

Do false alarm anti-predatory flushes provide a foraging benefit to subdominant species?

Darren M. EVANS¹, Graeme D. RUXTON² & David A. RUXTON³

¹Centre for Ecology and Hydrology, CEH Banchory, Hill of Brathens, Banchory AB31 4BW, United Kingdom; tel: +440 1330 826321, e-mail: dme@ceh.ac.uk

²Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, United Kingdom

³15 Old Hillfoot Road, Ayr KA7 3LW, United Kingdom

EVANS, D. M., RUXTON, G. D. & RUXTON, D. A., Do false alarm anti-predatory flushes provide a foraging benefit to subdominant species? *Biologia, Bratislava*, 59: 675–678, 2004; ISSN 0006-3088.

It is well known that birds often simultaneously take flight from a feeding site (flush), in response to a real or perceived predation threat. We hypothesised that such flushes would provide a means for subdominant individuals to alleviate the effects of competition for food. Specifically, we predicted that subdominant species would either be less prone to flushing and/or would return to feed after a flush more quickly than more dominant species. The main aim of this project was to test this hypothesis using garden birds feeding at provisioned feeders. We also sought to explore whether pseudo alarm calls were made by *Parus* species in order to reduce competition from dominant species, as has been previously reported. In our study, there was no evidence that instances with alarm calls differed from flushes without alarm calls with respect to the first bird to alight on the feeders after the flush. However, subdominant *Parus* species return more quickly to the foraging site after an anti-predatory flush. This can be interpreted as birds being prepared to risk returning too early to a site that may still have an active predator in order to take advantage of temporally reduced competition for food. Interestingly, increased predation rate is likely to increase the rate at which flushes occur and so increase the frequency with which subordinates can take advantage of such reduced competition. As such, this work provides a counter-example to the normally considered case where increased predation risk has a particularly detrimental effect on subdominants.

Key words: alarm calling, trade-off, competitive exclusion, garden birds.

Introduction

Most animals are vulnerable to predation during feeding, since foraging activities constrain the time (or attention) available for anti-predatory vigilance. Thus, foraging decisions of animals are classically considered to reflect a trade-off between predation risk and efficient foraging (SIH, 1980;

LIMA & DILL, 1990). Hence, increased risk of predation is generally considered to have an adverse effect on an individual's rate of food intake. This adverse effect might be expected to fall most heavily on subdominant individuals. For example, WHITFIELD (1985) found that sparrowhawks *Accipiter nisus* (L., 1758) preyed on juvenile redshanks *Tringa totanus* (L., 1758) and turnstones

Arenaria interpres (L., 1758) more than would be expected from the age composition of the species, an effect that he attributed to competition from adults forcing juveniles to forage in areas where predation risk was higher. Similar results were reported by HINSLEY et al. (1995) for sparrowhawks attacking great tits *Parus major* L., 1758 and blue tits *Parus caeruleus* L., 1758. The latter study demonstrated that subordinate juveniles were prepared to feed at higher-risk sites further from cover than dominant adults. For juveniles the increased predation risk is a price worth paying for reduced competition. It is well known that birds often simultaneously take flight from a feeding site (hereafter called a flush), in response to a real or perceived predation threat. We hypothesised that such flushes would provide another means for subordinate individuals to alleviate the effects of competition for food. Specifically, we predicted that subordinate individuals would either be less prone to flushing and/or would return to feed after a flush more quickly than more dominant individuals. The main aim of this project is to test this hypothesis using garden birds feeding at provisioned feeders.

We also wish to explore the effect of alarm calling by *Parus* species in the context of competition for food. MATSUOKA (1980) and MØLLER (1988) suggested that *Parus* species may emit alarm calls when no predator is present, referred to as a "false alarm". These calls are suggested to serve to cause species dominant to the *Parus* species to flush, thus allowing the caller access to a food source that was otherwise denied to it by competitive exclusion. However, HAFTORN (2000) comments that "false alarm calls used in similar contexts have so far never been recognised in Norway by me or Olav HOGSTAD despite lifelong experiences with winter feeding of birds (mainly tits)". Hence, we will explore whether the occurrence of an alarm call immediately prior to a flush was in any way predictive of the species of bird that returned first after the flush in our study.

Material and methods

The study took place between January and March 2001 in a garden located in Dumgoyne, a rural village in central Scotland (55°59' N, 4°24' W). Food (peanuts and mixed seeds) was provided from clear plastic feeders with perches, hung from a tree such that they were 2 m from the ground. For three hours each morning, the feeders were recorded using a video camera from a ground floor window in the adjacent building (3 m away). The same observer (DME) recorded the time of each flush (defined as the simultaneous flush of over

50% of the birds on the feeders and within a 5 m radius of them). If possible, the reason for the flush (generally traffic on a nearby road, human disturbance or over-flying birds) was recorded, along with any alarm calls that were heard. The videos were analysed by DAR. For each flush the numbers of each species immediately before the flush and immediately after were recorded, as well as the species of the first bird to alight on a feeder after the flush.

Results

Frequency of flushes

Flushes occurred 638 times in 56.5 h of observation. Hence a flush occurred on average every 319 ± 12 (SE) s [5.3 ± 0.2 (SE) min].

The species of birds returning after a flush

One species that is clearly unusual is the coal tit *Parus ater* L., 1758. Of the 563 flushes where the first returning individual could be identified, coal tits were present just before the flush on only 32 (6%) occasions (31 occasions with a single individual, and one pair). However, the first bird to return was a coal tit on 65 (11%) of occasions. If we use the relative frequencies of group sizes after all 563 flushes to calculate predicted values for the subset of cases where a coal tit was the first bird back, then we find that this distribution is significantly different from the one observed ($\chi^2 = 11.4$, $df = 4$, $P < 0.05$). By inspection, we can see that coal tits are more likely to be the first bird back if the number of birds remaining on the feeder is low.

Blue tits, chaffinches *Fringilla coelebs* L., 1758, great tits and greenfinches *Carduelis chloris* (L., 1758) make up 85% of first birds back (Fig. 1a). These four species also dominate the total numbers recorded on the feeder before a flush (Fig. 1b) and the total numbers flying at a flush (Fig. 1c). Of these species, the finches dominate the tits (FITZPATRICK, 1995; personal obs.). From these graphs we can see that, whether our expectation is drawn from the relative numbers of birds on the feeder *before* the flush (Fig. 1b) or birds that remain *during* the flush (Fig. 1c), tit species are first to return more often (Fig. 1a) than would be expected, and greenfinches much less often. These impressions are borne out by statistical testing (expectation drawn from total numbers: $\chi^2 = 207.9$, $df = 3$, $P < 0.001$; expectation drawn from fleeing numbers: $\chi^2 = 191.7$, $df = 3$, $p < 0.001$). An interesting comparison here is between the distribution of species types before (Fig. 1b) and after a flush (Fig. 1d). There is a

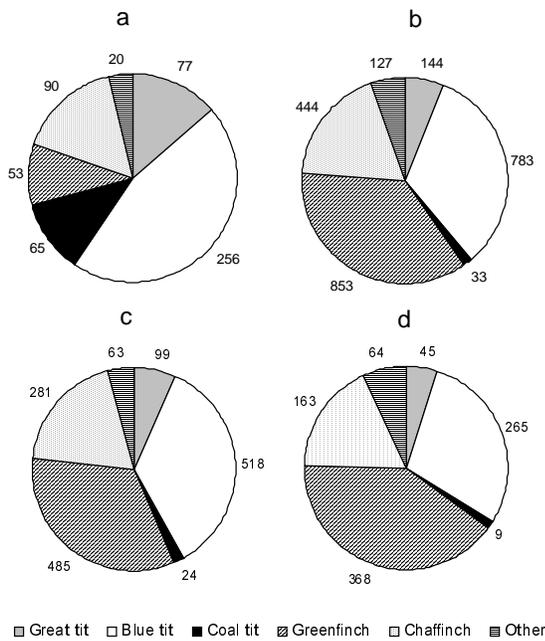


Fig. 1. Pie charts describing the breakdown by species of the first bird to return to the feeders after a flush (a), bird on the feeder just prior to a flush (b), birds that flew from the feeders during a flush (c), and birds that remained on the feeders during a flush (d).

significant difference between the two ($\chi^2 = 8.3$, $df = 3$, $P < 0.05$). Following a flush, the two finch species were more likely to still be at the feeder than blue tits and great tits.

Alarm calling

There were 186 flushes where a tit alarm call was heard just before the flush, and 374 flushes where no such call was heard. However, whether a call

was heard or not had no effect on the species identity of the first bird returning ($\chi^2 = 8.74$, $df = 4$, $P > 0.05$: the returning bird was categorised as either blue tit, great tit, coal tit, greenfinch or other).

Discussion

Despite 33% of flushes being preceded by a tit alarm call, there was no evidence that instances with alarm calls differed from other flushes with respect to the species of the first bird to alight on the feeders after the flush. Hence, it appears that our tits do not behave like the Japanese great, willow and marsh tits of MATSUOKA (1980) or the Danish great tits of MØLLER (1988). Rather, like those reported by HAFTORN (2000), there was no indication of deceptive use of alarm calling in our study system, even though blue and great tits were often seen to be competitively excluded from feeding by dominant greenfinches and chaffinches. From our observations (and other studies, e.g. BARLUENGA et al., 2001), the coal tit had the lowest dominance status of all the species regularly visiting the feeder, being regularly usurped even by other *Parus* species. One reason for the unusually high frequency with which it is the first bird to return after a flush could be that the reduced competition present just after a flush is attractive to this relatively subordinate species. This argument is supported by the comparison of the frequencies of different numbers of birds remaining on the feeder after the flush (Tab. 1).

It is well known that competition can drive subdominants to shift their foraging sites (e.g. ALATALO, 1981). This niche shift may be temporal rather than spatial: FITZPATRICK (1997) observed that subordinate species were the first to arrive at a garden bird feeder each day. Here

Table 1. Comparison between instances when the first returning bird was a coal tit compared to instances when it was another species, stratified according to the number of birds that did not flush but remained on the feeder throughout.

| Number of birds remaining on feeder | No. of cases when the first bird back was another species | No of cases when the first bird back was a coal tit | Predicted values based on all cases |
|-------------------------------------|---|---|-------------------------------------|
| 0 | 155 | 22 | 20.4 |
| 1 | 109 | 23 | 15.2 |
| 2 | 95 | 13 | 12.5 |
| 3 | 73 | 1 | 8.5 |
| 4+ | 66 | 6 | 8.3 |

we have demonstrated a similar effect on a much shorter temporal scale: subdominant species return more quickly to the foraging site after an anti-predatory flush. This can be interpreted as birds being prepared to risk returning too early to a site that may still have an active predator in order to take advantage of temporally reduced competition for food (see KOIVULA et al., 1995), although our study did not take into account the physiological differences between species (e.g. size, fat stores) and associated food demands. In addition, our study did not take into account the role of individual birds and it is possible that a certain proportion of individuals of each species might adopt a more 'risky' strategy than others. Future research could test for this using individually marked birds. Interestingly, increased predation rate is likely to increase the rate at which flushes occur and so increase the frequency with which subordinates can take advantage of such reduced competition. As such, this work provides a counter-example to the normally considered case where increased predation risk has a particularly detrimental effect on subdominants.

Acknowledgements

We thank D. HOUSTON for the kind use of his garden and M. MARQUISS for his comments on an earlier draft. This is dedicated to D. A. RUXTON who sadly died during the preparation of this manuscript.

References

- ALATALO, R. V. 1981. Interspecific competition in tits *Parus* spp. and the goldcrest *Regulus regulus*: foraging shifts in multispecific flocks. *Oikos* **37**: 335–244.
- BARLUENGA, M., BARBOSA, A. & MORENO, E. 2001. Differences in daily mass gain between subordinate species are explained by differences in ecological plasticity. *Ecoscience* **8**: 437–440.
- FITZPATRICK, S. 1995. Utilisation of provisioned peanuts by suburban tits in Belfast. *Irish Birds* **5**: 299–304.
- FITZPATRICK, S. 1997. The timing of early morning feeding by tits. *Bird Study* **44**: 88–96.
- HAFTORN, S. 2000. Contexts and possible functions of alarm calling in the willow tit, *Parus montanus*; the principle of "better safe than sorry". *Behaviour* **137**: 437–449.
- HINSLEY, S. A., BELLAMY, P. E. & MOSS, D. 1995. Sparrowhawk *Accipiter nisus* predation and feeding site selection by tits. *Ibis* **137**: 418–420.
- KOIVULA, K., RYTKÖNEN, S. & ORELL, M. 1995. Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate Willow Tits. *Ardea* **83**: 397–404.
- LIMA, S. L. & DILL, L. M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.
- MATSUOKA, S. 1980. Pseudo alarm calling in titmice. *Tori* **29**: 87–90.
- MØLLER, A. P. 1988. False alarm calls as a means of resource usurpation in the Great Tit *Parus major*. *Ethology* **79**: 25–30.
- SIH, A. 1980. Optimal behaviour: can foragers balance two conflicting demands. *Science* **210**: 1041–1043.
- WHITFIELD, D. P. 1985. Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**: 544–558.

Received July 17, 2003
Accepted November 13, 2003