Evidence for a rule governing the avoidance of superfluous escape flights

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When an imminent attack by a predator on a group of birds is signalled to non-detectors only by the departure of the detector, non-detectors may make time-wasting false-alarm flights in response to mistaken or non-predator-driven departures. The frequency of false-alarm flights might be reduced if group members assess the reason for single departures before responding. Immediate flights should only occur after multiple simultaneous departures, because these are only likely to be generated by an attack. The response delay between the detectors' departure and the next birds that respond should then be dependent on the number of detectors. On sparrowhawk attack, response delays in redshanks decreased significantly as detector number increased, controlling for raptor conspicuousness and proximity, and flock size and spacing. If response delay is modified because of risk dilution, it should increase with flock size and, consequently, the rate of alarm flights due to mistakes should decrease. However, response delay did not increase and flight frequency due to misidentification of non-raptors or non-predator-driven departures did not decrease with flock size. Significantly more feeding time was lost by birds in small flocks, suggesting that the dilution effect decreased the cost of each false-alarm flight rather than their frequency.

Keywords: anti-predation behaviour; collective detection; vigilance

1. INTRODUCTION

In larger groups, the probability of detecting an approaching predator increases because the instantaneous probability that at least one animal will be scanning increases (Pulliam 1973; Roberts 1996). Therefore, individuals can decrease their vigilance with increasing group size without increasing their risk of predation. This group-size effect is common in animals (Elgar 1989) yet it relies on the detecting animal communicating the presence of the predator to the rest of the group (Pulliam *et al.* 1982; Lima 1994). When an alarm call is not given, only the departure of the detector from the group signals the approaching predator (Cresswell 1994*b*; Lima 1994, 1995). However, departures from the group may also be non-predator driven, for example animals may leave the group for foraging reasons (Roberts 1997), and the frequency of these non-alarm departures may increase with flock size (Caraco 1980). Departures may also arise because an individual has mistakenly flown in response to an approaching non-predator. Although responding to all departures minimizes predation risk, time and energy can be saved if group members only respond to predator-driven departures (Ydenberg & Dill 1986). The key problem is when can a departure safely be ignored?

This paper explores the problem of how a bird which has not detected an approaching predator (the responder) reacts to the observed departure of a neighbour (the detector), where this departure may or may not be a genuine-alarm flight. In the absence of overt alarm signals, a single detection may go unheeded by other flock members and multiple detections may be required to sound the alarm (Lima 1994). Lima (1994) proposed that the probability of instant departure should depend on the number of birds departing simultaneously from a flock. Although single birds may commonly leave a flock for non-predator reasons, multiple simultaneous departures are likely to be for a common reason, most probably the approach of a predator. Therefore, birds may use a rule of thumb to determine whether to fly in response to a conspecific's departure: if some number of birds leave simultaneously, then make an escape response immediately, but if only one (or a few) birds leave, then assess the reason for the departure(s) before taking any action. Our study tests Lima's (1994) hypothesis and some consequent predictions.

(i) The delay (response delay) between the first birds which leave in response to a predator (detectors) and the next birds which respond (responders) decreases as the number of detectors increases.

(ii) If the rule of thumb is modified because of dilution of risk (Hamilton 1971), then the response delay should increase with flock size.

(iii) If the response delay increases with flock size then the frequency of mistaken identity alarm flights (to non-raptors) will decrease in larger flocks because individuals will be able to take more time to identify the potential cause of the departure of the detector and so recognize mistaken alarms. However, the rate of non-predator-driven departures may actually increase with flock size countering any effects of increased response delays on the overall rate of false-alarm flights (Roberts 1997).

(iv) If the frequency of false-alarm flights decreases with flock size then the amount of lost feeding time due to alarms should also decrease.

We tested these hypotheses with a well-studied system of common redshanks (*Tringa totanus*) feeding under a

high risk of predation from Eurasian sparrowhawks (*Accipiter nisus*) (Cresswell & Whitfield 1994; Hilton *et al*. 1999). The redshanks in the study system do not use alarm calls to signal departure (Cresswell 1994*b*). We measured (i) the response delay of redshanks in relation to the number of detectors during sparrowhawk attacks, and (ii) the frequencies of alarm flights due to mistakes (non-raptorial birds) and non-predator-driven alarm flights (those with no apparent cause) when not under attack. The data collected were observational and, therefore, variation in sparrowhawk conspicuousness between attacks could confound our results. Specifically, a decrease in the response delay as the number of detectors increased may simply reflect higher numbers of birds independently detecting more conspicuous sparrowhawks. However, if most birds react directly to the sparrowhawk rather than conspecifics we would predict that the response times would be independent of nearest-neighbour distance. In contrast, a prior analysis of the data presented in this paper has shown a positive relationship between nearest-neighbour distance and the average response time (Hilton *et al*. 1999). Lima's (1994) hypothesis can then also be used to determine further whether raptor conspicuousness is confounding any relationship between the number of detectors and response delay. According to Lima's (1994) rule of thumb, when there is one detector, conspecifics may scan for the source of the detector's departure before responding and, thus, if they fly, they actually respond directly to having detected the raptor themselves. Therefore, we would not predict a strong positive relationship between nearest-neighbour distance and response time when there is only one detector. In contrast, when there is more than one detector, the rest of the flock may respond directly to conspecifics' departures and, therefore, we predict a strong positive relationship between nearest-neighbour distance and response time in this case. As a final test of whether variation in sparrowhawk conspicuousness was confounding any relationship between the number of detectors and response delay, we tested whether there was any difference in the time taken for the rest of the flock to respond dependent on the number of detectors. If response delay is simply a consequence of increased conspicuousness (and more detectors throughout the flock respond) we would predict a faster average rate of response to attacks when there were more initial detectors.

2. MATERIAL AND METHODS

Data were collected from flocks of redshanks wintering at the Tyninghame estuary, Scotland (56°00′ N, 2°35′ W) during the first nine weeks of 1998 (period 1) and from October to February inclusive in 1989–1990 and 1990–1991 (period 2). Full site details are given in Whitfield (1985). Between 200 and 400 redshanks were observed foraging on a small saltmarsh where they were under a high risk of mortality from avian predators (Cresswell & Whitfield 1994).

During period 1 redshank flocks were videotaped feeding on a 17 ha area of saltmarsh from a distance of 30–300 m by a single observer (G.H.) using a Sony Hi-8 video camera with a frame resolution of 0.02 s. The area used in period 1 encompassed the area of observation in period 2. Sparrowhawks attacked the redshank flocks by flying out of the woods or

bushes surrounding the saltmarsh directly towards the redshanks (see Cresswell 1996). The camera was set to record continuously and an attack and response sample was collected opportunistically each time a sparrowhawk attacked the flock that was being videotaped. The direction of attack of the sparrowhawk was recorded at the time by the observer. Attacks probably came from two to three individual female sparrowhawks and the redshanks attacked on the saltmarsh were probably the same individuals (see Cresswell & Whitfield 1994). Flocks varied in size from seven to 61 birds and were defined according to Cresswell (1994*a*).

Thirty-eight attacks were successfully videotaped. For each attack, the redshank which flew first was identified and the video frame when that bird flew was defined as frame 0. Every other flock member was then scored for the frame number when it first took flight relative to the frame when the first bird of the flock took off: we call this time-period the response delay. We label all birds taking off in the first two frames as detectors and all others as responders. The distance of the bird's nearest neighbour (in body lengths) was recorded. The position of the bird within the flock was also recorded with respect to the direction of the approaching sparrowhawk. The flock was split into quarter areas so that approximately one-quarter of the birds were scored as being closest to the approaching sparrowhawk and one-quarter were scored as being furthest from the raptor (see Hilton *et al*. 1999).

During period 2, a single observer (W.C.) made 215 h of observations from a single point overlooking an area of saltmarsh of *ca*. 0.4 ha at a distance of between 20 and 40 m. A single, variable-sized flock of redshanks fed occasionally throughout two winters in this area and was watched opportunistically. On alarm, a flock (12–88 birds) would fly to a creek adjacent to the saltmarsh and then would run back into the feeding area after a few seconds. Alarm flights were of three types. Alarm flights in response to an aerial predator were flights during which a raptor was visible. Mistaken identity flights were flights in which a raptor was not visible but the response was associated with the approach of a non-raptorial species. Non-predator-driven flights were flights which occurred with no apparent cause. These classifications were probably accurate because the redshanks were watched from a 2 m high point immediately adjacent to the feeding area. From this point any raptor or other relevant species crossing the open saltmarsh within *ca*. 200 m of the flock was readily visible. After each alarm flight the time taken for more than 50% of the flock to resume feeding in the same area was recorded.

In period 2, there were 170 alarm flights from a predator (90 of these were attacks), 115 mistaken identity alarm flights and 572 non-predator-driven alarm flights. Hence, over 75% of the 913 alarm flights (some alarms consisted of more than one flight) were false-alarm flights. One hundred and thirty-eight hours of observations were used to assess the rates of false-alarm flights for different flock sizes containing 341 non-predator-driven alarm flights and 42 mistaken identity alarm flights. A sample was collected for any period of greater than 15 min where there was a constant flock size (within a class of ten birds, e.g. 11–20) without containing any raptor attacks. In total 115 samples were collected on 66 different days and the mean sample duration ($\pm$ s.e.) was 1.2 ± 0.1 h. The median rate of all false-alarm flights was $2.0\,\mathrm{h}^{-1}$ (range = 1.6–2.7 h), with $n = 115$ flock watches.

The data were analysed using SPSS (Norusis 1990). All analyses of false-alarm rates included $n = 115$ flock watches. All
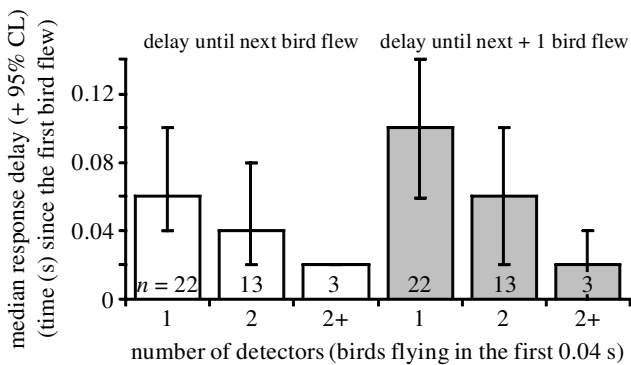
Figure 1. The median time in seconds ($+95\%$ confidence limits) between the flight of the first bird(s) (detectors) of the flock to fly and the next bird or birds (responders) and the next plus one responder(s) with respect to the number of detectors during an attack on redshanks by a sparrowhawk. The numbers in the bars indicate the sample sizes of attacks. As the number of detectors increased so the response delay until the next birds which flew decreased. There was significant variation in the response delay with the number of detectors (Kruskal–Wallis one-way ANOVA: delay until the next bird flew, $\chi_2^2 = 7.4$ and $p = 0.025$, and delay until the next plus one bird flew, $\chi_2^2 = 11.8$ and $p = 0.003$).

analyses of flocks attacked included $n = 38$ attacks, except in three cases (stated below) because of incomplete data. All probabilities are two-tailed. Medians are given with 95% confidence limits.

3. RESULTS

(a) *Hypothesis 1: does the response delay depend on the number of detectors?*

The response delay on attack decreased significantly as the number of detectors increased ($r_s = -0.42$, $n = 38$ and $p = 0.009$) (figure 1). The time between the first bird and the next plus one bird which flew also decreased significantly as the number of detectors increased ($r_s = -0.55$, $n = 38$ and $p < 0.001$) (figure 1).

The result that the response delay was dependent on the number of detectors was robust when controlling statistically for variation in flock size, spacing and the position of detectors. The number of detectors was independent of flock size (Kruskal–Wallis one-way ANOVA, $\chi_2^2 = 2.4$, $p = 0.30$ and $n = 38$ attacks, with classes as in figure 1). When we controlled for flock size, there was still a significant decrease in the response delay until the flight of the next bird (Kendall's partial correlation coefficient $= -0.32$, $n = 38$ and $p = 0.05$) and the next plus one bird (Kendall's partial correlation coefficient $= -0.47$, $n = 38$ and $p = 0.004$) dependent on the number of detectors. The number of detectors was independent of their mean nearest-neighbour distance within the flock (Kruskal–Wallis one-way ANOVA, $\chi_2^2 = 1.3$, $p = 0.51$ and $n = 34$ because spacing data could not be accurately determined for four attacks, with classes as in figure 1). When we controlled for mean nearest-neighbour distance, the decrease in the response delay until the flight of the next bird (Kendall's partial correlation coefficient $= -0.36$, $n = 34$ and $p = 0.04$) and the next plus one bird (Kendall's partial correlation coefficient $= -0.49$, $n = 34$ and $p = 0.004$) dependent on the number of detectors was still significant. The number
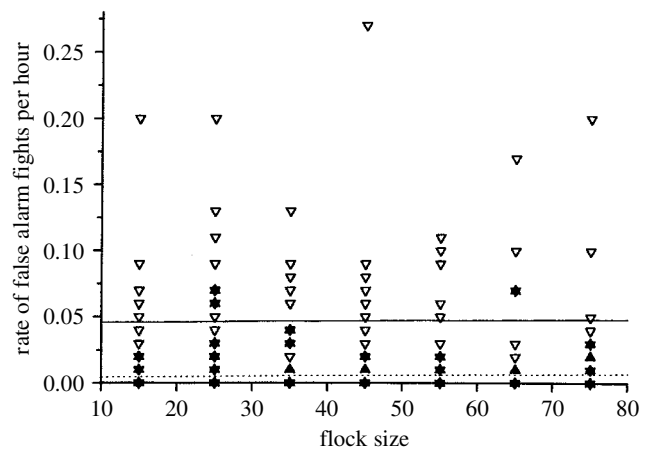

Figure 2. The rate of false-alarm flights per hour for $n = 115$ flock watches of redshanks in different flock size classes during periods without raptor attacks on the flock ($n = 138$ h). Filled triangles represent mistaken identity alarm flights (e.g. flights in response to non-raptor species): there was no relationship between flock size and the rate of mistaken identity alarm flights (the dotted line is the regression line). Open triangles are for non-predator-driven alarm flights (e.g. alarm flights with no apparent cause): there was no relationship between flock size and the rate of non-predator-driven flights (the solid line is the regression line).

of detectors was independent of their initial position with respect to the approaching raptor (Kruskal–Wallis one-way ANOVA, $\chi_2^2 = 1.9$, $p = 0.50$ and $n = 37$, because positional data could not be accurately determined for one attack, with classes as in figure 1). When we controlled for the proportion of birds which were in the quarter of the flock closest to the approaching raptor, the decrease in the response delay until the flight of the next bird (Kendall's partial correlation coefficient $= -0.32$, $n = 37$ and $p = 0.05$) and the next plus one bird (Kendall's partial correlation coefficient $= -0.46$, $n = 37$ and $p = 0.005$) dependent on the number of detectors was still significant.

(b) *Hypothesis 2: does the response delay increase with flock size?*

When controlling for the number of detectors, the response delay until the next bird flew (Kendall's partial correlation coefficient $= -0.27$, $n = 38$ and $p = 0.11$) and the next plus one bird flew (Kendall's partial correlation coefficient $= -0.11$, $n = 38$ and $p = 0.57$) was not dependent on flock size.

(c) *Hypothesis 3: does the frequency of mistaken identity or non-predator-driven alarm flights decrease with flock size?*

The frequency of mistaken identity alarm flights to non-raptors was independent of flock size ($r_s = 0.12$, $n = 115$ flock watches and $p = 0.21$), as was the frequency of non-predator-driven false-alarm flights ($r_s = -0.01$, $n = 115$ flock watches and $p = 0.91$) (figure 2).

(d) *Hypothesis 4: does the amount of feeding time lost decrease with flock size?*

The median amount of time during a continuous flock watch when a flock had left the feeding area (and was not feeding elsewhere) because of a false-alarm flight was 5%

Table 1. *The slope of a linear regression function fitted to the cumulative proportion of birds which flew during a 0.36 s period after any initial response delay (taken as median values from figure 1)*

(A period of 0.36 s was arbitrarily taken as representing 50% of the maximum 0.72 s for all birds in the study to take flight after the initial detection response. The sample sizes and classes are as in figure 1.)

number of detectors	regression gradient	standard error	r^2
one	0.052	0.002	0.97
two	0.053	0.003	0.94
more than two	0.052	0.005	0.85

(range, 0–9% and $n = 115$ flock watches). However, the proportion of time that was lost as a result of all false-alarm flights was dependent on flock size. Flock sizes of less than 20 lost proportionately more time (14%, range, 0–33% and $n = 23$ watches of flocks of 11–20 birds) than flocks of more than 70 (0%, range, 0–3% and $n = 11$ watches of flocks of > 70 birds) (Spearman's rank correlation of flock size and proportion of time not feeding $r_s = -0.24$, $n = 115$ flock watches and $p = 0.01$).

(e) *Is variation in the response delay simply a consequence of variation in sparrowhawk conspicuousness?*

If any observed response delay was simply a consequence of increased raptor conspicuousness then it is unlikely that there would be any interaction between the effects of nearest-neighbour distance and the number of detectors. The relationship between the mean response time (excluding detectors) and mean nearest-neighbour distance, controlling for flock size, when there was only one detector was relatively weak (Kendall's partial correlation coefficient = 0.02, $n = 19$ and $p = 0.93$) compared to the strong positive relationship when there were at least two detectors (Kendall's partial correlation coefficient = 0.62, $n = 15$ and $p = 0.019$; total $n = 34$ because the spacing data could not be accurately determined for four attacks). The observed relationship between nearest-neighbour distance and the response time may have been confounded because denser flocks had more vigilant individuals (and, therefore, faster overall response times). However, the relationship between nearest-neighbour distance and the number of vigilant individuals in a flock just before attack (controlling for flock size) acted in the opposite direction (Kendall's partial correlation coefficient = 0.74, $p = 0.003$ and $n = 15$ because the spacing data and vigilance data could only both be determined for a limited number of flocks). In addition, if any observed response delay was a consequence of increased raptor conspicuousness then we would expect an interaction between the speed of response of the whole flock and the number of detectors. The time taken for the whole flock to fly did not show significant variation with the number of birds flying in the first 0.04 s (Kruskal–Wallis one-way ANOVA, $\chi^2_2 = 2.8$, $p = 0.25$ and $n = 38$ attacks, with classes as in figure 2). After any response delay, redshanks should respond irrespective of the

number of detectors if they are responding mainly to flights of conspecifics. Therefore, the rate of increase in the proportion of birds flying (after any delay caused by the number of detectors) should be similar regardless of the number of detectors. If redshanks were responding to a more conspicuous sparrowhawk (where the number of initial detectors is an index of its conspicuousness) then the rate of increase in the proportion of birds flying should be greater when there are more initial detectors, as later flying birds will include both responders and new detectors. However, for our data, the rates of increase in the proportion of birds flying after any response delay were similar (table 1). Hence, we concluded that variation in sparrowhawk conspicuousness does not have an important bearing on our results.

4. DISCUSSION

The results of this study provide strong support for Lima's (1994) hypothesis of a simple rule of thumb where an individual in a flock only makes an immediate escape response if a certain number of neighbours leave simultaneously. When only one bird leaves, then other flock members delay flight, possibly to assess the reason for the single departure before taking any action. Several other factors also affected escape flight response times, such as whether a bird was scanning, proximity to the attacking raptor, spacing within a flock and flock size (Hilton et al. 1999) but these probably did not determine the relationship between the number of detectors and response delay. For example, multiple simultaneous departures are likely to be easier to detect by responders. Therefore, slower response times to single departures might simply reflect a detection failure. However, failure to notice a departure probably also depends on nearest-neighbour distance (Hilton et al. 1999) but the number of simultaneous detectors was not dependent on their spacing and the relationship between the number of detectors and the response delay was independent of the spacing of the responders. Similarly, the response delay was probably not simply because of variation in the conspicuousness of the raptor. All of the available evidence points to redshanks responding to conspecifics rather than directly to sparrowhawks. In addition, there was no evidence of a faster rate of response in flocks because of variation in the number of initial and later detectors (which we may have misclassified as responders). However, it is impossible to rule out completely the possibility that the relationship between the response delay and the number of detectors was not confounded by our misclassifying detectors as responders, but we found no evidence that such an effect was important.

Our second prediction, which was also based on Lima (1994; and see also Roberts 1997), was that the response delay should increase with flock size because of dilution of risk (Hamilton 1971): we found no evidence to support this prediction. The response delay may have been independent of flock size for several reasons. First, the overall flock response happened rapidly and so any changes in the response delay may have been too small to measure using our methods. Second, because the overall response is slower in larger flocks (Hilton et al. 1999) there may be less time available for a delay in larger

flocks. Third, if late-flying birds are preferentially targeted (see Bednekoff & Lima 1998) then the dilution effect is irrelevant because the assumption of equal risk for all birds does not apply. Finally, the response delay may have been apparently independent of flock size because of unmeasured delays where detectors may have delayed flight after detection. There are clear advantages in redshanks for a detector delaying flight because the best escape response on attack by a peregrine (*Falco peregrinus*) is not to fly, so correct identification of the approaching raptor is important (Cresswell 1993). However, if detector delay does increase with flock size, then we would predict that the frequency of mistaken identity alarm flights would decrease with flock size, but this was not observed.

Also relevant to a discussion of why the response delay was independent of flock size was the result that the frequency of non-predator-driven alarm flights was also independent of flock size. This is counter to other studies where the probability of simultaneous departures may have increased with flock size (Caraco 1980; Roberts 1997). If, for example, the probability of any individual leaving a flock is constant then the probability that two or more will leave simultaneously will increase with flock size. In redshanks at least, it seems that this effect is minor and, therefore, there may be less need for any reduction in sensitivity to alarm flights as a consequence of increasing flock size (see Roberts 1997).

In the absence of an effect of flock size on the response delay, we modify our third prediction and do not necessarily expect the frequency of mistaken identity alarm flights to decrease with flock size and no such relationship was observed. However, we did find that larger flocks returned to feeding much sooner than smaller flocks, suggesting that the dilution effect ameliorated the costs of each false-alarm flight rather than decreasing their frequency. Overall it is probably a safer strategy for redshanks to fly when in doubt even in a large flock, particularly if late-flying birds are targeted and the dilution effect does not apply (Bednekoff & Lima 1998). After the attack the dilution effect will apply to all birds and so flock size effects on the predation risk/foraging opportunity trade-off might then occur.

Redshanks appear to use a simple rule of thumb which may result in a decrease in the rate of false-alarm flights: only fly immediately after simultaneous departures. Without measurements from individuals which do not use this rule, it is impossible to determine whether it results in a decrease in the rate of false-alarm flights. However, the result that the frequency of mistaken identity alarm flights did not increase with flock size, despite the greater amount of scanning and potential for mistakes in larger flocks, suggests that a response delay rule may reduce the false-alarm flight frequency. Even with this rule, frequent false-alarm flights might still be expected. Although simultaneous non-predator-driven departures may be uncommon, simultaneous mistaken identity alarm flights probably occur often.

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