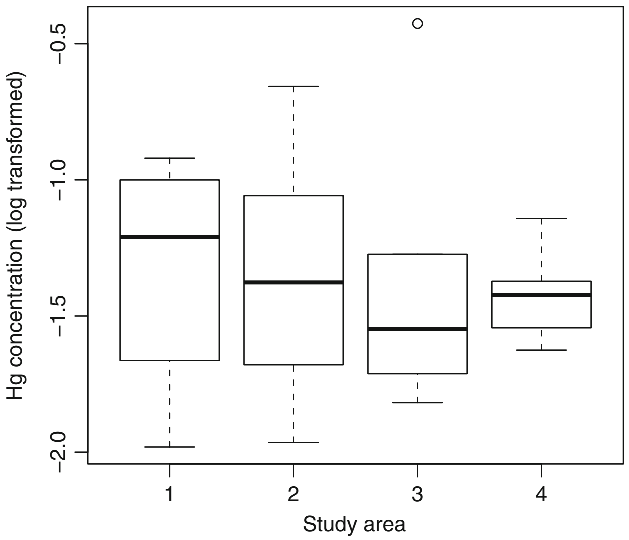

Fig. 5 Hg concentration (mg kg^{-1}) in primary consumers in the four study areas ($n_1 = 8$, $n_2 = 25$, $n_3 = 5$, $n_4 = 15$; see names in text). *Box* and *whisker plots* show the median, 25% quartiles and range

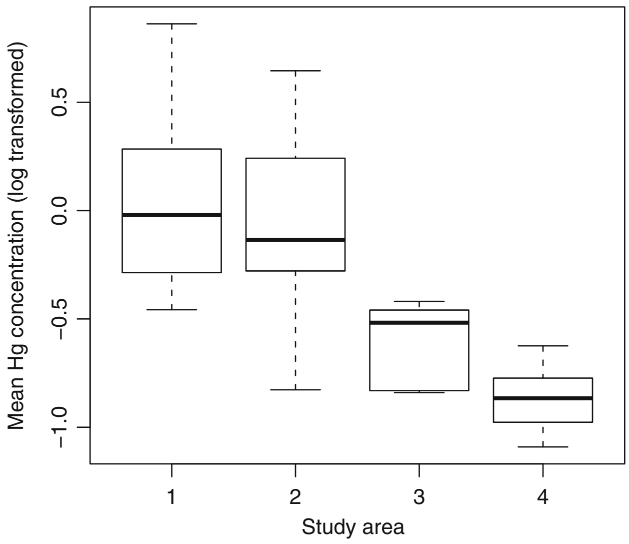

Fig. 4 Mean Hg concentration (mg kg^{-1}) in eagle owls in 33 territories in the four study areas (see names in text). *Box* and *whisker plots* show the median, 25% quartiles and range

($F = 11.05$, $DF = 3$, $P < 0.001$, $n = 33$), 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).

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; Rice1989), 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 ($\beta = 0.18$, $SE = 0.35$, $t = 0.502$, $P = 0.622$).

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 non-invasive 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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