# 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, *Petroica 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).
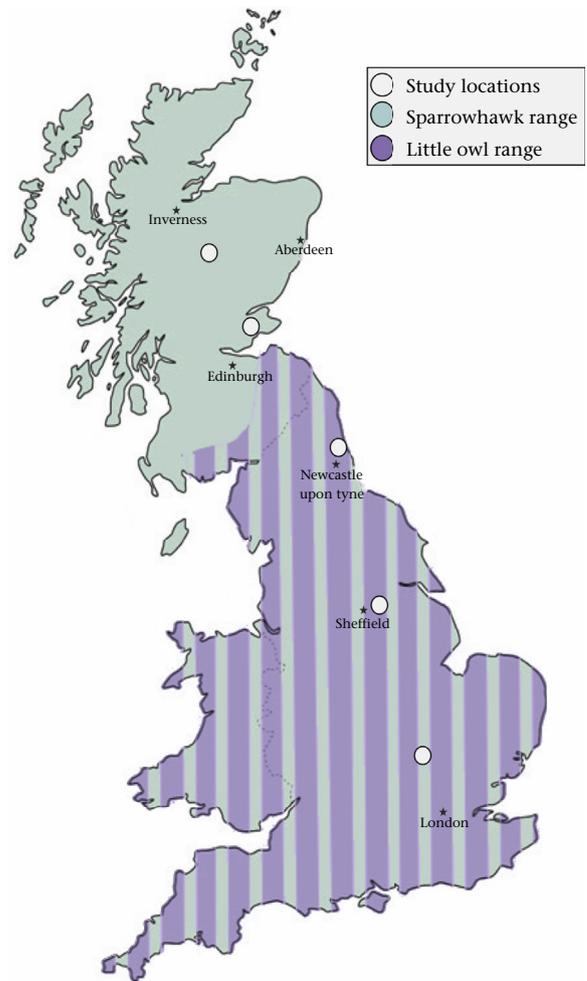


**Figure 1.** Map showing the locations of field sites as well as the ranges of sparrowhawks and little owls.

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.

## METHODS

### Study Sites and Species

We conducted predator presentations to blue tits and great tits at 56 feeders in five locations across the U.K. (three locations in England and two locations in Scotland), during January–March 2014 and 2015 (Fig. 1). The two locations in Scotland were all located outside the known range of little owls. Feeders were all placed within 0.5 m of dense leafy cover and filled with black-oil sunflower seeds.

### Stimuli

We used two species of predators to simulate predator encounters: a species present throughout the range of blue tits and great tits, and one present in only part of their range. We used the sparrowhawk as the familiar high-threat predator as it is found throughout the whole of the U.K. We used a little owl as a novel high-threat predator to some populations and as a familiar high-threat predator to other populations, as it is found only below the 56th parallel (south of Edinburgh) in the U.K. and therefore was unfamiliar to those tits in our study sites north of the 56th parallel (Brehm, 2007; Cramp, 1993; Forrester et al., 2007). Both predators are small, making them especially dangerous to the small birds (Dial et al., 2008; Templeton et al., 2005), including tits, which are known to make up part of their diet (Glue & Scott, 1980; Zawadzka & Zawadzki, 2001). Although crepuscular, little owls are often out during the day (Cramp, 1993; Forrester et al., 2007; Glue & Scott, 1980) so are likely to be encountered by tits.

We used taxidermy mounts for the predator simulations, each fitted with robotics that allowed the head to rotate in an approximation of the natural head movements of predatory birds to induce the desired response (for details, see Carlson et al., 2017; Patricelli & Krakauer, 2009). An Arduino computer board (Arduino Duemilanove from Arduino LLC, https://www.arduino.cc), on which we programmed a loop of 15 different rotation and time delay commands, controlled the head rotation. This computer was attached to a small servo in each mount that rotated the head. The servo ran for the duration of all predator presentations. We used two exemplars of each species (one juvenile male and one adult female sparrowhawk and two adult little owls of unknown sex) to help mitigate the effects of pseudoreplication, and as sex and age of the sparrowhawk mounts could potentially affect responses, we also included mount exemplar in the statistical models.

### Predator Presentation

We presented the model predators at feeders located in nature reserves and private gardens in English and Scottish countryside and forests. All feeders were stocked with food for at least 2 weeks prior to trials to allow the local birds to find and grow accustomed to them. Before an experiment began, we identified a concealed location to conduct our observations/recordings at least 4 m from the feeder. We then placed a 1.5 m high platform 2 m from the feeder. After we confirmed the presence of blue or great tits, we carried the mount (uncovered) from the observation spot and placed it on the platform with its body and head oriented towards the feeder, as head orientation can affect perceived predator threat (Book & Freeberg, 2015; Carter, Lyons, Cole, & Goldsmith, 2008). We began recording from the moment we exposed the mount. The trial began, however, when a bird of the target species met one of three criteria that suggested to us that it had seen the mount: (1) it approached within 7 m of the mount with its body and head oriented towards the mount for more than 20 s within 2 min, (2) it

approached within 5 m of the mount or (3) it displayed mobbing behaviour towards the mount (Altmann, 1956). We recorded continuously for 5 min after an individual of a target species met one of these criteria before removing the mount and stopping the trial. Recordings were made from an observation spot located in cover at least 4 m from the feeder. We vocally annotated the recordings with the numbers of individuals present for both species, and whether or not an individual met one of the above criteria to begin a trial proper. We recorded all predator presentations onto a Marantz PMD660 solid-state digital sound recorder (Marantz America, LLC., Mahwah, NJ, U.S.A.) with a sampling rate of 48 kHz and a bit depth of 24 bits using a hand-held Sennheiser ME 66 supercardioid microphone (Sennheiser Electronics, Hanover, Germany). We randomly assigned the order of predator presentation and the specific mount exemplar used at each feeder, and conducted all predator presentations from 1 h after sunrise to 1 h before sunset to reduce any stress associated with recovering from or preparing to roost overnight.

We conducted 48 trials where blue tits were present ($N = 15$ England, $N = 33$ Scotland) and 51 trials where great tits were present ($N = 13$ England, $N = 33$ Scotland).

### Acoustic Analysis

We used Raven Pro v1.5 (Bioacoustics Research Program, 2014) to analyse our recordings, using a frequency grid resolution of 23.04 Hz, a fast Fourier transformation (FFT) of 1050 samples and a Hann window function. We selected all calls by hand and assigned them to species using visual identification based on a catalogue of known vocalizations (Carlson et al., 2017). To test our above hypothesis, we compared the differences in call rate, as both species increase call rate in response to high-threat predators compared to low-threat or nonthreat stimuli (Carlson et al., 2017). Call rate was calculated as the number of calls divided by the number of individuals present per minute. This allowed us to control for the increased possibility of a call happening due to a larger number of individuals that could call during the mobbing event.

### Statistical Analysis

To test whether tit species called at different rates in response to familiar and unfamiliar predators, we tested for an interaction between predator type (sparrowhawk and little owl) and previous experience (England and Scotland). Because sparrowhawks are common throughout the study population and should be familiar, high-threat predators to the tit species we tested at all study sites, we used them as a positive control for a 'high-threat' response for which we could compare the response of each flock to the little owl. This allowed us to control for regional differences in overall mobbing response. We generated generalized linear mixed models with a Poisson distribution to test for the interaction of area and predator on the call rate (calls per individual per minute). We included mount order to control for order effects and mount exemplar to account for differences in mounts (as we had one male juvenile and one adult female sparrowhawk mount) as fixed effects. We also included as random effects the number of conspecifics present to control for differing flock sizes at each test site as well as feeder ID to take any small-scale local variation into account. To check for a significant interaction of experience (England and Scotland) and predator (sparrowhawk and little owl), we ran type III Wald chi-square tests. We used R (v.3.1.2) statistical software (R Core Team, 2014) and the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) for all statistical tests and all *P* values we report are two tailed.

*Ethical Note*

This research was approved by the University of St Andrews School of Biology Ethics Committee (01112013) and Scottish National Heritage, and followed ASAB/ABS Guidelines for the treatment of animals in research. Because of the increased food stress during the winter months, when this research was carried out, we conducted predator presentations between 1 h after sunrise and 1 h before sunset to allow birds to recover from and prepare for the cold night-time hours. Additionally, as it is potentially stressful to encounter predators, we restricted our predator presentations to 5 min once individuals responded. We removed the predators from sight and left the area as quickly as possible once 5 min had passed to allow the birds to recover and begin feeding normally again.

## RESULTS

The responses of tit species to little owls, relative to their responses to sparrowhawks, depended on whether they had prior experience with both predators (Fig. 2). Although the responses by both tit species looked similar, the relationship was significant only in blue tits (blue tits: $\chi^2_1 = 9.64$, $P = 0.002$; great tits: $\chi^2_1 = 3.26$, $P = 0.071$; Fig. 2).

In England (where little owls are common), neither tit species differentiated between the two model predators: blue tits and great tits called the same amount in response to a little owl as they did to a sparrowhawk (mean ± SD: blue tits: sparrowhawk: 4.71 ± 0.70; little owl: 5.14 ± 1.49; Fig. 2a; great tits: sparrowhawk: 6.28 ± 0.88; little owl: 4.89 ± 1.10; Fig. 2b). There were no order or mount effects for either tit species (blue tit: order: $\chi^2_1 = 5.04$, $P = 0.169$; mount: $\chi^2_1 = 2.27$, $P = 0.132$; great tit: order: $\chi^2_1 = 4.00$, $P = 0.261$; mount: $\chi^2_1 = 0.31$, $P = 0.577$).

In Scotland (where little owls are absent), however, responses of both tit species depended on whether the model was a little owl or a sparrowhawk: both species called at a lower rate (calls per individual per minute) in response to the little owl than in response to the sparrowhawk (blue tits: sparrowhawk: 7.07 ± 1.03; little owl: 2.34 ± 0.32; Fig. 2a; great tits: sparrowhawk: 9.75 ± 1.70; little owl: 3.73 ± 2.00; Fig. 2b).

## DISCUSSION

We observed population variation in response to the little owl, with those tit populations with prior experience treating it as more of a threat than naïve populations. In England, blue tits and great tits all reacted in a similar manner to the two predators (little owl and sparrowhawk), both of which were probably familiar to them. In Scotland, however, both tit species responded to the unfamiliar predator (little owl) differently from the way they responded to the familiar predator (sparrowhawk): blue tits and great tits called at a lower call rate to the little owl than they did to the sparrowhawk. A decrease in call rate for blue tits and great tits suggests that they considered the little owl to be of lower threat than the sparrowhawk (Carlson et al., 2017). This also suggests that the tits may need experience with a novel predator before they can recognize it as such. That blue tits and great tits responded in a similar way to both little owls and sparrowhawks in England suggests that they may perceive them as posing a similar threat.

It is not clear why tits in England responded to little owls as a high-threat species. Examining diets of each predator indicates that, like many other owl species found in the U.K., tits make up only a small portion of the little owl's diet (little owls: 4–15% frequency; short-eared owls, *Asio flammeus*: 0.1–14.5% total prey weight; long-eared owls, *Asio otus*: 0.4–12.8% total prey weight; barn owls, *Tyto alba*: 0.1–14.5% total prey weight; tawny owls, *Strix aluco*: 0–50% total prey weight; Cramp, 1993; Glue, 1967, 1974, 1977; Glue & Scott, 1980; Jedrzejewski, Jedrzejewska, Szymura, & Zub, 1996; Marti, 1976; Roberts & Bowman, 1986; Southern, 1953; Tome, 1994). In contrast, small birds make up a substantial portion of the sparrowhawk diet (~97% prey by weight; Newton, 1986). The response of the tits to the little owl could be due to a combination of two factors: (1) little owls fit the size criteria of a high-threat predator (Dial et al., 2008; Templeton et al., 2005) and are morphologically similar to tawny owls (the most dangerous owl to tits in the U.K.; Jedrzejewski et al., 1996; Southern, 1953); (2) although owls do not often hunt small birds, they do so occasionally. While morphological similarity alone may not be enough to cause a high-threat response to little owls, these attributes combined with previous experience of depredation events may have
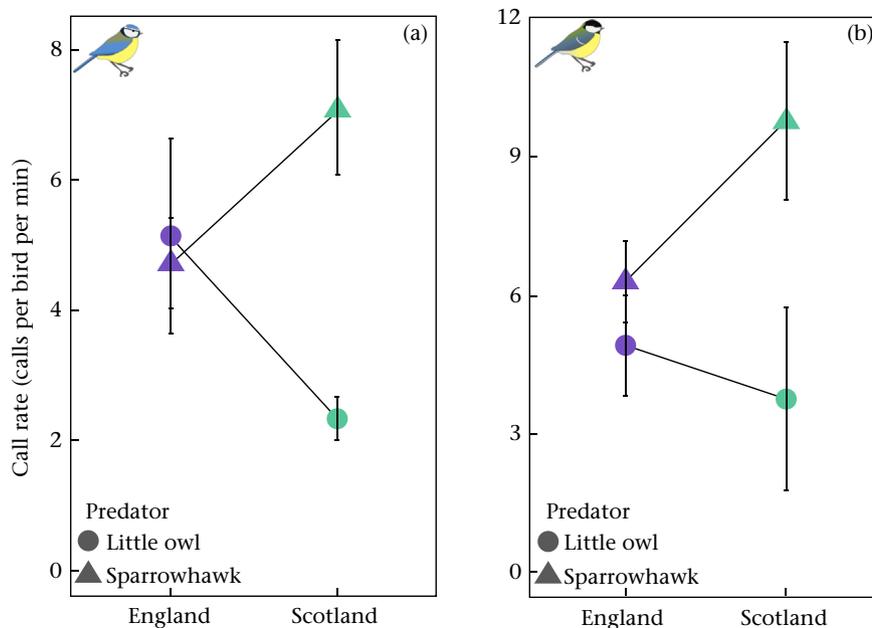


**Figure 2.** Mean ± SE call rate of (a) blue tits and (b) great tits in response to sparrowhawks and little owls in England (purple) and Scotland (teal).

triggered a response that exceeded the little owl's actual threat. Regardless, the differential response by naïve and experienced tits to little owls relative to sparrowhawks suggests that tits need some form of experience in order to 'recognize' a predator as a threat.

The lower response to the little owls (i.e. misidentification) by Scottish tits could be a result of the particular strategies that these tit species use to 'recognize' novel predators. There are three main ways in which novel predator recognition strategies may result in misclassification of a predator threat. First, tits may need to learn to identify each new predator. Tits may not 'recognize' novel predators at all but rather need to learn to identify each new predator species they encounter. Naïve blue tits and great tits misidentified the level of threat posed by the little owl similarly to many other species that learn about novel predators from other individuals. Naïve rhesus monkeys, for example, learn to exhibit a fear response to snakes after observing this response in others (Mineka et al., 2004). Other parid species can learn about novel predators by observing other individuals mobbing the novel predator (Baker, 2004). Black-capped chickadees, *Poecile atricapillus*, like blue tits and great tits, may have to learn about different predators, because in areas with resident screech-owls, *Megascops asio*, chickadees produce a shorter first D element than in areas without resident screech-owls (Saborse & Renne, 2012), suggesting that naïve chickadees underestimate the threat that screech-owls pose (Templeton et al., 2005).

Second, tits may 'recognize' novel predators by generalizing specific 'predatory features' (i.e. curved beak, long talons, etc.) across species. Therefore, tits may not recognize a new predator if that predator does not share salient 'predatory features' with other, familiar predators. The lack of apparent recognition of the little owl as a predator threat may be because any 'predatory features' (e.g. eye colour, beak shape, coloration, etc.) that are shared between little owls and sparrowhawks were not sufficiently similar to allow the tits to generalize from sparrowhawks to little owls. Although this is plausible, a number of other species can generalize from one predator to another. Tammar wallabies, *Macropus eugenii*, for example, which, after learning to fear a fox (*Vulpes vulpes*), were exposed to two unfamiliar animals, a domestic cat, *Felis catus*, and a goat, *Capra hircus* (Griffin et al., 2001). Wallabies' responses to the cat, but not to the goat, were similar to their responses to the fox, which suggests that they generalized predatory features from the fox to the cat but not to the goat (Griffin et al., 2001). Tits may also use combinations of features to identify predators (Beránková et al., 2014): wild adult great tits brought into captivity, for example, were as stressed by a sparrowhawk dummy with a pigeon beak as they were by a normal wooden sparrowhawk dummy (Beránková et al., 2014). Great tits and blue tits also responded to sparrowhawks the same irrespective of the dummy's chest barring. However, when presented with cuckoos, the barring on the chest determined whether they responded to the mount as a threat (barred) or a nonthreat (unbarred; Davies & Welbergen, 2008). However, it is also possible that, like Siberian jays, *Perisoreus infaustus* (Griesser, 2009), blue tits and great tits may classify hawks and owls as belonging to different classes of predators.

Finally, as great tits and blue tits do not generalize from sparrowhawks to little owls, yet appear to be capable of using 'predatory features' to recognize threats (Beránková et al., 2014), it is likely that tits generalize a novel predator's threat from familiar morphologically similar predators that are of a different threat level to that of the novel predator. While, like other species (Flasskamp, 1994; Griesser, 2009), blue tits and great tits probably can differentiate between different owl species (Curio et al., 1983), an unknown owl-like predator may be first classified as 'owl' before a specific level of threat is applied. The response of naïve blue tits and great tits to little owls was similar to their response to familiar low-threat predators like buzzards or nonthreats like partridges (Carlson et al., 2017), which may be because they generalized from previous experience with other, low-threat owls. While tit species will respond to other owls found in the U.K. with an antipredator response (Curio et al., 1983; Curio & Onnebrink, 1995), the diets of other owl species in Scotland (e.g. short-eared owl, long-eared owl, barn owl and tawny owl), contain few tits (Cramp, 1993; Glue, 1967, 1974, 1977; Glue & Scott, 1980; Jedrzejewski et al., 1996; Marti, 1976; Roberts & Bowman, 1986; Southern, 1953; Tome, 1994), making owls as a family generally low-threat predators.

Although it is unclear why the blue tits and great tits in England responded to little owls as they did to sparrowhawks, in Scotland they did treat the two predators differently. This difference in response of naïve Scottish tits to a novel predator suggests that prior experience with predators is important for individuals to associate novel predators with their appropriate level of threat. Whether this association is formed as the result of personal experience of a predation event, or through social or observational learning, also remains unclear (Baker, 2004; Curio, Ernst, & Vieth, 1978). Tits, due to their high propensity to mob and with their tendency to differentiate between predators of different threat levels, provide an ecologically and logistically useful system to examine the mechanisms by which species learn about novel predators.

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