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# The Role of Alarm Responses in the Formation of Mixed-Species Flocks of Heathland Birds

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**Summary.** Birds of ten species with similar short flight distances from a human intruder associated with stonechats (*Saxicola torquata*), which have large flight and alarm call distances. The attendants probably took advantage of the 'domain of safety' around the stonechat, produced by the difference in flight distance. Stonechats have no reciprocal advantage, and were not seen to initiate flocks.

Flocks were formed with both calling and silent stonechats. Benefits in the latter case probably include early warning of danger, but there may also have been a reduction in vigilance by attendants.

The relative flocking activity of attendant species (number of associations observed; percentage of incidents with silent stonechats; rate of warning calls by stonechats joined) was related to the species' average flight distance from an intruder (Fig. 1). Possible explanations are consistent with a correspondence between flocking tendency and the degree of benefit obtained.

## Introduction

There are many possible consequences from joining a temporary group (see reviews by Morse 1977; Bertram 1978). One benefit is the reduction of risk from predators by relying on other group members' vigilance, which provides an early warning of danger (Lazarus 1972, 1979; Pulliam 1973; Powell 1974). As a result, individuals may divert less effort to vigilance from other activities such as foraging (Pulliam 1973; Silliman et al. 1977; Abramson 1979; Caraco 1979a, b; and references in Lazarus 1979).

In this paper data are presented on flocks of heathland birds and on responses to danger by members of the species involved. This helps to identify the circumstances under which individual birds could benefit by making use of the vigilance and alarm signals of others and suggests why species differ in their tendencies to flock.

It is assumed that individual birds have characteristic, species-specific responses to the approach of potential predators or other forms of disturbance. When an intruder reaches a certain critical distance, the animal flees ('flight distance'), and before this it may give a call or other alarm signal. Unless an animal's ability to detect predators is nearly perfect, it would always be expected to pay attention to alarms given by another. However, if the warner has a greater flight distance than the attendant, it may be beneficial for the attendant to move close to the warner. The former could enjoy a 'domain of safety' (cf. Hamilton's (1971) 'domain of danger') around the latter, defined by the difference between their flight distances. So long as an attendant was within that radius of the animal giving the warning, it could be sure that an intruder would not approach closer than its limit of tolerance while the warner remained. It would thus be relieved of some of its need for vigilance.

These arguments appear to provide an adequate explanation for the behaviour of several heathland bird species forming associations with stonechats (*Saxicola torquata*), which have large flight distances and are particularly vigilant.

## Methods

Fieldwork was conducted 1977–1979 at Ashdown Forest, Sussex, UK. The area consists of lowland heath, a vegetation mosaic dominated by gorse (*Ulex europaeus* and *U. minor*), heather (*Calluna vulgaris, Erica cinerea* and *E. tetralix*), bracken (*Pteridium aquilinum*) and purple moor-grass (*Molinia caerulea*), with scattered pine (*Pinus sylvestris*) and birch trees (*Betula* spp).

During watches on known individual stonechats, all incidents

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were recorded when birds of other species associated with them, defined as one bird flying to perch close to another (<ca. 5 m away), and remaining for at least 10 s. Some associations were maintained by birds repeatedly following stonechats; these moves were not counted as separate incidents.

For each association, some or all of the following information was recorded: (i) the numbers and species of birds involved; (ii) which bird initiated the association (i.e. flew to join a solitary bird); (iii) the distance between bird and observer when the association began, measured later in paces (1 pace $\simeq$1 m); (iv) which birds foraged or called while the association lasted; (v) the sex of the stonechat. Further information on the stonechats' behaviour, including call-rates and breeding data, was taken from a concurrent study (Greig-Smith 1980).

For each species, at least five undisturbed birds were observed to determine the proportion of time spent hidden in vegetation by timing with a stopwatch during watches of up to 5 min. The responses of birds to a human disturbance were assessed by walking slowly towards a bird and measuring (in paces) the distance at which it made its first alarm call, or flew away from me. Each bird was assessed only once on each occasion, and data on flight distances were gathered separately for hidden and exposed birds.

## Results

Birds of 15 species were seen associating with stonechats, but the most frequent were willow warblers *Phylloscopus trochilus,* whitethroats *Sylvia communis* (combined with records of lesser whitethroats *S. curruca* because the two species were not always distinguished), reed buntings *Emberiza shoeniclus,* yellowhammers *E. citrinella,* linnets *Acanthis cannabina,* redpolls *A. flammea,* meadow pipits *Anthus pratensis* (combined with tree pipits *A. trivialis*), and dunnocks *Prunella modularis.* All but a very few of 290 associations were clearly initiated by birds other than stonechats, and male stonechats were joined more frequently (130 occasions) than females (62), despite an approximately equal sex ratio in the population. Associations were usually brief, rarely involving more than four attendants, and in these flocks both foraging and aggression were very infrequent.

On 178 occasions (68%) birds joined a stonechat that was calling, usually rising from hidden positions in the vegetation as soon as the calls began. Previous work had shown that these calls, of two kinds, are given to defend the stonechats' offspring by warning nestlings to be silent and by distracting predators (Greig-Smith 1980). The remaining 84 flocks (32%) formed when the stonechat was silent, and making no other obvious signs of alarm. On many such occasions, the attendants hid in nearby vegetation rather than perching exposed beside the stonechat.

On average, male and female stonechats make a similar number of defence calls (Greig-Smith 1980), and when attendants joined a single calling stonechat, it was as likely to be a male (76 of 128 occasions) as a female (52 of 128 occasions) ($\chi^2_1=2.21$, $P>0.10$, compared with numbers expected from the average sex ratio of 1.12 males to 1 female). In contrast, when they joined a single silent stonechat, it was much more frequently a male than a female (49 of 57 versus 8 of 57 occasions, $\chi^2_1=25.15$, $P<0.001$).

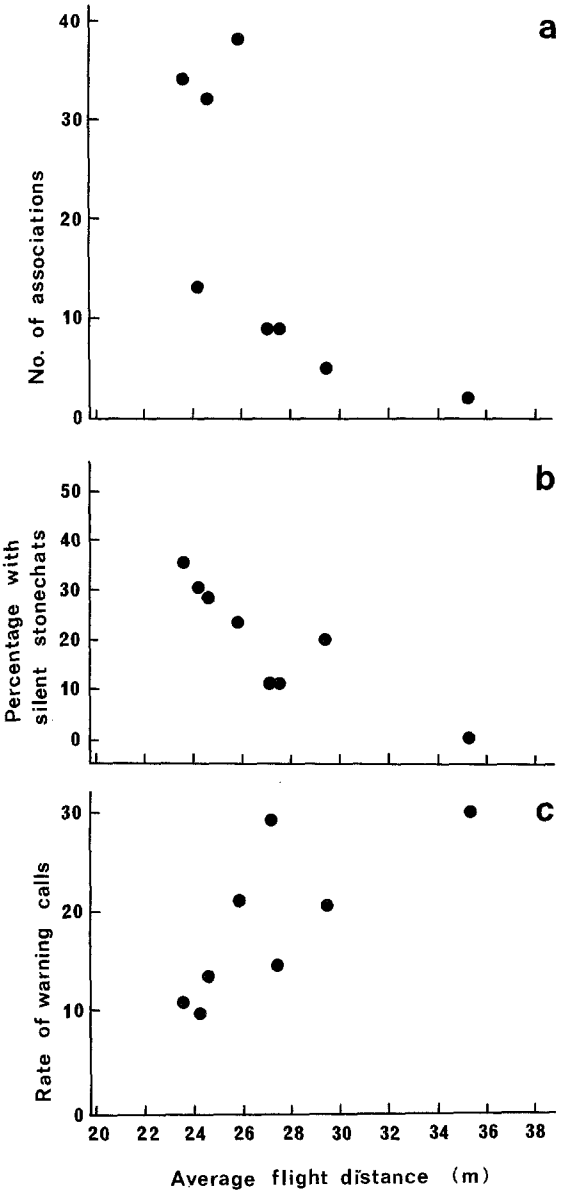


**Fig. 1a–c.** Correlations across species of average flight distance of exposed birds, against **a** the number of times that birds were seen in association with stonechats, **b** the percentage of associations that were with a silent rather than a calling stonechat, and **c** the average rate of warning calls given by stonechats during associations. From left to right, the species are *E. shoeniclus, Anthus* spp combined, *Sylvia* spp combined, *P. trochilus, A. flammea, A. cannabina, E. citrinella, P. modularis*

The disturbance experiments showed that stonechats on average gave alarm calls at $101\pm26$ m ($n=22$) from the observer, and flew at $57\pm26$ m ($n=17$). These distances are much greater than the corre-

**Table 1.** Spearman rank correlations between three attributes of species that might influence the value of flocking, compared with five measures of flock behaviour

| | Average flight distance of exposed birds | Average flight distance of hidden birds | Percentage of time spent hidden in vegetation |
|---|---|---|---|
| No. of associations with stonechats | −0.82* | 0.61 | −0.07 |
| Average rate of warning calls by stonechats | 0.72* | −0.14 | 0.46 |
| Average rate of distraction calls by stonechats | 0.55 | −0.14 | 0.39 |
| Percentage of associations with silent stonechat | −0.91** | 0.22 | −0.07 |
| Average distance from intruder at start of association | −0.36 | −0.33 | −0.32 |

* indicates $P<0.05$, ** indicates $P<0.01$

sponding average distances for other species, which varied from 29 to 41 m (alarm call distance), 24 to 35 m (flight distance of exposed birds), and 11 to 15 m (flight distance of hidden birds). Associations with stonechats were formed at distances averaging 35–58 m. The relatively slight inter-species variation in these averages (excluding stonechats) demonstrates that the species share similar responses to intruders.

Variation between species in their flocking tendencies might correspond to differing degrees of benefit obtainable from the behaviour. Correlations were sought with differences between the flocking behaviour of species, for three factors that might influence its value: the average proportion of time spent hidden, flight distance for hidden birds, and flight distance for exposed birds. The results (Table 1) provide three statistically significant relationships, all showing a trend across species with flight distance of exposed birds. This measure was negatively correlated with the number of associations observed, and with the percentage of associations in which the stonechat concerned was silent. It was positively correlated with the average rate of warning calls by the stonechats that were joined (see Fig. 1). There were no relationships with either the average rate of stonechat distraction calls, or the average distance from the observer that flocks formed.

## Discussion

The association of other species with stonechats, noted elsewhere by Tallowin and Youngman (1978) and Harpum (1978), cannot be accounted for in terms of feeding advantages, or certain anti-predator effects such as confusing the predator (Neill and Cullen 1974) or seeking cover in a group (Hamilton 1971). The behaviour is, however, entirely consistent with the 'domain of safety' argument outlined above. All the attendant species had much shorter flight distances than the stonechats, which also gave warnings well in advance; indeed, only 2 or 257 measured flight distances overlapped the range of stonechat call distances (50–145 m). The stonechats, which were not seen to initiate associations, could not gain any such advantage, and thus the flocks apparently involve a one-sided benefit to the attendant birds. It is better to regard the associations as exploitation than cooperation, which is often assumed when discussing groups (Morse 1977; Bertram 1978).

Joining a silent stonechat would ensure that a bird would both receive an early warning of danger, and be in the safest place to assess it, i.e. near the source of the warning. Birds might then be expected to reduce their own vigilance, relying on the stonechat. Practical difficulties precluded an adequate test of this possibility, but a small sample of data for reed buntings and meadow pipits showed that birds near silent stonechats tended to remain hidden longer before rising to look around or fly off (mean = 5.8 min, $n=6$) than solitary birds (mean = 2.1 min, $n=11$) (Mann-Whitney $U=11$, $P<0.025$, one-tailed). This suggests that there may indeed have been a reduction in vigilance, though further data are clearly required.

The tendency for attendants to join silent male stonechats more often than females may be attributed in part to the fact that females were sometimes unavailable while incubating, but may also reflect males' greater vigilance. Males habitually perched higher than females, and usually responded first when territories were entered by a human (e.g. on 108 of 129 occasions).

Flocking was apparently most developed in those species that were most tolerant of an intruder's approach, i.e. with smallest flight distance. They formed associations most frequently, did so relatively most often with silent stonechats (reflecting their use of the stonechats as insurance against future danger), and joined stonechats giving the lowest average rates of warning calls, i.e. in situations of low as well as high risk (Fig. 1).

Several explanations can be offered for the importance of flight distance in predicting species' flocking behaviour. First, a small flight distance would provide a relatively large domain of safety. Second, birds with small flight distances would receive relatively early warnings. Third, the species with smallest flight dis-

tance are the least vigilant, and would be most vulnerable out of flocks. The three species that associated most often did indeed spend a high proportion of time hidden, where their detection ability would be impaired. However, exposed birds usually gave clear signs of having seen me well before flying; also, this argument predicts a stronger correlation for hidden flight distance than for exposed flight distance. Finally, birds might tolerate the close approach of intruders because of strong fidelity to an area (e.g. if dispersed in small all-purpose territories). It might then be advantageous to employ flocking as a means of improving detection of potential disturbance. This might be a lower priority for wide-ranging birds such as linnets and redpolls (see Newton 1972).

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