Wild fledgling tits do not mob in response to conspecific or heterospecific mobbing calls

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Mobbing, where birds harass a predator through a combination of vocalizations and stereotyped behaviours, is an effective anti-predator behaviour for many species. Mobbing may be particularly important for juveniles, as these individuals are often more vulnerable than adults. Although the component behaviours of mobbing are often considered to be un-learned, there are few confirmatory data, and the developmental trajectory of mobbing is unknown. In this study, we tested whether conspecific or heterospecific mobbing calls initiated mobbing behaviour in juvenile Blue Tits *Cyanistes caeruleus*. We located wild adult and recently fledged juvenile Blue Tits and presented them with playback recordings of adult conspecific (Blue Tit) and heterospecific (Great Tit *Parus major*) mobbing alarm calls. Although adult birds readily mob in response to these types of playbacks, juveniles did not exhibit characteristic mobbing behaviour. Some juveniles did, however, exhibit individual components of mobbing behaviour found in mobbing, despite not producing adult-like mobbing behaviour in response to either conspecific or heterospecific playback. These results suggest that, although birds might be capable of mobbing as juveniles, the associations between the non-vocal stereotyped mobbing behaviours and mobbing calls may be learned.

Keywords: alarm calls, anti-predator behaviour, Blue Tits, *Cyanistes caeruleus*.

Mobbing is a widespread behaviour, found in many taxa, that involves harassing (or even physically attacking) a predator, emitting loud aggressive vocalizations and engaging in stereotyped aggressive threat displays (Dominey 1983, Crofoot 2012, Suzuki 2016, Carlson *et al.* 2017a). While costly due to the increased attraction of predators to the area (Krams 2001, Krams *et al.* 2007), there are a range of benefits that may accrue from mobbing. These include increasing the survival chances of the mobbing individuals by driving off a predator (Pettifor 1990) or alerting naïve individuals, including kin, to the predator's presence (Griesser 2013), allowing them to escape more quickly,

thereby decreasing the chances of being killed (Ekman 1986, Pavey & Smyth 1998), and learning about unknown predators (Curio *et al.* 1978, Baker 2004, Onnebrink & Curio 2008, Carlson *et al.* 2017b, Griesser & Suzuki 2017). Indeed, mobbing is frequently used by experimenters to assess whether or how different species 'recognize' or learn about novel predators (Mateo & Holmes 1997, Hanson & Coss 2001, Kullberg & Lind 2002, Magrath *et al.* 2014). Additionally, as heterospecifics that share the same predators often eavesdrop on mobbing calls, so mobbing calls and eavesdropping behaviour are also the focus of research into information networks in species communities (Templeton & Greene 2007, Magrath *et al.* 2009, Goodale & Ruxton 2010, reviewed by Templeton & Carlson 2019).

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Mobbing may be a particularly important anti-predator strategy in young birds and fledglings. Although juveniles often have relatively poor coordination and manoeuvrability, they can, and do, mob from the safety of dense cover. The data on mobbing by juveniles, however, are sparse and contradictory (Shedd 1982, Buitron 1983, Sternalski & Bretagnolle 2010). Juvenile birds sometimes appear to respond to predators with fear (Rydén 1980, Göth 2001, Hollén & Radford 2009), but naïve individuals do not always respond to predators as a threat (Curio 1993, Kullberg & Lind 2002, Hollén & Radford 2009). Most work, however, on the development of anti-predator behaviour has been focused on the production and response to aerial/flee alarm calls (Rydén 1980, Rajala et al. 2003, 2011, Davies et al. 2004, Madden et al. 2005, Platzen & Magrath 2005, Magrath et al. 2006, Hollén et al. 2007, Hollén & Radford 2009) rather than on mobbing calls. Additionally, most of the data on the development of anti-predator behaviour come from responses of very young animals still in the nest, rather than from those in the wild with some experience of predators or observing mobbing behaviour (Kuhlmann 1909, Rydén 1980, Davies et al. 2004, Madden et al. 2005, Suzuki 2011, Haff & Magrath 2012). While it has been rare to track the development of mobbing behaviour, it appears that the association between mobbing calls (both conspecific and heterospecific) and a novel predator are learned in many species (Curio et al. 1978, Vieth et al. 1980, Baker 2004, Onnebrink & Curio 2008, Griesser 2009, Carlson et al. 2017b, Griesser & Suzuki 2017). The development of the mobbing response (mobbing calls and behaviour) remains poorly understood.

Here, then, we conducted a playback experiment to wild juveniles to determine whether young birds mob and, if so, whether the form of mobbing is immediately adult-like in appearance or follows a more gradual developmental trajectory, and whether acoustically similar heterospecific mobbing calls elicit similar behaviour. If mobbing is entirely unlearned, we would expect juveniles to be able to produce complete adult-like mobbing behaviour, as opposed to partial or no mobbing behaviour. Similarly, if the response to heterospecific mobbing calls is unlearned, then juveniles should produce adult-like mobbing behaviour in response to both conspecific and heterospecific mobbing calls, rather than

responding to conspecific but not heterospecific mobbing calls. We chose to investigate juvenile mobbing in Blue Tits Cyanistes caeruleus as they are abundant, readily mob predators, nest in artificial nestboxes, and mobbing by adults of the family Paridae is especially well described (Cramp 1993, Ficken et al. 1994, Templeton et al. 2005, Bartmess-LeVasseur et al. 2010, Courter & Ritchison 2010, Randler 2012, Suzuki 2012, 2014, Carlson et al. 2017a).

METHODS

Study sites and species

To test whether post-fledging juveniles respond to mobbing calls, we conducted a playback experiment to juvenile and adult Blue Tits in eight locations in St Andrews, Fife, Scotland (56°19′52.4886″N, 2°50′18.4236″W) from 29 June to 5 August 2015. Mobbing behaviour is generally relatively stable within (Shedd 1982, 1983, Clucas et al. 2004, Avey et al. 2008) and predictable across (Shedd 1982, 1983) seasons, and although factors such as increased predation or decreased resources could impact mobbing behaviour, any seasonal changes would probably affect both adult and juvenile mobbing similarly, making these variations unlikely to affect our data.

Post-fledging core areas used by juveniles and their parents range from about 10 000 to 20 000 m^2, and their home-ranges cover around 40 000–80 000 m^2 (van Overveld et al. 2016). To ensure that we tested different birds during trials in each area, trial locations were between 250 and 500 m apart, except for two trials where the sites were separated by only 100 m. These two trials occurred consecutively to ensure that the birds tested were not the same. To avoid bias of either very young or much older juveniles dominating our samples, we aimed to sample juveniles over a range of ages. To increase our chances of sampling an even range of ages, we re-visited each of the eight locations four times (separated by 4–12 days) during a 38-day period. As most of the juveniles in this population were not ringed, we could not be sure of an individual's exact age, but by re-visiting the same locations we increased our chances of re-sampling the same family group again: in other words, birds that had aged a specific amount between repeated trials. This increased our chances of a more even age representation but also

increased our chances of sampling an individual more than once (i.e. a repeated measures design that requires us to control for intra-individual variability). To account for possible pseudoreplication we treated each location as a repeated individual and controlled for this in the analysis.

Stimuli

We conducted auditory playbacks to determine whether Blue Tit juveniles mob in response to hearing conspecific or heterospecific mobbing calls. We chose to conduct playbacks rather than model predator presentation for two reasons. First, Blue Tits respond quickly, aggressively and reliably to playback of conspecific and heterospecific mobbing calls, whereas their responses to predator presentations depend on discovery of the predator (a fairly low rate other than at feeding stations, which are not typically available to birds in the summer). Secondly, due to the mobile nature of juvenile flocks as well as their height in the canopy, predator presentations presented a logistical problem because predicting where the flock was moving to or would be present on a sufficiently fine scale was difficult. Thirdly, acoustic signals travel farther in forested habitats compared with visual signals, increasing the certainty that our target individuals received the signal even in the absence of a behavioural response. We used three different call types for the playbacks: (1) conspecific calls: an adult Blue Tit mobbing a Eurasian Sparrowhawk *Accipiter nisus* (Fig. 1a); (2) heterospecific calls: an adult Great Tit *Parus major* mobbing a Sparrowhawk (Fig. 1b); and (3) control calls: a Common Wood Pigeon *Columba palumbus* producing territorial calls (Fig. 1c), which occur frequently in the study area throughout the year. We chose to present both Blue Tit and Great Tit mobbing playbacks as we expected that, if the association between mobbing calls and stereotyped physical movements was learned, the Blue Tits would exhibit a mobbing response to Blue Tits but not Great Tits, whereas if the response was an un-learned response to the general structure of the mobbing calls, Blue Tits would respond similarly to both stimuli. We made three exemplars of each treatment to reduce the effects of pseudoreplication. We created playback sound files from series of non-overlapping calls of varying length, extracted from recordings of each tit species mobbing a Sparrowhawk mount. For playback recording

examples see Supporting Information Audio S2–S4); recordings of Wood Pigeons were obtained from Xeno-canto (https://www.xeno-canto.org; XC94613, XC94614, XC130994, XC183441, XC183442). We simulated natural calling rates for each species in our playback recordings: mobbing calls were separated by an average ($\pm$ se) of 0.49 ± 0.03 s for Blue Tits and 0.88 ± 0.07 s for Great Tits across all sound files and had an average of 20.11 ± 1.88 elements/call for Blue Tits and 10.32 ± 0.33 elements/call for Great Tits (Carlson *et al.* 2017a,2017b,2017c). The Wood Pigeon recordings had a natural call rate of 3.5 calls/min with calls separated by an average of 10.00 ± 0.03 s and an average 13.33 ± 0.03 elements in each call. Wood Pigeon calls comprised repetitions of a single call, as their calls are stereotyped for each individual. For the Blue and Great Tit playbacks we included five different calls repeated in the same order for each audio file with call rates of 33.5 calls/min for Blue Tits and 33.5 calls/min for Great Tits. All playback files were generated from .wav file recordings and were saved as .wav files with a bit depth of 24 bits per sample and a sampling rate of 48 kHz. Each sound file consisted of 2 min of playback.

Playback

We presented each focal juvenile individual with all three playback stimuli sequentially. To do this, we went to each location and waited until we heard fledglings/juveniles (allowing us to find a cohesive fledgling flock – usually accompanied by one or occasionally two adults) and then chose a single focal fledgling to follow (the first we saw if there was more than one fledgling). We then placed a FoxPro Wildfire 2 speaker (FoxPro Inc., Lewistown, PA, USA) between 3 and 6 m away from the focal individual (and the other flock members), retreated at least 4 m from all birds in the flock, and played one of the three stimuli via remote control. The calls were all played at natural levels (~80 dB at 1 m SPL, determined using a Casella Cel-24XSPL sound pressure level meter), and the order each individual flock received the three stimuli, as well as the exemplar used, was randomized. Due to the potential stress of mobbing events and the demands on parent birds to feed their young, and on young to acquire food, we minimized any negative impact of the playbacks on the birds by limiting the duration of each
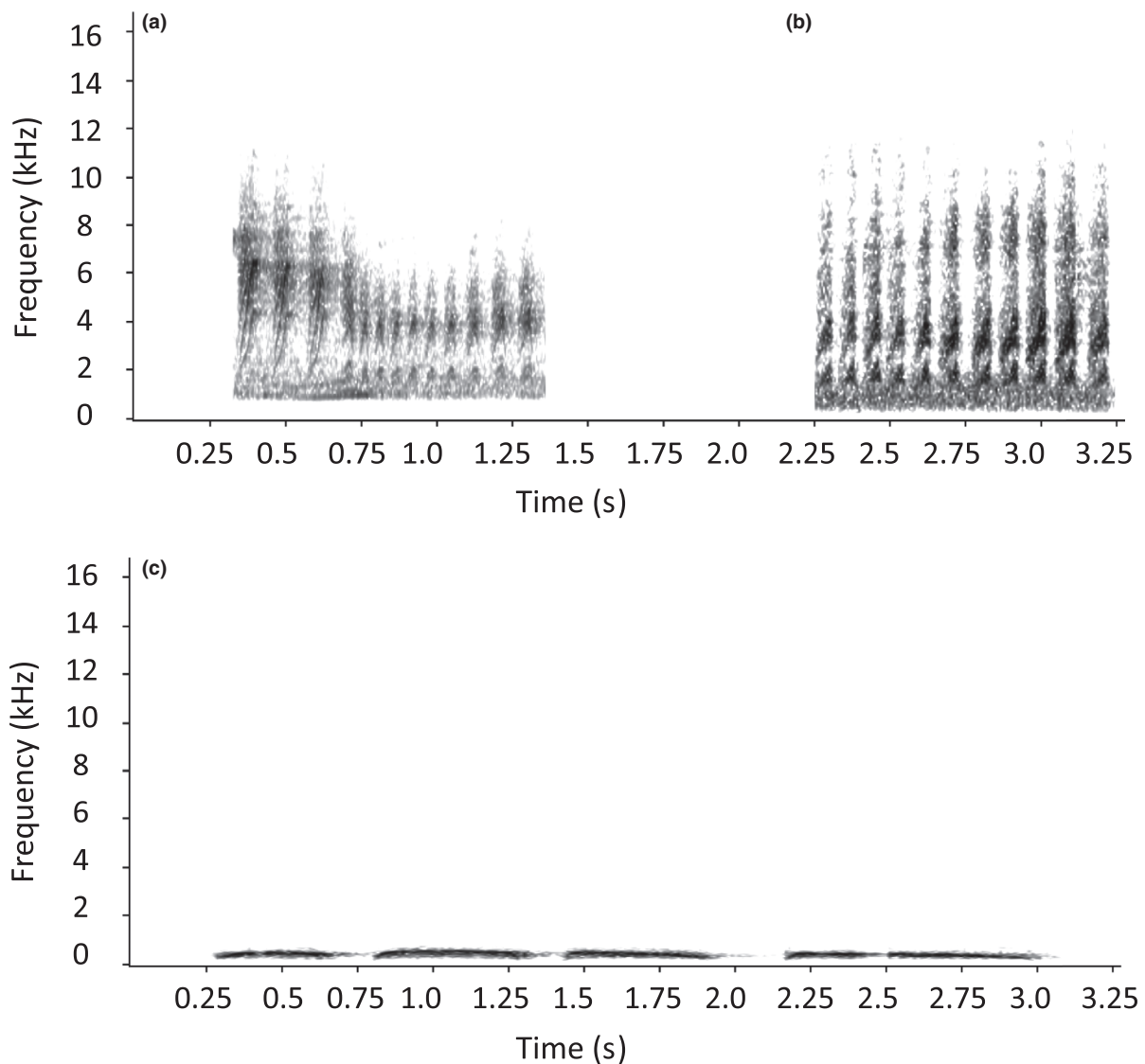
Figure 1. Spectrograms of (a) Blue Tit and (b) Great Tit mobbing calls, and (c) control Common Wood Pigeon calls from the playback sound files. Spectrograms were generated in Raven Pro v1.5 with a Hann window function, a fast Fourier transform (FFT) size of 1050 samples, and a frequency grid resolution of 21.5 Hz.

playback to 2 min. Although individuals were not colour-ringed, adults were easily differentiated from juveniles by plumage colour.

We recorded all behavioural and vocal responses of the focal juvenile using a Sennheiser ME 66 super-cardioid directional shotgun microphone (Sennheiser Electronics, Hanover, Germany) and a PMD 661 Marantz solid-state digital sound recorder (Marantz America, LLC., Mahwah, NJ, USA). We also noted the number of adults and whether they mobbed in response to the playback (see mobbing definition below). Adult

mobbing was a binary variable (either adults mobbed or did not). Although this way of counting adult mobbing might increase the chances of recording an adult mobbing (if there was more than one adult), in practice if one adult mobbed, the others would usually join in, lowering this possibility. All recordings were made with a sampling rate of 48 kHz and a bit depth of 24 bits. After each playback was finished we followed the focal fledgling for 20–30 min at which time we conducted the next trial. We did this to ensure that the same individual was sampled for all playback

treatments, while simultaneously providing enough time between playbacks to reduce carryover effects from previous mobbing playbacks. When possible, we did this for all three stimuli on the same day. If none of the birds in the area changed their foraging behaviour in response to the control playback, we waited only 5 min before presenting the focal individual with the next playback ($n = 8$). We did this to increase the likelihood that we tested the same individual with all three treatments before losing track of it and we saw no evidence that this decision influenced future responses (see Statistical analysis). For individuals for which we were not able to complete three consecutive presentations ($n = 5$, three of which remained incomplete), we returned to the same location the next day to complete the remaining treatment(s). Although this meant that we could not be sure we were sampling the same bird again, we still treated every trial in a particular location as though it were from the same bird to account for any possible pseudoreplication. We made this choice because we felt it was more conservative to treat different individuals as the same (admittedly thereby possibly introducing more variability into their behaviour due to individual differences) than to treat the same individual as different individuals (pseudoreplication). The first set of trials ($n = 7$) did not include control trials, and three split-day trials where experimenters could not re-locate the flock with 2 days of repeated visits together resulted in 10 subjects that were not presented with a control treatment.

Behavioural responses

We used Raven Pro v1.5 acoustical software (Bioacoustics Research Program 2014) to analyse vocalizations produced by target individuals and annotated recordings with a running commentary of behaviour, including the number and age of other Blue Tits. We recorded four component mobbing behaviours that are produced by adults in concert during mobbing events (Carlson *et al.* 2017c). These include one vocal behaviour (mobbing calls) and three non-vocal behaviours (flip-flopping, wing-flicking and approaching the playback speaker; see Table 1 for more detailed descriptions; Carlson *et al.* 2017c). During and after the playback, we recorded all behaviours of the focal juvenile and recorded whether adults that were present mobbed in response to the playback. We defined mobbing as mobbing vocalizations accompanied by at least one of the component stereotyped physical behaviours (Hinde 1952, Clemmons & Lambrechts 1992, Carlson *et al.* 2017a,2017c).

Statistical analysis

To test whether age (juvenile or adult) or playback (conspecific, heterospecific or control) affected the proportion of trials in which individuals mobbed, we generated generalized linear mixed models with a binomial distribution using the lmer function of the lme4 package in R. Our model included whether an individual mobbed (i.e. produced mobbing vocalizations accompanied by at least one of the non-vocal mobbing behaviours: flip-flopping, wing-flicking or approaching) as the response variable, with age (juvenile or adult), trial (which of the four successive trials in each location), exemplar (the playback exemplar) and order (the order of the playbacks) as fixed effects, and we included the location as a random effect. To test for a significant effect of our variables we ran a type III chi-square test.

To test whether the component behaviours of mobbing exhibited by juvenile Blue Tits differed in response to different playback stimuli (control, conspecific, heterospecific), we generated four binomial generalized linear mixed models (GLMMs), one for each tested behaviour. However, although the nature of the data is best tested using a binomial GLMM, as the sample size was relatively small and there was complete separation (i.e. some playbacks never received a specific behavioural response, e.g. no juveniles mob called, flip-flopped or wing-flicked to control playbacks) the model was therefore unable to evaluate the scaled gradient. Because of this problem, and the

Table 1. Descriptions of adult Blue Tit mobbing calls and stereotyped physical behaviours exhibited during mobbing (Hinde 1952, Clemmons & Lambrechts 1992, Carlson *et al.* 2017a,2017c)

Behaviour	Description
Mobbing calls	Broadband mobbing calls (Fig. 1a)
Flip-flop	Moving the whole body back and forth rapidly while remaining perched
Wing-flick	Flicking wings open and closed rapidly while remaining on perch
Approach	Moving or flying in the direction of the playback

fact that other models (e.g. linear mixed models) were not a good fit, we did not run further statistical tests on these data, but we report the proportions of trials in which juveniles exhibited these component behaviours.

RESULTS

Blue Tit age (adult or juvenile) explained a significant amount of variation in the propensity to mob in response to different playbacks ($\chi^2 = 18.97$, df = 1, $P < 0.001$): fledglings mobbed during one of 80 trials (control: 0/21 trials, Great Tit: 0/31 trials, Blue Tit: 1/28 trials), whereas adults mobbed during 31 of 66 trials (control: 5/16 trials, Great Tit: 8/26 trials, Blue Tit: 18/24 trials; Fig. 2a). Adults mobbed more in the first trials than they did in the last trials ($\chi^2 = 10.59$, df = 3, $P = 0.014$; Table S1). There were no exemplar or order effects (exemplar: $\chi^2 = 0.84$, df = 2,

$P = 0.656$, order: $\chi^2 = 1.01$, df = 2, $P = 0.605$; Table S1).

Although only one fledgling Blue Tit (from the second set of trials, and therefore probably not the oldest of the fledglings tested) exhibited complete mobbing behaviour in response to any playback, other fledglings exhibited individual components of mobbing to varying degrees in response to the three different playbacks (Fig. 2b). The fledglings produced mobbing calls only once, in response to a conspecific Blue Tit playback (control: 0/21, 0%, Great Tit: 0/31, 0%, Blue Tit: 1/28, 4%). Juveniles rarely flip-flopped (control: 0/21, 0%, Great Tit: 1/31, 3%, Blue Tit: 7/28, 25%) or wing-flicked (control: 0/21, 0%, Great Tit: 8/31, 26%, Blue Tit: 11/28, 39%) but, when they did, they did so only in response to mobbing playbacks. Blue Tit fledglings frequently approached mobbing, but not control, playbacks (control: 3/21, 14%, Great Tit: 23/31, 74%, Blue Tit: 19/28, 68%).
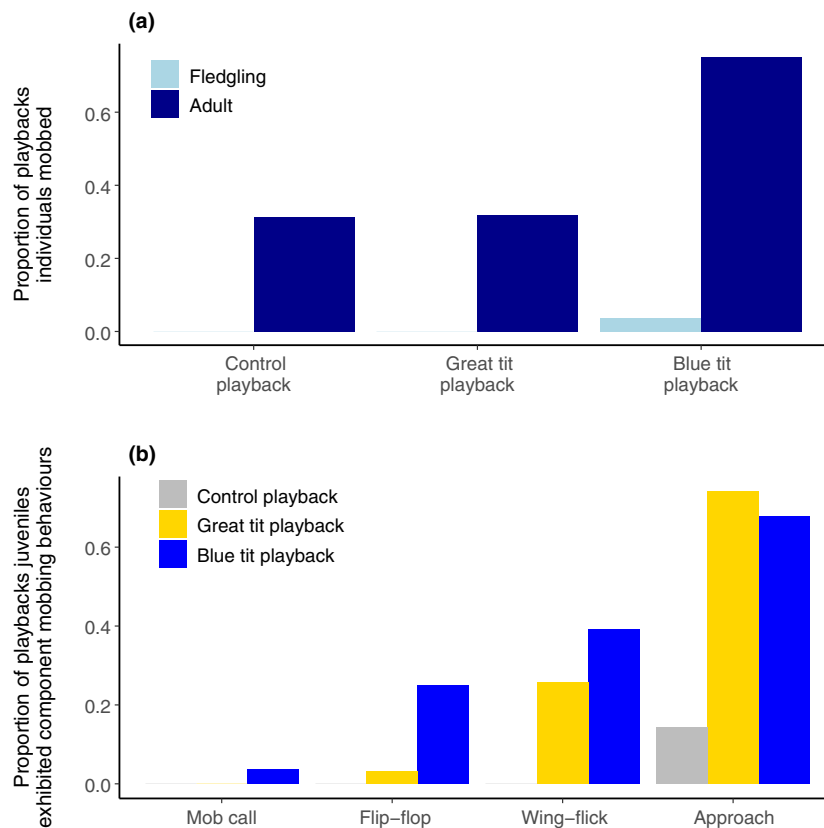

Figure 2. The proportion of trials in which (a) juveniles (light) and adults (dark) produced mobbing behaviour (see text for definition), and (b) juveniles produced individual components of mobbing in response to playbacks.

DISCUSSION

Only one of the focal juvenile Blue Tits mobbed in response to playbacks of either conspecific or heterospecific mobbing calls. They did, however, produce some of the non-vocal components found in adult mobbing (i.e. flip-flopping, wing-flicking and approaching the speaker), although they tended to produce these non-vocal behaviours only in single sporadic events. The lack of adult-like mobbing behaviour in juvenile Blue Tits could be due to three possible causes: (1) they are unable to mob due to physical inability and must learn to produce the mobbing actions and combinations; (2) there is a developmental trajectory over which juveniles master the component behaviours, then assemble them into the appropriate response (possibly by learning); (3) they choose not to mob as mobbing is dangerous and they are less dexterous than adults.

As juvenile Blue Tits could produce the component behaviours that adults collectively use during mobbing, juvenile Blue Tits are at least physically capable of mobbing. This rules out physical inability as a reason for the lack of adult-like mobbing behaviour. Similarly, the presence of these conspicuous mobbing behaviours accompanied by other kinds of calls (i.e. begging and contact calls) suggest that juveniles neither make an effort to hide themselves as a response to parental mobbing calls nor learn to change from nestling (i.e. silence) to full-grown behaviour (i.e. mobbing or fleeing) in response to adult mobbing as some species do (Platzen & Magrath 2005, Magrath *et al.* 2006). This suggests that, although Blue Tit fledglings may not be bold enough to physically attack a predator (as some adults do) while mobbing, their suppression of a mobbing response is also unlikely to be an attempt to hide themselves and avoid detection by the predator.

The production of components of mobbing may be evidence, however, that adult-like mobbing develops in parts over time rather than as a whole. By 'practising' component mobbing behaviours (i.e. producing each sporadically and infrequently), relatively uncoordinated juveniles may increase their dexterity. However, this does not explain why juveniles performed component mobbing behaviours only in mobbing situations during the mobbing playbacks and not in response to control playbacks. Blue Tit juveniles could have produced component behaviours in other contexts, but we did not see it when we followed the juveniles for extended periods between playback trials. This suggests that these behaviours are probably restricted to mobbing contexts. 'Practising' may be part of a developmental process of organizing the component behaviours of mobbing into the correct order, duration and timing. The presence of mobbing adults provides juveniles with exposure to the complete set of adult mobbing behaviours, allowing them to be repeatedly exposed to the correct set and intensity of mobbing behaviour. Additionally, as Blue Tit juveniles appeared to respond mostly in much the same way to both conspecific and heterospecific mobbing calls, it is not clear whether they learn to associate Blue and Great Tit mobbing calls and behaviour with one another (Haff & Magrath 2012, Potvin *et al.* 2018) or fine-tune their responses in order to differentiate between these acoustically similar calls (Clemmons 1995, Davies *et al.* 2004). Juveniles may also learn about predators during this period. As many bird species learn to associate novel predators with their degree of threat by observing conspecific mobbing behaviour and vocalizations (Curio *et al.* 1978, Baker 2004, Griesser 2009, Carlson *et al.* 2017b, Griesser & Suzuki 2017, Potvin *et al.* 2018), this juvenile 'practising' during adult mobbing events may help juveniles not only to learn the correct form of mobbing, but also to associate the information in mobbing vocalizations, mobbing behaviours and degree of threat with predators with which they have had little or no experience.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Model summary of the model describing the proportion of Blue Tit juveniles and adults that mob in response to each playback including: random effect variance, model estimates, degrees of freedom and z-values.

Audio S2. Sound file of one of the Blue Tit mobbing playbacks presented during trials.

Audio S3. Sound file of one of the Great Tit mobbing playbacks presented during trials.

Audio S4. Sound file of one of the Wood Pigeon control playbacks presented during trials.