SHORT COMMUNICATIONS

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INTERSPECIFIC AGGRESSION AND NEST-SITE COMPETITION IN A EUROPEAN OWL COMMUNITY

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Interspecific killing among predators of the same guild has been extensively reported, but is still relatively unstudied (Mikkola 1983, Kostrzewa 1991, Palomares and Caro 1999). Although Mikkola (1983) summarized 1363 cases of owls killed by other owls, it was not always clear whether birds were taken as prey or killed for other reasons. Indeed, some of these owls may have been killed during defense of nest sites, as food competitors, or a few may have been found dead and scavenged. Others may have been killed, but not actually eaten. Palomares and Caro (1999) pointed out that interspecific killing may remove potential predators or their offspring, free up resources that would otherwise be consumed by competitors or provide energetic benefits as prey, although atypical in the diet.

On the other hand, Jaksic and Braker (1983) and Marti et al. (1993) showed that predator assemblages can be organized in feeding guilds (i.e., clusters of species within which interspecific dietary overlap is more extensive), although they did not take into account the habitat dimension of these respective niches. Herrera and Hiraldo (1976) showed a weak clustering effect due to interspecific dietary overlap in owl communities in the Iberian Peninsula. In this case, we would expect that spatial segregation would be the most common dimension of resource partitioning in the owl community (Schoener 1974, Nilsson 1984, Danielson 1991, Venier and Fahrig 1996).

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Competition among species is difficult to assess, and in spite of great interest in such interactions, the actual influence of direct and indirect effects of this process is still far from clear (Palomares and Caro 1999). Mikkola (1983) explained that existing data are too circumstantial to allow an evaluation of the important benefits related to the competition. As several factors may be influencing population dynamics, the importance and degree of interspecific killing among raptors needs to be assessed by long-term, intensive studies exploring owl interactions Bizkaia offers a unique opportunity to examine this issue in Europe, as the owl population has been studied for over a decade (e.g., Zuberogoitia and Campos 1998, Zuberogoitia and Martinez 2000, Zuberogoitia 2002). Here, we report rates of interspecific aggression and nest-site competition among seven species of owls that we censused during the above-mentioned research.

METHODS

Study Area. This work was conducted in Bizkaia, in northern Spain (43°22′N, 2°41′W) between 1992–2002. This is a 2300-km^2 area covered primarily by forest (70%), mainly conifers, especially Monterey pine (*Pinus radiata*), which occupies 53% of the forested area (Departamento de Ordenación del Territorio y Medio Ambiente 2001). In Bizkaia, Tawny Owls (*Strix aluco*) reach one of the highest densities found in Europe, with 1700 known territories (Zuberogoitia and Campos 1998, Zuberogoitia 2002). The lowlands and rural areas are surrounded by old fields and agriculture, where owls more characteristic of open space live (e.g., Barn Owl [*Tyto alba*], Little Owl [*Athene noctua*], Scops Owl [*Otus scops*]), with 407, 272, and 26 known territories, respectively (Zuberogoitia 2002). The rest of the owl guild is comprised of Long-eared Owls (*Asio otus*), with nine known territories; Short-eared Owls (*Asio flammeus*), present only dur-

Table 1. Number and proportion of total playbacks and territories where interspecific attacks occurred. For calculating the percentages we considered all the cases when we used the broadcast method (2056) and used the number of known territories for each attacked species.

	ATTACK ON TAPE RECORDER		ATTACK ON ANOTHER OWL		
PREY	*N*	PERCENT	*N*	PERCENT	ATTACKER
Little Owl	4	0.2	1	0.4	Barn Owl
	2	0.1	1	0.4	Tawny Owl
Long-eared Owl	2	0.1	1	0.1	Tawny Owl

ing the migratory fluxes and winter; and Eagle Owls (*Bubo bubo*) with three territories.

Survey Methods. We used three different techniques to assess competition and aggression among owls. The first was the playback method, conducted between December 1992 and December 1996, that we used to elicit territorial vocalizations from the seven owl species at 2056 point count stations and recorded the number of interspecific attacks on the broadcast speaker. Scops Owls were surveyed between April and September because they do not winter in the study area; otherwise, we surveyed all species twice a week throughout the year ($\bar{x}$ = 7.26 count stations, SD = 2.13). We broadcasted taped vocalizations (male, female, and owlet vocalizations recorded in a continuous format) according to the size of the owl (smallest to largest) for 5 min, and then assessed reactions of owls during the subsequent 10 min. The broadcast speaker was placed 1.5 m above the ground, while two to four observers surrounded it separated by 10–20 m. Surveys began at dusk, continued for an average of 5 hr, and were performed in all kinds of weather except during very windy (>35 km/hr) and stormy nights. Further details about survey methods are described by Zuberogoitia and Campos (1998), Zuberogoitia and Martínez (2000, 2001), Martínez and Zuberogoitia (2002), and Martínez et al. (2002).

Second, we reviewed our notes made during 3084 hr observing behavior of owls in our study area, from which instances of interspecific interactions involving physical contact among owl species were tallied. Finally, following Zuberogoitia and Campos (1998), we located breeding sites of 181 Barn Owls, 83 Little Owls, 77 Tawny Owls, nine Scops Owls, and three Long-eared Owls, and examined nest-site competition among these species. We considered that competition for nest sites existed when one species displaced another from its nest before the end of the nesting season.

Data Analysis. We calculated relative frequency and proportion of interspecific attacks during the 2056 point counts and recorded species of both the attacker and target species. Independent of the call broadcasts, we calculated number of interspecific attacks observed incidentally during the study period. We used number of territories of each species as the total sample when calculating proportion of territories at which attacks occurred. For example, one attack involving a Little Owl in its territory is 1/272, as there were 272 known territories of this species. Third, we calculated frequency and proportion of species that were expelled from their nests by another species.

RESULTS

We registered eight cases of owls attacking the playback station while broadcasting the call of a different species (Table 1), and three cases of interspecific aggression observed incidentally. Most attacks were aimed at Little Owls, and the main aggressors were Barn and Tawny owls. We also documented interspecific competition for breeding sites. Tawny Owls displaced Barn Owls six times (3.3% of the recorded nests), and all such cases occurred during the egg-hatching period. However, we also found evidence that many owl species within the guild did not interact with each other aggressively, even though they nested in close proximity. In five cases, two or three different species shared the same building for breeding (Table 2). All bred successfully, and we did not record predation or aggressive behaviour among them.

DISCUSSION

The frequency of direct attacks by an owl species on another and the frequency of interspecific attacks to playback stations were very low. Tawny Owls appeared to be the most aggressive species of the guild, attacking Little

Table 2. Number of cases in which two or more owl species nested in the same building at the same time. The percentage data were obtained considering all nests monitored for each species.

N		PERCENT		PERCENT		PERCENT
2	Little Owl	2.4	Barn Owl	1.1	Tawny Owl	2.6
2	Little Owl	2.4	Barn Owl	1.1		
2	Barn Owl	1.1	Tawny Owl	2.6		

and Long-eared owls and expelling Barn Owls from their nests. Similarly, Tawny Owls can show a high degree of intraspecific competition, as territoriality is often the cause of fights that can lead to the killing of an intruder (Zuberogoitia and Martínez 2000). Hence, it may not be surprising that such an aggressive species would defend its resources vigorously against other species.

Barn Owls were also aggressive against other species. All observed cases were aimed at Little Owls, although the frequencies of such interactions were almost negligible. Our results are similar to those of Mikkola (1983), who found that the only owls killed by Barn Owls were Little Owls, but very infrequently. In our study areas in Valencia (eastern Spain), we also have witnessed two cases of resident male Barn Owls expelling Long-eared Owls from their territories after brief aerial fights (J.A. Martínez and I. Zuberogita, unpubl. data). According to Mikkola (1983), shortage of suitable breeding places for owls may lead to interspecific conflicts. Natural cavities are in short supply, and therefore, presumably a limited resource for owls in Bizkaia, which helps explain why owls tend to breed in alternative sites. Such sites include vaults of churches, attics of houses, and piles of hay or branches (Zuberogoitia 2002). Thus, both interspecific and intraspecific competition for such limited resources would be expected (Newton 1979), especially if food availability is high, and the structural characteristics of the habitat suit the hunting mode of several species. Tawny Owls are extremely abundant in our study area despite that availability of suitable nest holes is low because of timber harvesting (Zuberogoitia 2002). Accordingly, these owls recently have increased use of anthropogenic structures (mainly buildings) for nesting. Barn Owls also select buildings for nesting (Zuberogoitia 2002), but they seem to be at a disadvantage when confronted by the more aggressive Tawny Owls in competition for nest sites. Nevertheless, Bunn et al. (1982) described a single case of a pair of Barn Owls chasing away a Tawny Owl that had entered a barn where they were nesting.

Therefore, even if we were not monitoring all the nests in the owl guild, our results suggested that competition between Tawny Owls and Barn Owls occurred at least at the nest-site level, although sharing of structures supporting breeding sites occurred occasionally. Current land management practices favoring timber plantations over deciduous woods (which provide natural cavities for forest owls) have created Tawny Owl hunting habitat artificially by increasing the availability of edges within woods (Zuberogoitia 2002). In these habitats, Tawny Owls have adapted to breeding in diurnal-raptor nests and even in buildings, which may support a high density of Tawny Owls (Zuberogoitia 2002) competing for a limited number of nest sites with less aggressive, open-space dwellers such as Barn Owls, Little Owls, and Scops Owls (Taylor 1994, Zuberogoitia 2002).

Jaksic (1988) wondered about effects of removing dominant owls on the abundance and diversity of local predator assemblages. For example, Eurasian Eagle-Owls can kill smaller owls and raptors (Mikkola 1983, Saurola 1995) or influence the composition of predator guilds (Sergio et al. 2003). Whether the wide range of habitats occupied by Tawny Owls and their high density in Bizkaia are also a consequence of the lack of competition by a larger owl is still an open question.

AGRESIÓN INTERESPECÍFICA Y COMPETENCIA POR SITIOS DE NIDIFICACIÓN EN UNA COMUNIDAD EUROPEA DE BÚHOS

RESUMEN.—La depredación entre depredadores de una misma comunidad no ha sido bien estudiada. Con objeto de comprender la frecuencia y la magnitud de las agresiones interespecíficas en una comunidad europea de rapaces nocturnas, analizamos la frecuencia de contactos agresivos (ataques) y apropiaciones de nidos entre las siete especies de búhos presentes en un área de 2300 km^2 ubicada en Bizkaia (España) entre 1992–2002. Reprodujimos reclamos previamente grabados de las siete especies en 2056 puntos de censo, comenzando con los de la especie más pequeña y finalizando con los de la más grande. Durante los reclamos registramos (1) la frecuencia con la que se producían ataques interespecíficos, y (2) las especies implicadas. Sólo registramos ocho ataques, los cuales fueron dirigidos a especies de menor tamaño que la especie atacante. Además, durante más de 3000 horas de observaciones de rapaces nocturnas en el área de estudio, registramos tres casos de ataque directo de una especie contra otra. Por último, constatamos siete casos de competencia directa por los lugares de nidificación, en los que una especie fue desplazada del nido por otra especie antes de finalizar el periodo reproductivo. Sugerimos que el nivel de agresión está relacionado con el tamaño de la especie, de forma que las especies de mayor tamaño atacan a las más pequeñas. Sin embargo, las agresiones son muy poco frecuentes, por lo que nuestros datos sugieren que estas especies rara vez compiten directamente entre sí de forma directa o apropiándose de los nidos. En cambio, las especies podrían estar compitiendo de foma menos evidente.

[Traducción de los autores]

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PREY PARTITIONING BETWEEN MATES IN BREEDING BOOTED EAGLES (*HIERAAETUS PENNATUS*)

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KEY WORDS: *Booted Eagle*; Hieraaetus pennatus; *food partitioning*; *forest*; *prey provisioning*; *reversed size dimorphism (RSD)*.

Reversed sexual-size dimorphism (RSD) is widespread in raptors and owls, with females being larger than males (Newton 1979). Several researchers have proposed that this trait is driven by different selective forces acting on breeding adults (Mueller and Meyer 1985, Massemin et al. 2000, Simmons 2000). However, no explanation has gained universal acceptance (Bildstein 1992). One of the most popular explanations is the prey-partitioning hypothesis or female supplementary feeding hypothesis (Reynolds 1972, Korpimäki 1985), which suggests that RSD is advantageous because it allows females to hunt larger prey, widening the prey base available for the pair and reducing intersexual competition for food (Snyder and Wiley 1976, Andersson and Norberg 1981, Massemin et al. 2000). Several authors (e.g., Snyder and Wiley 1976,

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