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ARTICLES

Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance?

FABRIZIO SERGIO*, LUIGI MARCHESI†, PAOLO PEDRINI† & VINCENZO PENTERIANI*
*Estación Biológica de Doñana, Sevilla
†Trento Natural History Museum, Trento

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Intraguild predation is increasingly reported as a population-limiting factor for vertebrate predators. However, long-term coexistence of the intraguild prey with its predator is a common occurrence usually maintained by some form of predator avoidance, which may be achieved through distance-sensitive avoidance (selection of sites as far as possible from the intraguild predator), and/or habitat-mediated avoidance (avoidance of habitats associated with high predation risk). The former is expected when the distribution of the predator is heterogeneous, leaving gaps which can be exploited by the prey, while the latter is expected at high predator densities, when few predation refugia are available. To date, few studies have focused on such switch in predator avoidance under changing scenarios of intraguild predator density. To test this hypothesis, we censused tawny owls (*Strix aluco*, body mass ~0.4–0.7 kg) and their intraguild predator, the eagle owl (*Bubo bubo*, ~1.5–4 kg), in 12 areas of the Alps. As predicted, tawny owls were indifferent to predator distance in an area of low predation risk, they switched to distance-sensitive avoidance in an area of medium predator density and to habitat-mediated avoidance in an area of high predator density with few available refugia. Actual predation rates were low, but increased with proximity to the intraguild predator nest. Similarly, tawny owl breeding output declined with closeness to an eagle owl nest. Habitat loss associated with predator avoidance translated into population effects, leading to a negative relationship between the densities of the two owl species. The spatial gaps in tawny owl distribution caused by eagle owls indirectly favoured other owl species, resulting in higher diversity of the overall owl community and suggesting that eagle owls acted as keystone predators. Our results suggest that intraguild predation may alter habitat choices and affect density, productivity and guild structure of vertebrate mesopredators. Such effects are probably more common than previously thought.

Keywords: *Bubo bubo*; competition; eagle owl; interactions; predation refugia; *Strix aluco*; tawny owl

Intraguild predation, the killing by a predator of species that use similar resources and are thus potential competitors, has been reported as ubiquitous in terrestrial and aquatic food webs (Polis & Holt 1992). Increasing evidence suggests that intraguild predation may affect the distribution and limit the populations of top predatory species, including such diverse taxa as arthropods, carnivores, birds of prey, fish and amphibians (e.g. Huang & Sih 1991; Hileman & Brodie 1994; Creel et al. 2001; Petty et al. 2003), with pronounced repercussions on guild structure and community diversity and stability (review in Polis et al. 1989).

In vertebrates, intraguild predation systems are usually asymmetrical and size based, with a larger, dominant species (intraguild predator or killer) preying on a smaller one (intraguild prey or victim) (Polis & Holt 1992; Palomares & Caro 1999). Usually, the much greater body

Correspondence: F. Sergio, Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., Avda. de María Luisa s/n., Pabellón del Perú, Apdo 1056, 41013 Seville, Spain (email: fsergio@ebd.csic.es). L. Marchesi and P. Pedrini are at the Raptor Conservation Research Unit, Trento Natural History Museum, via Calepina 14, 38100 Trento, Italy.

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size or harming potential of the killer species prevents the evolution by the prey of antipredator defences (characteristics of prey that reduce the probability of predation once the prey is in the perceptual field of the predator; Hileman & Brodie 1994), so that coexistence is favoured by some form of predator avoidance, that is any mechanism that lowers the probability that the prey occupies the foraging microhabitat of the predator (Hileman & Brodie 1994). Predator avoidance can be attained in three main ways: (1) temporal segregation: the intraguild prey alters its activity times so as to avoid those of the intraguild predator, a mechanism generally regarded as unsuccessful (e.g. Jaksic 1982; Fedriani et al. 1999); (2) distance-sensitive avoidance: independently of habitat, the intraguild prey selects sites as far as possible from the intraguild killer, exploiting discontinuities in the distribution of the predator (Kostrzewa 1991; Palomares et al. 1996; Durant 1998). Such predation refugia are usually dependent on landscape heterogeneity and predator density (Durant 1998; Sergio et al. 2003a); (3) habitat-mediated avoidance: the intraguild prey avoids habitats associated with high predation risk, such as those preferred by the intraguild killer (e.g. Fedriani et al. 2000).

Overall, predator avoidance must be a frequent and effective mechanism in intraguild predation systems, because long-term coexistence of the intraguild prey with its killer species has been frequently reported (Holt & Polis 1997). However, despite its importance, there have been relatively few studies focusing on predator avoidance in vertebrate intraguild predation systems and most of them were conducted on mammals. Despite the enormous amount of research dedicated to birds of prey, surprisingly few studies were conducted on this group (Kostrzewa 1991; Hakkarainen & Korpimäki 1996; Sergio et al. 2003a; Sunde 2005), and none of them discriminated between different forms of predator avoidance. Here, we show that the tactic used by tawny owls, *Strix aluco*, to avoid their intraguild predator, the eagle owl, *Bubo bubo*, depends on the type of resource overlap between the two species and the density of the killer, which dictates the amount of locally available enemy-free space.

The eagle owl, the largest owl in the world (body mass ~1.5–4 kg), is a food and habitat generalist frequently reported to prey on other raptor species (Mikkola 1976, 1983). It is a sit-and-wait predator typically foraging in open habitats or at the edge of woodland (Penteriani 1996). In the Alps, eagle owls prefer low-elevation open areas and wetlands, and their diet is dominated by rats, hedgehogs and edible dormice, *Glis glis* (Marchesi et al. 2002a; Sergio et al. 2004a). The latter arboreal mammal is typically snatched from the top of the tree canopy (L. Marchesi & F. Sergio, personal observation). Previous analyses have shown that eagle owls can limit the populations of other raptors (Sergio et al 2003a, 2004b; Busche et al. 2004).

The tawny owl is a medium-sized (0.4–0.7 kg) generalist predator, usually hunting through a sit-and-wait tactic within woodland or at its margin (Galeotti 2001). In the Alps, it shows wide flexibility in habitat use, nesting on cliffs, trees and buildings and occupying all the available woodland types at almost any elevation, with a diet dominated by edible dormice, and by woodland mice and voles (Marchesi et al. 2006). Its characteristic and persistent territorial call makes it a potentially easy prey for a nocturnal predator foraging by auditory cues such as the eagle owl.

Based on the above, tawny owls may be expected to be vulnerable to eagle owl predation in three main circumstances: (1) during territorial advertisement near their nest; (2) when foraging at the edge between woodland and open areas; and (3) when foraging in habitats preferred by dormice (the main prey shared by the two species), where casual encounters with the intraguild killer will be more likely. Under such scenario, predation is probably best avoided by distance-sensitive nest site selection. However, this may be ineffective or unfeasible if predator density is too high and continuous, leaving too little enemy-free space. In such conditions, we may expect tawny owls to make the best of a bad job by avoiding habitats associated with high predation risk the nearer to an eagle owl nest (i.e. an interaction between habitat selection and proximity to eagle owls). Finally, tawny owls have been frequently reported to prey upon and compete with other owl species (e.g. Mikkola 1976, 1983; Nilsson 1984). Therefore, the gaps in tawny owl distribution produced by eagle owls could represent spatial refugia for other owl species, indirectly enhancing the diversity of the overall owl assemblage.

Based on the above, we developed the following predictions: (1) the two species show pronounced diet overlap, mainly because of one prey item, the edible dormouse; (2) the edible dormouse selects specific habitat features, where encounter rates between the two species (i.e. predation risk) are likely to be higher; (3) mechanisms to avoid the intraguild predator will vary with predator density; more specifically, we predicted a switch from indifference to distance-sensitive avoidance, to habitat-mediated avoidance along a three-step gradient of increasing predator density; (4) proximity to the intraguild killer affects the breeding output of the intraguild prey; (5) at the population level, the densities of the two species are negatively correlated; and (6) the diversity of the owl assemblage increases with eagle owl abundance.

METHODS

Study Areas

Tawny owls were censused in 2002 and 2003 in three plots chosen on the basis of eagle owl abundance: (1) Mount Baldo, a 55-km^2 plot holding no eagle owl territories, the nearest being located 2.1 km from the border of the area; (2) Adige Valley, a 210-km^2 plot with medium eagle owl density (2 pairs/100 km^2); and (3) Noce Valley, a 250-km^2 plot with high eagle owl density (3 pairs/100 km^2).

All the three areas had mountain slopes covered by extensive forests interspersed with vineyards and apple orchards at lower elevation and with managed grassland at middle elevations. Cliffs, the main nesting substrate for both species, were plentiful throughout all areas. Forests were managed for timber harvest by two main silvicultural practices: coppice woodland (Matthews 1989) at lower elevation and high forest at higher elevation. In 2002 and 2003, tawny owls were censused in another nine quadrats, each of 100 km^2, randomly scattered throughout the