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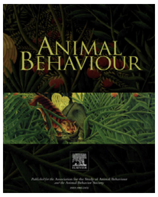

Mobbing behaviour varies according to predator dangerousness and occurrence

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Animals possess various antipredator behaviours to reduce their risk of predation. Whereas most prey make considerable effort to avoid their predators, sometimes individuals approach and mob predators as a group. Among the types of predators that elicit mobbing, raptors such as hawks and owls are one of the more consistent targets. We conducted playback experiments to investigate the strength of mobbing behaviour according to the perceived risk associated with either predator dangerousness or local predation pressure. We first determined whether mobbing is specific to dangerous predators or more broadly directed at predatory species. We experimentally investigated whether prey can discriminate the level of dangerousness of two owl species. Our results indicate that prey adjusted the strength of their mobbing behaviour according to the perceived risk: passerine birds mobbed the Eurasian pygmy owl, *Glaucidium passerinum* (i.e. a dangerous predator) but not the boreal owl, *Aegolius funereus* (i.e. a far less dangerous species). Second, we compared mobbing behaviour in similar habitats differing in predation pressure (with or without pygmy owls). Working on identical bird communities, we revealed that mobbing varied in relation to the local presence of the predator. Where the pygmy owl was absent, calls of this dangerous predator failed to elicit mobbing among passerine birds although they responded strongly to a playback of a mobbing chorus. This study provides experimental evidence that intense predation increases the expression of cooperative mobbing in passerine birds.

Typically, once a predator has been detected, prey move away while emitting alarm signals. When hearing alarm calls, animals either flee to hide or remain motionless. More surprisingly, in some situations, prey do not flee but mob predators. Mobbing is defined as movements of prey towards the predator involving both attacks with stereotyped behaviours and easily localizable calls that quickly draw a crowd of both conspecific and heterospecific prey against the predator (Curio, 1978; Hartley, 1950; Hurd, 1996; Randler & Vollmer, 2013). The principal benefit of mobbing is to cooperatively chase the predator away (‘move-on hypothesis’, Curio, 1978; Pettifor, 1990; Flasskamp, 1994; Pavey & Smyth, 1998) although such strategy is not without risk (Curio & Regelmann, 1986; Dugatkin & Godin, 1992; Sordahl, 1990).

Even though mobbing is not uncommon among vertebrates, how predation risk drives the expression of this behaviour is still poorly understood. Most studies have suggested that animals adjust the strength of their mobbing behaviour according to the perceived risk associated with either predator dangerousness or local predation pressure (Graw & Manser, 2007; Kaplan, Johnson, Koboroff, & Rogers, 2009; Kobayashi, 1987; Koboroff, 2004; Koboroff, Kaplan, & Rogers, 2013). Predator dangerousness, i.e. the rate at which predators kill prey, can greatly vary between predator species, while predatory pressure mostly depends on the abundance of a local predator species. Although mobbing is thought to correlate positively with predator dangerousness, studies on mobbing have only compared prey responses to predators and nonpredatory species (Kobayashi, 1987; Koboroff, 2004; Lind, Jöngren, Nilsson, Schönberg Alm, & Strandmark, 2005). For example, Lind et al. (2005) has experimentally shown that great tits, *Parus major*, do not mob the European robin, *Erithacus rubecula*, i.e. a nonpredatory species, but approach and mob Eurasian pygmy owls, *Glaucidium passerinum*, a predator that is particularly dangerous for great tits. However, inoffensive species such as the European robin can be easily discriminated acoustically from predatory species. Hence, it is still unclear whether mobbing is specific to dangerous predators or more broadly directed at predatory species whatever their dangerousness. It is thus important to investigate the accuracy of prey discrimination facing predatory species of different dangerousness levels (see for instance Griesser, 2009 working at an intraspecific level on the Siberian jay, *Perisoreus infaustus*). Many studies have emphasized that local predation pressure is an excellent predictor of the strength of mobbing

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responses, with birds exhibiting stronger mobbing responses in locations where predators are common and weaker responses where predators are rare (Sandoval & Wilson, 2012; Tilgar & Moks, 2015). This is in agreement with the study of Reudink, Nocera, and Curry (2007) suggesting that birds mob only predatory species they have previously experienced. Interestingly, studies also indicate that prey respond to mobbing calls even in areas where their natural predator is absent (Johnson, McNaughton, Shelley, & Blumstein, 2004; Randler, 2012) suggesting that the convergent features themselves would facilitate interspecific communication (Marler, 1955, 1957). Nevertheless, it is worth noting that comparing behavioural responses between different localities should be interpreted with caution. For instance, prey communities may vary greatly between localities which can make comparisons irrelevant. This can be particularly problematic if the prey species richness or the relative abundance of the most commonly preyed on species vary according to predator occurrence. Unfortunately, to our knowledge, previous studies did not control for such variations in prey communities between the compared sites.

In this study, we conducted a series of playback experiments to determine whether passerine mobbing behaviour depends on local predation risk. First, we studied birds' responses to two morphologically similar owl species to evaluate whether mobbing is specific to predator dangerousness. We used passerine responses to the Eurasian pygmy owl (hereafter pygmy owl), a predator specialized in passerine birds which constitutes an ideal model species for studying mobbing behaviour (Kellomäki, 1977; Kullberg, 1995; Muller & Riols, 2013; Solheim, 1984; Sotnar, Pacenovsky, & Obuch, 2015). We also used the boreal owl, *Aegolius funereus*, a less dangerous species as indicated by the low prevalence of birds in its diet (Korpimäki, 1986). We predicted that passerines should respond more strongly to the pygmy owl than to the boreal owl. Second, we tested mobbing in two forest patches, one with and one without pygmy owls, in the same mountain range and with identical bird communities, to compare mobbing behaviour with different predation pressures. We predicted that birds would not mob in response to predator vocalizations where the predator was absent, because owl calls are not associated with predation. However, it was important to control for the possibility that the absence of response was due to a loss of mobbing ability; hence, in both forest patches (with or without pygmy owls), we tested whether birds responded to the playback of a mobbing chorus.

METHODS

Site and Species Studied

The study was conducted in mixed deciduous-coniferous forests in the Jura mountains (Ain, France) in two study areas. The first is located near Oyonnax (46°15′N, 5°39′E, mean altitude 850 m) where the Eurasian pygmy owl, a dangerous predator of passerine birds, and the boreal owl, a less dangerous predator of passerine birds, are both common. The second study area, in which owls are absent, is located 40 km away from the first (45°57′N, 5°20′E, mean altitude 260 m). Four listening sessions were performed at each site to control for owl occurrence using site occupancy models (Appendix 1). While owls were detected in each site of the first area ($N = 20$), none was detected in the second area ($N = 15$), confirming previous information (Lengagne & Bulliffon, 2014) and making the two sampled areas (hereafter referred as area with owls versus area without owls) highly relevant to investigate the influence of owl predation exposure on mobbing. The distance between the different sites was at least 500 m to avoid a responding individual contributing more than once to the analyses. At each of the 35 sites, bird species diversity was surveyed through a 20 min acoustic census of about 100 m radius around the observer. A census was performed before any experiment (Blondel, Ferry, & Frochot, 1970). In total, 32 passerine species were identified in the area where pygmy owls were present and 22 where pygmy owls were absent. In all cases, we focused on the eight bird species that were most commonly preyed on by pygmy owls (Muller & Riols, 2013): common chaffinch, *Fringilla coelebs*, coal tit, *Periparus ater*, European crested tit, *Lophophanes cristatus*, great tit, blue tit, *Cyanistes caeruleus*, goldcrest, *Regulus regulus*, common firecrest, *Regulus ignicapilla*, and European robin. This passerine community did not vary significantly between the two study areas (see Appendix 2, Fig. A1).

Experimental Design

Data were collected during playback experiments conducted between May and July 2014 (experiment 1) and between September and November 2014 (experiment 2).

Response specificity (experiment 1) was tested in different sites of the area with owls ($N = 20$). For this purpose, we applied a crossover design: at each site, the bird community was offered a broadcast sequence of the following three experimental stimuli, pygmy owl calls, mobbing chorus and boreal owl calls. This study design is particularly convenient for minimizing the error variance resulting from the subject effect (i.e. the bird community present at the site), since the relative effect of stimuli can be assessed within each bird community (Jones & Kenward, 2003). A latency period of 5 min was systematically observed between each experimental test (see test procedure for the complete description) in order to avoid carryover effects (i.e. residual effects of the experimental stimuli tested during the previous period on the next one). The sequence order of the three playback stimuli was also alternated between sites to avoid any bias that could result from the sequence order.

The goal of experiment 2 was to test whether mobbing behaviour of passerine birds varied in relation to predator presence. For this purpose, we selected 15 sites in the area without owls and 15 of the 20 sites in the area with owls that were previously used in experiment 1. Experimental tests were performed as in the first experiment except that the broadcast sequence included only two experimental stimuli: the pygmy owl calls and the mobbing chorus.

Test Procedure

Two observers with binoculars were positioned opposite each other at vantage points at least 10 m from the playback (i.e. focal zone) and collected data for 13 min (duration of a test). During the first 5 min we identified and counted all the birds present in the focal zone close to the loudspeaker; these observed birds were excluded from counts in subsequent analyses. Such observations were rare (2.2% of total observed birds). Then, during the 3 min playback, we quantified the birds' response using the number of species observed within a 10 m radius of the loudspeaker. After the playback, observers waited for 5 min before beginning the next test.

Experimental Stimuli

We broadcast playbacks via an amplified loudspeaker (SMC8060, Beyma) connected to a digital playback device (WAV player). Playbacks were restricted to 0600–1200 hours, which corresponds to a period of high activity in birds. To avoid pseudoreplication, we first tested whether prey response was specific to a particular soundtrack or generalizable to various soundtracks of the same species. For both owl species, we downloaded from online databases of avian sounds (http://www.xeno-canto.org) two soundtracks recorded in two populations located on both sides of the species' range in order to encompass the call variation range that a local prey community