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Hoo are you? Tits do not respond to novel predators as threats

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To combat the threat of predation, prey species have developed a variety of ways to recognize and respond appropriately to novel predators. While there is evidence that predator recognition does not require learning in certain species, learning appears to play an important role for other species. In systems where learning is important, it is less clear whether predator identification requires prior experience with specific predators or, whether general experience with predators provides sufficient tools for identifying similar species of novel predators. Here we test whether wild-living adult birds recognize a dangerous predator that occurs in only part of their geographical range. We presented taxidermy mounts of little owls, *Athene noctua*, and sparrowhawks, *Accipiter nisus*, to blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*. All populations of both tit species co-occur with sparrowhawks, but populations differ in their prior experience with little owls. We found that tits that overlap geographically with little owls responded to little owls using the same intensity of mobbing behaviour exhibited toward sparrowhawks. In populations with no historical contact with little owls, however, both blue and great tits treated little owls as a lower threat than sparrowhawks. These results suggest that blue tits and great tits do not generalize 'predatory features' to novel predators and instead need prior experience with specific predators before they assign the correct level of threat.

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Predation is a major source of mortality for most animals and even when not the cause of loss of life it can have multiple negative indirect effects on prey (Caro, 2005; Cresswell, 2008; Preisser, Bolnick, & Benard, 2005). Rapid and accurate identification of predators allow prey both to reduce immediate predation risk and to modulate appropriately their antipredator responses without unnecessarily reducing time spent on other important behaviours, such as foraging or searching for mates (Caro, 2005; Creel, Schuette, & Christianson, 2014; Cresswell, 2008; Lima, 1998). When individuals encounter a novel species, they need to determine the degree to which it poses a threat and respond appropriately. Recognizing that a novel species is not a predator and thereby avoiding costly antipredator behaviour may be nearly as important as recognizing another novel species as a predator and taking evasive action to avoid being injured or eaten (Caro, 2005; Creel et al., 2014; Cresswell, 2008; Lima, 1998).

Because of the importance of predator recognition for survival, considerable effort has been invested in examining how different species respond to novel predators (Griffin, 2004; Sih et al., 2010). The literature provides evidence for a variety of responses by naïve prey. For example, captive-born greater rheas, *Rhea americana*, do not discriminate between predators and nonpredators (de Azevedo, Young, & Rodrigues, 2012), and captive-born rhesus monkeys, *Macaca mulatta*, do not respond appropriately to predatory snakes (Mineka, Davidson, Cook, & Keir, 2004). Nevertheless, many conservation programmes have succeeded in training naïve prey to respond appropriately to novel predators that they previously did not view as a threat (Griffin, Blumstein, & Evans, 2000). For example, with training, naïve New Zealand robins, *Petrocia australis*, mobbed mammalian predators (Maloney & McLean, 1995). But some species do appear to make appropriate responses, even when naïve. For example, captive-born Atlantic salmon, *Salmo salar* L., increased their opercular rate, a sign of increased stress in response to predators (Hawkins, Armstrong, & Magurran, 2004), even when they had no prior experience of the predator (Hawkins, Magurran, & Armstrong, 2004), and both zoo-reared black tailed

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prairie dogs, *Cynomys ludovicianus*, and naïve wild-living California ground squirrels, *Spermophilus beecheyi*, engage in stereotyped snake-directed behaviour in response to moving snakes (Owings & Coss, 1977; Owings & Owings, 1979). Most of the experiments in which predator recognition has been investigated have been conducted on young juveniles in the laboratory, or in captive situations where the test animals have never been exposed to predators of any kind (Ferrari, Messier, & Chivers, 2007; Göth, 2001; Griffin, Evans, & Blumstein, 2001; Kullberg & Lind, 2002; Veen, Richardson, Blaakmeer, & Komdeur, 2000).

Antipredator behaviour in captive animals (Hinde, 1954b) or by juveniles (Francis, Hailman, & Woolfenden, 1989; Hinde, 1954a; Rajala, Ratti, & Suhonen, 2003; Shedd, 1982) may not, however, be representative of the way in which free-living adults recognize and respond to predators, particularly if prior experience of other predators shapes responses to novel predators. But if a novel predator shares similar 'predatory features' with known predators, a prey species may be able to generalize those features across predators and identify a novel predator appropriately (Beránková, Veselý, Sýkorová, & Fuchs, 2014; Davies & Welbergen, 2008). Great tits, *Parus major*, and blue tits, *Cyanistes caeruleus*, for example, responded to sparrowhawk, *Accipiter nisus*, models that had their plumage coloration modified as they did to a model sparrowhawk without plumage modifications (Veselý, Buršíková, & Fuchs, 2016), while other species appear to use specific 'predatory features' (Beránková et al., 2014) to identify predators. These include combinations of beak shape, eye colour and body shape (Beránková et al., 2014), coloration and body size (Beránková, Veselý, & Fuchs, 2015), breast barring and eye colour (Trnka, Prokop, & Grim, 2012) and texture (Němec et al., 2014). By generalizing specific features from a familiar feature or suite of features associated with known predators, individuals can respond appropriately to a novel predator.

To test whether wild-living adults that have general experience with predators can recognize a novel predator as a threat, we examined adult prey species from different populations that vary in the presence of a particular predator. Specifically, we presented foraging winter flocks of two species of tits (blue tits and great tits), which are found throughout the U.K., with two different species of predators (sparrowhawks and little owls, *Athene noctua*).

We chose these two predators as they differ in their historical distribution in the U.K. Sparrowhawks are both currently and historically common throughout the U.K. (Cramp, 1993; Forrester et al., 2007; Perrins, 1979). Sparrowhawks have been present in the U.K. since time immemorial (Newton, 1986) and although their population numbers were quite low in the 1950s and 1960s, they are now quite common (Cramp, 1993; Glue & Scott, 1980). Little owls, on the other hand, are restricted to England and Wales, and are mostly absent from Scotland, found only below the 56th parallel, south of Glasgow and Edinburgh (Cramp, 1993; Forrester et al., 2007; Perrins, 1979; Fig. 1). Historically, little owls were introduced to the U.K. around 1870 (Altringham, O'Brien, & Sydney, 1994) and, although they are present in smaller numbers than sparrowhawks, they are common enough to be familiar to tit species in their ranges (Robinson et al., 2016). The sparrowhawk is a high-threat predator that specializes in hunting small birds and it elicits a strong antipredator mobbing response from tit species (Cramp, 1993; Forrester et al., 2007; Newton, 1986; Perrins, 1979). Although the little owl only infrequently eats small birds (Altringham et al., 1994; Cramp, 1993; Hounsome, O'Mahony, & Delahay, 2010), it is of similar size to sparrowhawks and it elicits mobbing in great tits (Curio, Klump, & Regelmann, 1983). We, then, considered that both species could be perceived as a threat (Dial, Greene, & Irschick, 2008; Templeton, Greene, & Davis, 2005).

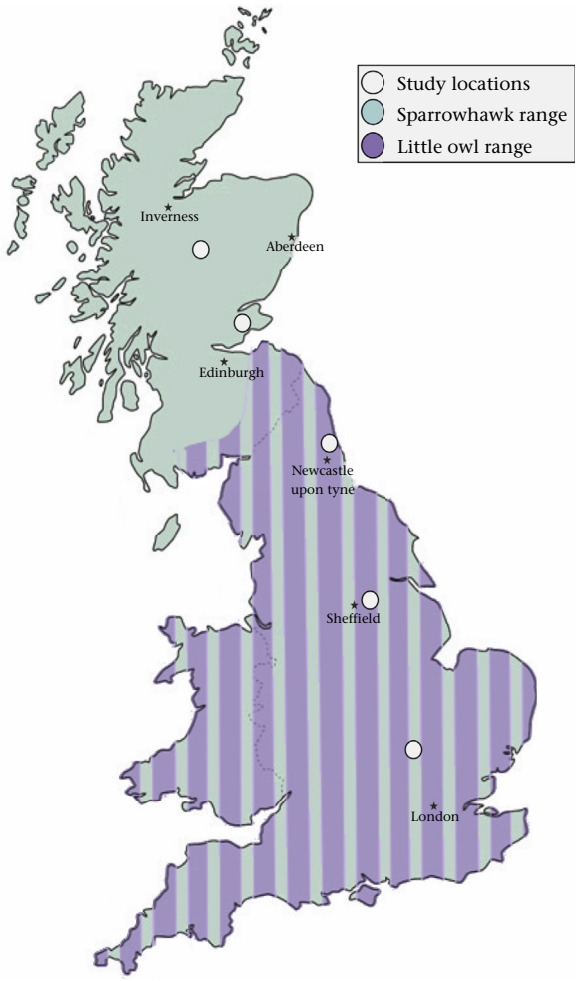

Figure 1. Map showing the locations of field sites as well as the ranges of sparrowhawks and little owls.

As sparrowhawks and little owls are common within their own ranges, but have different distributions, southern populations of tits should have prior familiarity with both predators, but northern populations should only have experience with sparrowhawks. This difference in exposure provided the opportunity to test wild populations with experience of predators in their ability to respond appropriately to a novel predator. As both predators were likely to elicit an antipredator mobbing response in tits, we were able to use the mobbing vocalizations associated with this behaviour (Carlson, Healy, & Templeton, 2017) to assess the level of threat that blue tits and great tits perceived the sparrowhawk and little owl mounts to represent. Mobbing vocalizations in blue tits and great tits contain information about the degree of threat a predator poses (Carlson et al., 2017). If the tits do not recognize novel predators as a threat, then inexperienced birds (those in Scotland) should respond to the familiar predator much more strongly (with increased call rate; Carlson et al., 2017) than to the novel model. However, if inexperienced birds (those in Scotland) recognize the threat of a novel predator, then their responses to the little owl and the sparrowhawk should not differ from the responses of experienced birds (those in England). No difference in response to the little owl and the sparrowhawk between experienced (English) and inexperienced (Scottish) birds could be taken as evidence that birds generalize from familiar predators to novel stimuli.

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