Running Head: Social Cues and Foraging Rates

### **Public Information Affects Foraging Patch Use by Mixed Species Flocks of Tits in High Risk, Open Environments**

MEGAN J. BARNES & COLIN M. BEALE

*Department of Biology, University of York, YO10 5DD*

Social cues can improve estimates of foraging site predation risk beyond that of individual assessment alone as they provide current, accurate, information, and the importance of these cues may be greater in higher risk environments. We assessed the foraging behaviour of mixed species flocks of tits in both high risk, open environments and lower risk, closed environments in winter by measuring foraging intensity on standardised feeders. Responses to acoustic playback of bird calls differed in open and closed sites suggesting that reliance on social cues is dependent on the habitat. Audible social cues from known species, and to a lesser extent unfamiliar calls at a similar pitch, were most important in evaluating safety in open, riskier sites, with more seeds eaten when playback was present at open-site feeders compared to silent controls, but no difference observed between treatments in closed environments.

**Keywords:** Acoustic playback, *Aegithalos caudatus,* *Cyanistes caeruleus*, giving up density, *Parus major*, social cues.

An animal’s ability to accurately determine the quality of a habitat patch can strongly influence its survival and reproduction (Valone 2007). As well as an individual’s own experience of searching and sampling a resource (Valone 1991), social information, including observing the foraging success of others, can provide additional information about the availability and safety of a resource compared to individual information alone (Danchin *et al.* 2004, Valone 2007). However, the relative contribution of each mechanism is probably context dependent (Kendal *et al.* 2004). This ‘public information’ (Valone 1989) can influence an individual’s decision-making during foraging (Templeton & Giraldeau 1995, 1996, Ward & Zahavi 2008), such as indicating the location of food sources (Krebs 1974) and the predation risk (Danchin *et al.* 2004).

Predation risk is a major factor impacting the behaviour of foragers, altering feeding and habitat use (Altendorf *et al.* 2001, Abdulwahab *et al.* 2019). Predators are relatively rare, so individual assessment of perceived safety may depend largely on vegetation type (Altendorf *et al.* 2001). For some species, a feeding patch located close to trees provides cover and protection against predators (Brown *et al.* 1992, Abdulwahab *et al.* 2019), while others prefer areas far from trees to enable early predator detection (Cresswell 1994). When deciding to forage in higher risk areas, social cues may prove more important than at other times, because they could provide up to the minute information about the actual predation risk. Certainly, birds such as Starlings *Sturnus vulgaris* use visual cues of foraging success differently depending on local context (Templeton & Giraldeau 1995, 1996), but the importance of social cues may vary with vegetation structure in a way that we do not think has been tested previously.

Foraging in a group allows resource patches to be located more quickly (Aplin *et al.* 2015) and increased group vigilance and predator detection (Pulliam 1973). This reduces the time an individual spends being vigilant, allowing increased foraging, so contact calls may be an important social cue (Suzuki & Kutsukake 2017). The formation of mixed species flocks of birds is common in winter (Sridhar *et al.* 2009). In the UK, such flocks often include Great Tits *Parus major*, Blue Tits *Cyanistes caeruleus* and Long-tailed Tits *Aegithalos caudatus* (Morse 1978). These birds typically forage in woodland, seeking cover in dense vegetation when predators are present (Perrins 2012). Tits alter their behaviour to forage at sites with the least predation risk (Suhonen 1993) and preferentially forage close to the cover of trees (Todd & Cowie 1990). Both visual and auditory cues can be important (Kress 1983), but auditory cues have previously been shown to have a larger impact than visual cues when providing public information (Brandl *et al.* 2019). Species of tit are likely to avoid more open areas where predation risk is higher compared to closed habitats (Todd & Cowie 1990). With playback of sympatric species calls and perhaps other bird calls at a similar frequency at open sites, there is likely to be increased foraging at these feeders as calls can indicate a safe environment (Templeton & Giraldeau 1995). To assess this, six feeders were set up, three in the open and three in a closed woodland area, with one of three playback treatments applied: silence; control (Grey Partridge *Perdix perdix* call with a modified peak frequency to match that of the Long-tailed Tit call); and a Long-tailed Tit call. The weight of seeds eaten from the feeders in a day with each treatment were measured.

### **METHODS**

### **Study Location**

The University of York Heslington East Campus (53.9485° N, 1.0311° W: Fig. S1) consists of *c*. 10-year-old planted parkland with woods and open areas. Great, Blue and Long-tailed Tits are common residents and form mixed-species flocks (Morse 1978). In a limited study area with two small woodland patches, we set up three pairs of feeders in open areas and the nearby woodland (henceforth termed ‘bush’) between 18 January 2020 and 12 February 2020. Open sites averaged 21m from the nearest woodland. Pairing reflects both close physical distance and the treatment received: members of each pair consisting of bush and open feeder received the same treatment at one time. We noted weather conditions each day.

### **Feeders**

Each feeder was an open tray on a 1.83m pole that was filled between 07:30 and 08:00 each morning with a mix of 300g of gravel and 100g of seeds (Extra Select, Sunflower Hearts Wild Bird Food), adapted from Brown *et al.* (1992) (Fig. S2). The chrome pole prevented squirrels climbing the feeder. As the seeds are eaten, finding further seeds in the gravel becomes more time consuming for the birds, hence the seeds remaining were used as an accurate index of foraging intensity (the giving up density, *sensu* Brown (1988) and Brown *et al.* (1992)). We removed the remaining seeds and gravel at 15:30 (finishing the last feeder at 16:00) and separated them using flotation in water. Seeds were dried overnight and weighed the following morning to estimate the giving up density.

**Acoustic Playback**

To test our hypothesis, we needed to provide audible cues of foraging birds at some feeders and appropriate controls at others. We used the calls of Long-tailed Tits as the social cue, a silent control and a second control of a Grey Partridge call, modified to play at the same frequency as the Long-tailed Tit call (Fig. S3). Each location received a different treatment on a given day, with both feeders in each location receiving the same treatment. The treatment was rotated every two days until we had 49 measurements, with at least 14 at each site. We downloaded calls from Xeno-Canto as mp3 files (Xeno-canto.org, recordings of Long-tailed Tit by David W, [www.xeno-canto.org/196355](http://www.xeno-canto.org/196355) & Grey Partridge by Roels E www.xeno-canto.org/143118, accessed November 2019), and edited them using Audacity v 2.4.2 (Audacity Team 2020). One Long-tailed Tit track and one Grey Partridge track were used. The Long-tailed Tit file was unfiltered and contained typical social calls from three birds, the partridge track contained calls from a single male - a custom noise removal filter was applied before processing. We modified the peak frequency of the Grey Partridge call so that it matched that of the Long-tailed Tit, creating a control where we could test whether an unknown noise of similar frequency to small birds contained the same information a real call might have. We created 1-minute-long files by cutting the start/end of the 1:10 and 1:03 minute tracks and matched peak amplitudes. We played these continuously for the duration of each experiment, with no silent gaps, on outdoor wireless speakers (NBY Portable Bluetooth Speakers), played on full volume, with a transmission distance of 10m. This resulted in a call average volume of 68.8dB (max 83.4dB) for Grey Partridge and of 56.6dB (max 72.2dB) for Long-tailed Tit at 1m. Speakers were attached beneath the feeding tray (Fig. S2a). Speakers were still playing at the end of each day.

**Data Analysis**

All analyses were conducted in R v 3.6.3 (R core team 2020). We fitted a general linear model with a Gaussian link function predicting giving up density, with covariation indicating location (a factor with three levels indicating the treatment pair), plus the interaction of vegetation type and treatment. We assessed significance by comparing the full model with a reduced model with no interaction using ANOVA, followed by Tukey post hoc tests using the package multcomp (Hothorn *et al.* 2020). We assessed goodness of fit using visual inspection of the residuals and standard diagnostics.

### **RESULTS**

Observations at each visit confirmed that it was predominantly species of tit using the feeders. We found a significant interaction between treatment and habitat on the number of seeds remaining (χ2 = 2281.6, df = 2, *P* = 0.03: Fig. 1). After 8 hours of feeding, open plots retained more seeds than bush plots only in the silent and control treatments (Tukey post hoc test, *P* < 0.001, *P* = 0.014 respectively), but were similar when the Long-tailed Tit calls were playing. In open habitats, playing the Long-tailed Tit calls resulted in the largest reduction in giving up density (46.2%) when compared to the silent group (Tukey post hoc test, *P* = 0.002). Effects of the Grey Partridge control call were intermediate (Fig. 1). Locations were significantly different (χ2 = 7827.5, df = 2, *P* < 0.001), but treatments were paired and we undertook a balanced rotation of treatments so weather and site effects were controlled.

### **DISCUSSION**

We found evidence that birds respond differently to the sound of bird calls in open and closed habitats. After 8hrs of feeding, more seeds remained in open than woodland sites (on average 25.8g fewer seeds remained in woodlands), as in previous findings (Brown *et al.* 1992, Altendorf *et al.* 2001, Abdulwahab *et al.* 2019). The Long-tailed Tit call increased foraging rates, but only in open sites. This suggests that species of tit in the mixed flocks may use social cues differently depending on the habitat in which they are foraging. The control sound of the Grey Partridge also altered foraging behaviour in the open habitats (though not by as much as the Long-tailed Tit calls), but this did not differ significantly to the silent treatment. This could perhaps indicate that calls in the frequencies used by Long-tailed Tits may be enough to trigger behavioural responses in foraging passerines.

Consistently more seeds were eaten in woodland than in the open habitats suggesting that these areas are already considered safe foraging areas. This may be in part due to the presence of natural social cues. If, as hypothesised, playback indicates a safe foraging site, a small decrease in seeds remaining would still be expected with the additional playback provided in the closed habitats. This was not seen, perhaps due to these environments having many sympatric calls already present, resulting in the playback treatment having no effect. It is also possible that calls were less audible in the closed woodlands than open landscapes, which could also explain the lack of response to playback here.

At open sites, the Long-tailed Tit call reduced the weight of seeds remaining so that it was not significantly different to that of the woodland sites, suggesting that this ‘conspecific cueing’ (Stamps 1988) and use of public information (Valone 1989) affects how a forager makes decisions about where to feed. Public information has previously been suggested to be more important than individual assessment when deciding the quality of a location in the Black-Throated Blue Warbler *Setophaga caerulescens*, which could be encouraged into poor quality habitats using just playback (Betts *et al.* 2008), but our results suggest this effect may be sensitive to environmental conditions. Such responses suggest that both social information and individual assessment are important in acquiring information about the safety of a foraging site.

When playing the Grey Partridge call altered to match the pitch of the Long-tailed Tit, the weight of seeds remaining were intermediate between the amount left at silent and treatment feeders (but did not differ significantly from either), suggesting noises of the correct frequency alone could increase the perceived safety of foraging areas to some degree. Pitch is a key cue for many birds (Rothenberg *et al.* 2014) and species that co-occur often respond to the alarm calls of heterospecifics (Magrath *et al.* 2007), especially those that resemble their own call (Meise *et al.* 2018). Consequently, it may be advantageous for species of tit to respond to the frequency-modified partridge calls played.

There are some caveats to our interpretation. Firstly, we only used one call from each treatment species, so it is possible that responses are specific to the chosen call (Long-tailed Tits certainly use calls to identify individuals; Leedale *et al.,* 2020). Future work could test calls from other individuals. Similarly, although we mainly observed Great Tits, Blue Tits and Long-tailed Tits at our feeders, other birds did sometimes use the feeders too, so our results may not exclusively reflect tit foraging behaviour.

Overall, we conclude that the social influences of bird calls on foraging decisions are most important in open habitats, corresponding to higher risk sites for the birds in our study. Birds rely on audible social cues from known species and (to a lesser degree) unfamiliar calls of a similar pitch, in order to evaluate safety of a feeding site, using social cues more when foraging in riskier areas. The mitigation of foraging risk by increased reliance on social cues is likely to be important in the foraging decisions of many bird species.

We thank Gordon Easton for facilitating access to field sites on campus and the Department of Biology at the University of York for funding field equipment.

**DATA AVAILABILITY**

The data that support the findings of this study are available in the supplementary material of this article. Analysis can be found at <https://colab.research.google.com/drive/16y--R80RFRbCCDmxL9F_bPgFe_wb-mh0?usp=sharing>

**REFERENCES**

Abdulwahab UA, Osinubi ST, Abalaka J. 2019 Risk of predation: a critical force driving habitat quality perception and foraging behavior of granivorous birds in a Nigerian forest reserve. *Avian Research* 10, 33. (doi:10.1186/s40657-019-0173- 6)

Altendorf KB, Laundré JW, López González CA, Brown JS. 2001 Assessing Effects of Predation Risk on Foraging Behavior of Mule Deer. *J. Mammal.* 82, 430–439.

Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518(7540),538-541. (doi:10.1038/nature13998)

Audacity Team (2020). Audacity(R): Free Audio Editor and Recorder [Computer application]. Version 2.4.2 retrieved 21st Feb 2020 from <https://audacityteam.org/>

Betts MG, Hadley AS, Rodenhouse N, Nocera JJ. 2008 Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proc. Biol. Sci.* 275, 2257–2263. (doi:10.1098/rspb.2008.0217)

Brandl HB, Griffith SC, Laaksonen T, Schuett W. 2019 Begging calls provide social cues for prospecting conspecifics in the wild Zebra Finch (Taeniopygia guttata). *Auk* 136. (doi:10.1093/auk/ukz007)

Brown JS, Morgan RA, Dow BD. 1992 Patch use under predation risk: II. A test with fox squirrels, Sciurus niger. *Ann. Zool. Fennici* , 311–318.

Brown JS. 1988 Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 22, 37–47. (doi:10.1007/BF00395696)

[Cresswell, W. 1994 Age-Dependent Choice of Redshank (*Tringa totanu*s) Feeding Location: Profitability or Risk? *J. Anim. Ecol.* 63: 589–600.](http://paperpile.com/b/ZSkR8A/iPDQ)

Danchin E, Giraldeau L-A, Valone TJ, Wagner RH. 2004 Public information: from nosy neighbors to cultural evolution. *Science* 305, 487–491. (doi:10.1126/science.1098254)

Hothorn T, Bretz F, Westfall P. 2008 Simultaneous Inference in General Parametric Models. Biometrical Journal, 50(3), 346–363.

Kendal RL,Coolen I, Laland KN. 2004 The role of conformity in foraging when personal and social information conflict, Behav. Ecol.15(2), 269–277. ([doi:10.1093/beheco/arh008](https://doi.org/10.1093/beheco/arh008))

Krebs JR. 1974 Colonial Nesting and Social Feeding as Strategies for Exploiting Food Resources in the Great Blue Heron (Ardea Herodias). *Behaviour* 51, 99–134. (doi:10.1163/156853974X00165)

Kress SW. 1983 The Use of Decoys, Sound Recordings, and Gull Control for Re-Establishing a Tern Colony in Maine. *Colonial Waterbirds* 6, 185–196. (doi:10.2307/1520987)

Leedale AE, Simeoni M, Sharp SP, Green JP, Slate J, Lachlan RF, Robinson EJH, Hatchwell BJ. 2020 Cost, risk, and avoidance of inbreeding in a cooperatively breeding bird. *Proc. Natl. Acad. Sci.* 117, 15724-15730. (doi: 10.1073/pnas.1918726117)

Magrath RD, Pitcher BJ, Gardner JL. 2007 A mutual understanding? Interspecific responses by birds to each other’s aerial alarm calls. *Behav. Ecol.* 18, 944–951. (doi:10.1093/beheco/arm063)

Meise K, Franks DW, Bro-Jørgensen J. 2018 Multiple adaptive and non- adaptive processes determine responsiveness to heterospecific alarm calls in African savannah herbivores. *Proc. Biol. Sci.* 285. (doi:10.1098/rspb.2017.2676)

Morse DH. 1978 Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. *Ibis* 120, 298-312. ([doi:10.1111/j.1474-919x.1978.tb06790.x](https://doi.org/10.1111/j.1474-919X.1978.tb06790.x))

[Perrins, C. 2012. British Tits (Collins New Naturalist Library, Book 62). HarperCollins UK.](http://paperpile.com/b/ZSkR8A/BkOc)

Pulliam HR. 1973 On the advantages of flocking. *J. Theor. Biol.* 38, 419–422. (doi:10.1016/0022-5193(73)90184-7)

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rothenberg D, Roeske TC, Voss HU, Naguib M, Tchernichovski O. 2014 Investigation of musicality in birdsong. *Hear. Res.* 308, 71–83. (doi:10.1016/j.heares.2013.08.016)

Sridhar H, Beauchamp G, Shanker K. 2009 Why do birds participate in mixed- species flocks? A large-scale synthesis. *Anim. Behav.* 78, 337–347. (doi:10.1016/j.anbehav.2009.05.008)

Stamps JA. 1988 Conspecific Attraction and Aggregation in Territorial Species. *The American Naturalist* 131, 329–347.

Suhonen, J. 1993 Predation Risk Influences the Use of Foraging Sites by Tits. *Ecology,* 74(4), 1197-1203. (doi:10.2307/1940490)

Suzuki TN, Kutsukake N. 2017 Foraging intention affects whether willow tits call to attract members of mixed-species flocks. *R Soc Open Sci* 4, 170222. (doi:10.1098/rsos.170222)

Templeton JJ, Giraldeau L-A. 1995 Patch assessment in foraging flocks of European starlings: evidence for the use of public information. *Behav. Ecol.* 6, 65–72. (doi:10.1093/beheco/6.1.65)

Templeton JJ, Giraldeau L-A. 1996 Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behav. Ecol. Sociobiol.* 38, 105–114. (doi:10.1007/s002650050223)

Todd, A, Cowie, RJ. 1990 Measuring the risk of predation in an energy currency: field experiments with foraging blue tits, Parus caeruleus. *Animal Behaviour* 40(1), 112-117.

Valone TJ. 1991 Bayesian and prescient assessment: foraging with pre-harvest information. *Anim. Behav.* 41, 569–577. (doi:10.1016/S0003-3472(05)80897-8)

Valone TJ. 2007 From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behav. Ecol. Sociobiol.* 62, 1–14. (doi:10.1007/s00265-007-0439-6)

Valone. 1989 Group foraging, public information, and patch estimation. *Oikos* 56, 357–363. (doi:10.2307/3565621)

Ward P, Zahavi A. 2008 The importance of certain assemblages of birds as ‘information centres’ for food-finding. *Ibis* 115, 517–534. (doi:10.1111/j.1474- 919X.1973.tb01990.x)

**Figure Legends:**

**Figure 1.** The weight of the seeds remaining is dependent on both the treatment and habitat. All weights of seeds remaining plotted as circles, light grey represents bush habitats, dark grey represents open habitats. Treatments were Silent (no calls), Control (frequency-modified Grey Partridge calls) and Sound (Long-tailed Tit calls). Boxplots show median and inter quartile range. The same letter represents no significant difference between groups, e.g. all with the letter ‘a’ are not significantly different from one another.

Figure S1. Study Location

Figure S2. Feeders

Figure S3. Calls for Playback.