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The function of distress calls given by tufted titmice (*Parus bicolor*): an experimental approach

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Abstract. I studied the response of tufted titmice (*Parus bicolor*) to distress-call playbacks to discern the function of distress calls given in a non-breeding context. At baited locations, titmice were presented with three different stimuli: (1) a hawk model, (2) a distress-call playback, and (3) a hawk model in association with a distress-call playback. The reactions of titmice to these stimuli were measured in terms of the number of titmice attracted to the stimuli, time spent by titmice in the area around the stimuli, and the number of visits made by titmice to the area around the stimuli. Titmice approached closer to and spent more time near the source of the distress call when the call was not associated with a hawk model than when a hawk model was present. In either case, the approach of titmice was slow and cautious. Exposure to a hawk model in the absence of a distress-call playback caused titmice either to mob the model or ignore it. Titmice recognized the hawk model more often when it was associated with a distress-call playback than when it was presented alone. These observations are in accordance with predictions of the hypothesis that distress calls warn other birds of danger. Conversely, many observations contradicted the hypothesis that distress calls are calls for help.

When a predator seizes a victim, a period of time often elapses between capture and death. During this interval, avian prey display a range of behaviours presumably aimed at either increasing their own chances of escape or enhancing the fitness of their kin. One fairly common avian behaviour in such circumstances is distress calling. Distress calls are loud, harsh vocalizations of long duration that cover a wide range of frequencies, making them easy to locate (Stefanski & Falls 1972b; Högstedt 1983). Although distress calling is a widespread behaviour, considerable interspecific variation occurs in the proportion of individuals that emit distress calls when handled by a human. In some species all individuals give distress calls, while in other species only some or no individuals do so. The calling frequency of a species is relatively constant from location to location and from year to year (Perrone 1980; Högstedt 1983) and is usually independent of handling effects (Inglis et al. 1982; but see Balph 1977).

Four hypotheses have been proposed to explain why birds give distress calls: (1) the call startles the predator into releasing the caller (Driver & Humphries 1969); (2) it attracts other predators that squabble with the original predator, increasing the caller's escape opportunities (Curio 1976); (3) it warns kin of the nature and location of danger, increasing the inclusive fitness of the caller by increasing the individual fitness of its kin (Rohwer et al. 1976); (4) it is a call for help directed at kin or reciprocating non-kin (Rohwer et al. 1976). My study quantifies the response of birds to distress calls and thus focuses on hypotheses (3) and (4), which I will hereafter refer to as the warning hypothesis and the call-for-help hypothesis, respectively.

According to the warning hypothesis, birds responding to a distress call are expected to approach the source of the call cautiously and no closer than would be necessary to gain information about the predator. For a distress call to function as a warning to kin, birds related to the caller would have to be in the vicinity when the call is given. Birds that live in close proximity to kin would thus be expected to call more frequently than birds that are solitary or live in unrelated groups. Thus, the correlation between sedentariness and calling frequency noted by Inglis et al. (1982), Perrone (1980) and Rohwer et al. (1976), and the correlation between flocking propensity and calling frequency noted by Greig-Smith (1982) both support the warning hypothesis.

Unlike the warning hypothesis, the call-for-help hypothesis proposes that conspecifics respond to

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distress calls for the sake of the caller, not for any direct personal gain. Responding birds incur some risk by attempting to save the caller. Predictions of this explanation are that responding birds will rapidly approach a predator associated with a distress call and will attack or distract it. Also, assuming no reciprocity, only related conspecifics will be attracted to a distress call. Like the warning hypothesis, the call-for-help hypothesis predicts a positive correlation between stability of kin groups and calling frequency and is supported by the correlations between sedentariness and calling frequency, and flocking propensity and calling frequency stated above.

In further support of the call-for-help hypothesis, Stefanski & Falls (1972a) presented evidence that dependent, juvenile white-throated sparrows (*Zonotrichia albicollis*) direct distress calls at their parents as calls for help. Recorded distress calls played near a tethered predator at intervals during the breeding season when young birds were vulnerable to predation elicited a strong response by parent birds. The parents both attacked the predator and performed distraction displays around it. Furthermore, white-throated sparrows responded only to the call of a conspecific or a heterospecific that gave a call very similar to their own (Stefanski & Falls 1972b).

Most of the published work investigating the function of distress calls emitted by non-breeding birds has concentrated on correlating species' calling frequencies with variables such as sedentariness and flocking propensity. Only Perrone (1980) has previously attempted to quantify the reaction of birds to distress calls during the winter. The purpose of this study was to address the warning and call-for-help hypotheses by subjecting birds to a series of distress-call playbacks performed under various experimental conditions. I studied tufted titmice (*Parus bicolor*) because they are locally abundant, can be attracted to a location by bait and invariably give distress calls when handled (Norris & Stamm 1965; Rohwer et al. 1976). Additionally, yearling titmice often remain with their parents throughout their first winter, making it likely that some birds in each flock are related (Van Tyne 1948; Laskey 1957; Brackbill 1970; Tarbell 1983).

METHODS

The study was conducted between 15 January and 20 February 1983 in a rural wooded region of eastern Monroe County in southern Indiana. A titmouse distress call was recorded from a hand-held titmouse using a portable Panasonic RQ-309AS cassette recorder. A continuous 5-min distress-call recording was obtained in this manner. Playbacks were conducted using a remote Nagra speaker with the volume set at approximately the natural volume for a titmouse distress call.

In order to concentrate titmouse activity in a relatively small area, piles of whole sunflower seeds and cracked corn were put on the ground at numerous locations along low-usage roads. A standardized procedure was employed for performing all trials. I approached a baited location by car and parked where the bait-pile and surrounding area were clearly visible. I then set up an experimental trial by placing at the centre of the bait-pile either: (1) a 1-m perch supporting a covered hawk model, (2) an empty 1-m perch with a speaker at its base, or (3) a 1-m perch supporting a covered hawk model with a speaker at its base. With one such set-up in place I returned to the car, which I used as a blind, and allowed the birds to resume normal activity. This typically required only about 60 s.

When the birds were once again feeding, I recorded 5 min of undisturbed activity data. Immediately following such a control trial, I began an experimental trial by uncovering the hawk model by means of a string running to the car, starting the playback, or both, depending on which of the three trials was being conducted. (The six trial types will hereafter be referred to as hawk control, playback control, hawk/playback control, hawk experimental, playback experimental, hawk/playback experimental.) Regardless of the trial type, the transition from a control trial to an experimental trial did not entail leaving the car a second time. With the experimental trial started, 5 min of activity data were again taken on the birds.

All three experimental treatments were performed at each location, but I allowed at least 48 h between the presentation of any two stimuli. I also rotated the order in which the three stimulus types were presented at the trial sites so that no sequence received preference.

The hawk model used in these trials was a stuffed merlin (*Falco columbarius*) mounted in an upright, life-like position. Merlins are small-bird specialists that have been reported to take such woodland birds as nuthatches, warblers, and vireos (Bent 1938). They occur in Monroe County in the winter

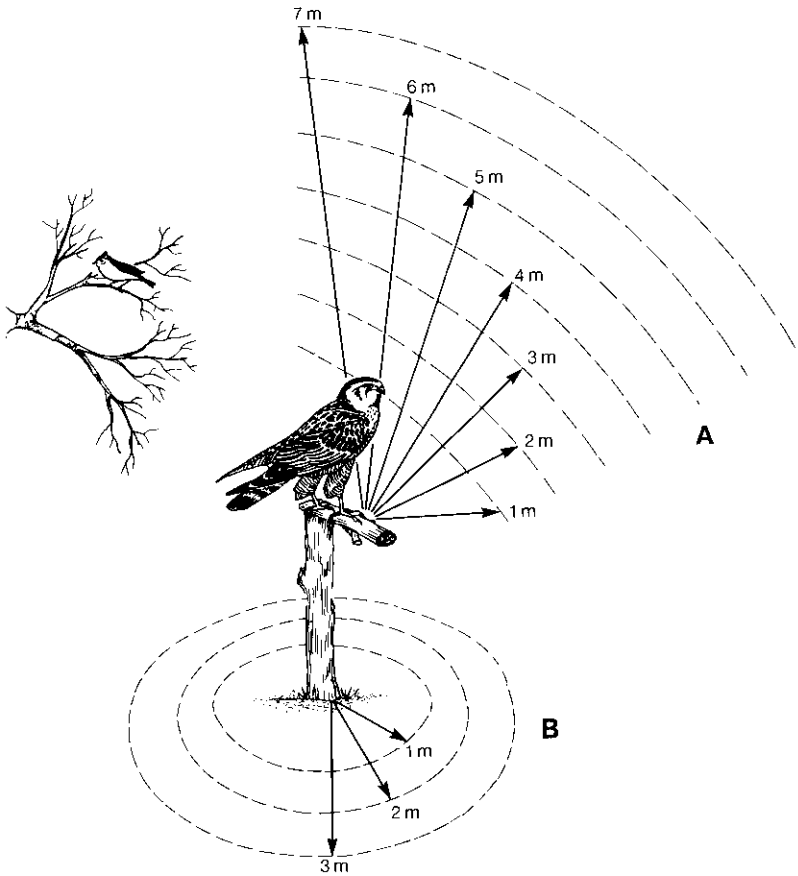

Figure 1. The experimental set-up used to record the reactions of titmice to stimuli presented in this study. A: 1-m intervals in three-dimensional space centred at the stimulus. B: 1-m intervals on the ground centred directly below the stimulus.

(personal observation) and are presumed to be natural predators of tufted titmice.

To quantify the pattern of movement of the birds during the 5-min observation periods, the area around the bait-pile was imagined to be divided into 1-m intervals falling into two groups. The first set of intervals consisted of planar concentric circles with radii of 1, 2, and 3 m centred at the point on the ground directly below the crossbar of the perch (Fig. 1). Birds were placed in one of these inverval categories only when they were standing on the ground. The second interval set, which used the crossbar of the perch as its centre-point, consisted of concentric spheres with radii from 1 to 7 m (Fig. 1). Birds were placed in this set only when they were perched off the ground. All 10 distance intervals were thus mutually exclusive. While conducting trials, I estimated interval boundaries by using pre-established reference points within the study area. Although the density of perches across the seven distance intervals was not always uniform for any one trial site, there was no trend across sites for certain intervals to have more or fewer perches and, for all trial sites, each distance interval had several places for birds to perch.

During both control and experimental trials, I recorded data by noting (1) the total number of titmice present during the trial period, (2) the number of seconds spent by titmice in each of the 10 distance intervals during the 5-min trial period (hereafter referred to as titmouse seconds), and (3) the number of times titmice entered each of the 10 distance intervals during the 5-min trial period (hereafter referred to as titmouse visits). It should be re-emphasized that titmouse-seconds data consisted of the cumulative time spent by all titmice in

each of the 10 distance intervals. One titmouse spending 30 s 1 m from the crossbar of the perch yielded the same titmouse-seconds datum as three titmice each spending 10 s 1 m from the perch crossbar. Titmouse-visits data similarly recorded the cumulative visits by all titmice to each distance interval. For purposes of analysis, data were standardized within treatments by dividing titmouse seconds by the number of titmice present to yield titmouse seconds per bird. Likewise, titmouse-visits data were standardized to yield titmouse visits per bird.

RESULTS

When undisturbed, titmice concentrated their activity on the ground at the bait-pile and 2–3 m from the perch crossbar off the ground (Figs 2, 3). Exposing titmice to a hawk model initially caused them to flush to the treetops outside the observation sphere. One of two responses followed. They either ignored the model and resumed feeding or they mobbed it from beyond 3 m. The former response occurred during five out of 14 trials, the latter in the other nine trials.

At the start of a distress-call playback, titmice in the area flushed up into the surrounding trees, even when dense cover was readily available near the ground. If the distress call was associated with a hawk model, the birds remained completely outside the 7-m observation sphere or briefly approached the perimeter of it. Few titmouse seconds were recorded closer than 5 m from the crossbar of the perch during hawk/playback experimental trials (Figs 2F, 3F).

When a tufted titmouse distress call was played in the absence of the model, the titmice in the vicinity slowly moved back into the study area after flushing to the surrounding trees. The birds generally approached to within 2–4 m of the speaker, where they remained for the duration of the playback. Rarely did a titmouse perch on the ground during a playback (Figs 2D, 3D).

Unlike the bimodal reaction of titmice in the hawk experimental trials, the reaction of titmice to both the playback presented alone and the playback in association with the hawk model appeared to be consistent between trials. This can be demonstrated by comparing the playback and hawk/playback experimental treatments on a trial-by-trial basis. At 13 of 14 locations the total number of titmouse seconds, summed over all distance intervals, was greater in the playback experimental trial than in the hawk/playback experimental trial ($\chi^2 = 10{\cdot}28$, $df = 1$, $P < 0{\cdot}001$). Moreover, at 12 of 14 trial sites, titmice approached closer to the speaker in the playback experimental trial ($\chi^2 = 7{\cdot}14$, $df = 1$, $P < 0{\cdot}01$), and at 13 of 14 sites titmice paid more visits (pooled over all distance intervals) to the

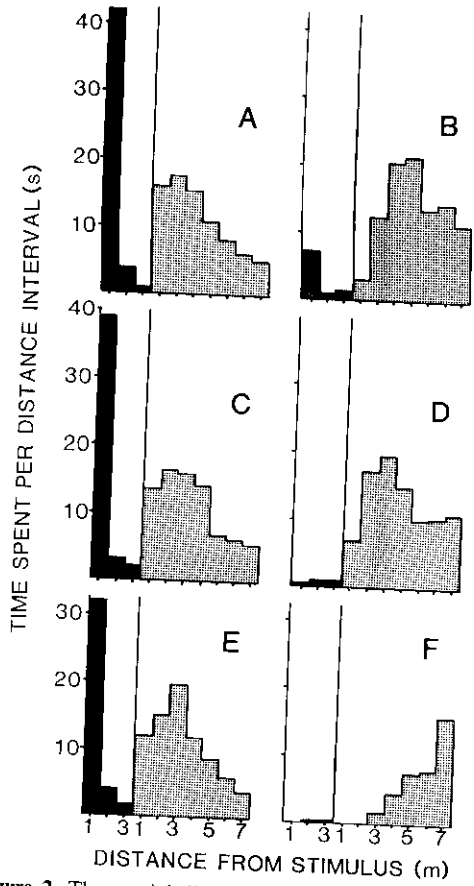

Figure 2. The spatial distribution of seconds spent by tufted titmice in a study area before and during the presentation of three different stimuli. Data are the average time spent per bird per distance interval for all 14 trials. A: undisturbed before presentation of a hawk model; B: hawk model presented; C: undisturbed before presentation of a distress-call playback; D: distress call played; E: undisturbed before simultaneous presentation of a hawk model and a distress-call playback; and F: simultaneous presentation of a hawk model and a distress-call playback. The black region represents the distance intervals on the ground, centred at a point directly below the stimulus. The stippled region represents the distance intervals off the ground in three-dimensional space, centred at the stimulus.

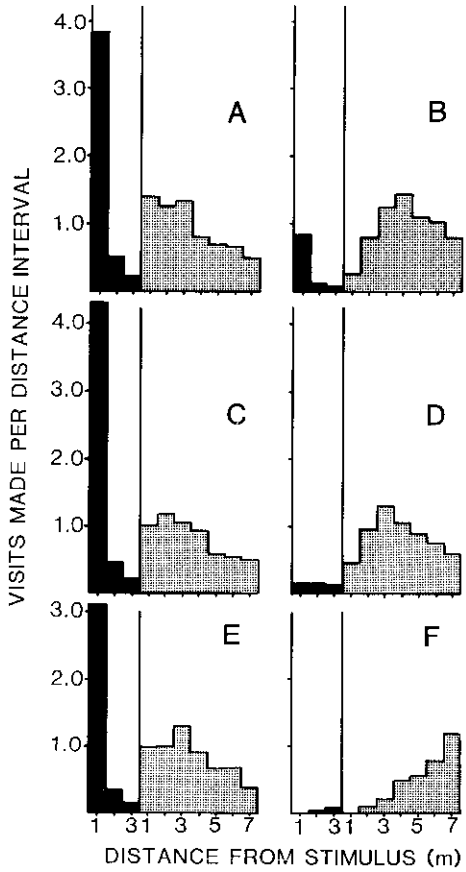

Figure 3. The spatial distribution of visits made by tufted titmice to a study area before and during the presentation of three different stimuli. Data are the average number of visits per bird per distance interval for all 14 trials. A: undisturbed before presentation of a hawk model; B: hawk model presented; C: undisturbed before presentation of a distress-call playback; D: distress call played; E: undisturbed before simultaneous presentation of a hawk model and a distress-call playback; and F: simultaneous presentation of a hawk model and a distress-call playback. The black region represents the distance intervals on the ground, centred at a point below the stimulus. The stippled region represents the distance intervals off the ground in three-dimensional space centred at the stimulus.

study area during the playback experimental trial than during the hawk/playback experimental trial ($\chi^2 = 10{\cdot}28$, $df = 1$, $P < 0{\cdot}01$). The one behavioural anomaly occurred at the sixth trial site, where no titmice were recorded in the 7-m observation sphere during the 5-min playback experimental trial.

Statistical Analysis

In the following analysis I used a two-tailed sign test for paired comparisons, a Friedman's test for homogeneity for multiple comparisons, and a Kolmogorov–Smirnov two-sample comparison for comparisons of distributions. For the latter comparisons, critical values were calculated using a Bonferoni correction for number of comparisons made (Siegel 1956). To justify pooling data across the 14 different sites used in this study, I tested for a site effect by comparing the number of titmouse seconds per bird, summed over all intervals, recorded during the three control treatments using sites as treatments and controls as blocks. I found no differences in the 14 sites ($N = 14$, $T = 1{\cdot}22$, $P > 0{\cdot}30$).

To establish that the baseline activity of titmice was consistent, I made comparisons among the three control treatments. I found no differences in the number of titmice present ($N = 14$, $T = 0{\cdot}45$, $P > 0{\cdot}30$, Table I), in the number of titmouse seconds per bird, summed over all intervals ($N = 14$, $T = 0{\cdot}27$, $P > 0{\cdot}30$), or in the number of titmouse visits per bird, summed over all intervals ($N = 14$, $T = 0{\cdot}07$, $P > 0{\cdot}30$). The three control treatments also did not differ in their distribution of

Table I. Number of tufted titmice present at study sites during various control and experimental procedures

	Treatment*					
Site	HC	PC	HPC	H	P	HP
1	5	8	6	6	2	0
2	6	9	9	6	10	3
3	1	3	4	6	5	2
4	4	6	5	4	2	2
5	2	5	6	2	3	2
6	5	4	7	4	0	1
7	8	10	7	9	4	3
8	5	4	4	4	5	0
9	8	3	3	7	5	5
10	4	5	6	7	3	1
11	5	6	6	4	3	0
12	7	7	6	3	9	4
13	8	7	6	6	10	2
14	4	3	5	3	4	2
Total	72	80	80	71	65	27

* HC: hawk control; PC: playback control; HPC: hawk/playback control; H: hawk experimental; P: playback experimental; HP: hawk/playback experimental.

titmouse seconds per bird across the three on-the-ground intervals and the seven off-the-ground intervals ($P > 0{\cdot}05$ for all comparisons, Table II).

Comparisons among the three experimental treatments and between these and the corresponding control treatments also reinforce the patterns that can be seen in Figs 2 and 3. Significantly fewer titmouse seconds per bird (summed over all intervals) were recorded during the playback experimental and hawk/playback experimental treatments than during the corresponding control treatments ($N = 14$, $P = 0{\cdot}012$ and $P < 0{\cdot}001$, respectively). The hawk experimental treatment did not differ from its respective control treatment ($N = 14$, $P = 0{\cdot}42$). All experimental treatments showed fewer titmouse visits per bird than their corresponding controls ($N = 14$, $P < 0{\cdot}012$ for all comparisons). Similar comparisons between experimental treatments showed significantly fewer titmouse seconds per bird during hawk/playback experimental treatments than either hawk or playback experimental treatments ($N = 14$, $P < 0{\cdot}05$). There was no significant difference in titmouse seconds per bird between hawk experimental and playback experimental treatments ($N = 14$, $P > 0{\cdot}05$). All three experimental treatments dif-

Table II. Maximum deviation values from a Kolmogorov–Smirnov two-sample comparison of the spatial distribution of seconds spent by tufted titmice in 1-m intervals either off the ground 1–7 m from a stimulus, or on the ground 1–3 m from a point directly below the stimulus

	Maximum deviation values											
	Ground intervals†						Off-ground intervals†					
	HC	PC	HPC	H	P	HP	HC	PC	HPC	H	P	HP
HC	—	0·020	0·024	0·109	—	—	—	0·053	0·068	0·265*	—	—
PC	—	—	0·011	—	0·651*	—	—	—	0·039	—	0·105	—
HPC	—	—	—	—	—	0·865*	—	—	—	—	—	0·599*
H	—	—	—	—	0·556*	0·781*	—	—	—	—	0·113	0·429*
P	—	—	—	—	—	0·225	—	—	—	—	—	0·485*
HP	—	—	—	—	—	—	—	—	—	—	—	—

* $P < 0{\cdot}05$.

† HC: hawk control; PC: playback control; HPC: hawk/playback control; H: hawk experimental; P: playback experimental; HP: hawk/playback experimental.

Table III. Maximum deviation values from a Kolmogorov–Smirnov two-sample comparison of the spatial distribution of visits made by tufted titmice to 1-m intervals off the ground 1–7 m from a stimulus, or on the ground 1–3 m from a point directly below the stimulus

	Maximum deviation values											
	Ground intervals†						Off-ground intervals†					
	HC	PC	HPC	H	P	HP	HC	PC	HPC	H	P	HP
HC	—	0·026	0·021	0·028	—	—	—	0·053	0·068	0·261*	—	—
PC	—	—	0·005	—	0·518*	—	—	—	0·040	—	0·138	—
HPC	—	—	—	—	—	0·861*	—	—	—	—	—	0·449*
H	—	—	—	—	0·469*	0·817*	—	—	—	—	0·112	0·327
P	—	—	—	—	—	0·348	—	—	—	—	—	0·381*
HP	—	—	—	—	—	—	—	—	—	—	—	—

* $P < 0{\cdot}05$.

† HC: hawk control; PC: playback control; HPC: hawk/playback control; H: hawk experimental; P: playback experimental; HP: hawk/playback experimental.

fered from each other in the number of titmouse visits per bird.

To verify the patterns of the distributions of time and visits in experimental treatments in Figs 2 and 3, I compared both on-the-ground and off-the-ground distributions between control and experimental treatments and among experimental treatments. The playback and hawk/playback experimental treatments differed significantly from their corresponding controls in their on-the-ground distribution of titmouse seconds per bird ($P<0{\cdot}05$). The hawk experimental treatment did not differ from its control (Table II). The same comparisons with off-the-ground distributions showed that the hawk and hawk/playback experimental treatments differed significantly from their controls ($P<0{\cdot}05$) but that the playback experimental treatment did not (Table II). I compared on-the-ground distributions among experimental treatments and found that the hawk experimental differed from both playback and hawk/playback experimental treatments ($P<0{\cdot}05$) but that the latter two treatments did not differ from each other (Table II). Finally, I compared the off-the-ground distributions of the three experimental treatments and found that the hawk/playback experimental treatments differed from both the hawk experimental and playback experimental treatments but that the latter two were not significantly different. Distributional comparisons of visits/bird data were conducted in an identical manner with similar results (Table III).

DISCUSSION

If a distress call is perceived as a warning by birds in the vicinity of the call, one could imagine two possible responses by these birds. They could take evasive action by freezing or fleeing the area, or they could cautiously approach the source of the call to learn the nature and location of the danger. Knowing the whereabouts and identity of the predator causing the prey's call would aid a responding bird in avoiding capture by that predator and could help it recognize and avoid similar predator types in the future.

Several species of birds have been found to gather information about potential danger in a manner similar to that proposed for birds responding to distress calls. For instance, Kruuk (1976) showed that in initial trials, more herring gulls (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) were attracted to a predator associated with a dead gull than to a predator without such an additional stimulus. In subsequent trials, however, both species avoided the predator that had been associated with the dead gull. Similarly, a study of European blackbirds (*Turdus merula*) revealed that mobbing may result in the cultural transmission of the ability to recognize a predator type (Curio et al. 1978). Naive birds learned to associate mobbing calls with a novel, harmless type of bird and later recognized the harmless species as danger. In a similar fashion, birds responding to distress calls could associate these calls with danger and learn what types of predators to avoid.

The response of titmice to the various types of stimuli presented in this study follows a pattern one would expect if the responding birds perceived the distress call as a warning. When a hawk model was presented in association with a distress call, titmice approached only to the periphery of the 7-m sphere of observation (Figs 2F, 3F). Presumably, in these trials, the titmice were able to discern the nature and location of the danger associated with the distress call with minimal approach. Interestingly, Shedd (1982) reported that American robins (*Turdus migratorius*) behave in a similar manner when responding to an owl model during the non-breeding season or on a territory other than their own. Under such circumstances, robins quietly approach the model, observe it, and then retreat.

When a distress call was played without a hawk model, titmice slowly approached to within 2–4 m of the speaker and concentrated there during the remainder of the playback (Figs 2D, 3D). My interpretation of the behaviour is that playing a distress call in the absence of any recognizable danger creates an unnatural situation. At the start of the playback, birds flush to the treetops and look for the source of danger associated with the call. When they fail to see the stimulus they move toward the source of the call in an attempt to locate the danger. Finally, unable to discern either the source of the call or an object of danger, the titmice concentrate a few metres from the speaker until the playback is stopped.

Further evidence that the titmice in this experiment regarded the distress-call playbacks as warnings is the difference in frequency with which the birds appeared to recognize the hawk model under the two circumstances in which it was presented. In 35·7% (five out of 14) of the trials in which a hawk model was presented alone, titmice apparently did

not recognize it as a threat. In these five trials, they approached very close to the model as they fed from the bait-pile. In contrast, in 100% (14 out of 14) of the trials in which a hawk model was associated with a distress-call playback, titmice apparently did recognize the hawk model as a threat. They remained away from the model throughout the trial period. This is what one would expect if the distress call caused the birds to look for danger.

In contrast to the predictions of the warning hypothesis, the predictions of the call-for-help hypothesis were consistently contradicted by the results of this study. Assuming that death in the grasp of a predator is relatively rapid, titmice that intended to assist the caller would have to come to the caller's aid quickly. Then, by direct attack or distraction, the helping titmice would have to get the predator to release the caller before the caller was seriously injured. This is exactly the response that Stefanski & Falls (1972b) observed when they exposed breeding white-throated sparrows to predator models associated with distress calls. Such behaviour is quite different from the slow, cautious approach of tufted titmice observed in this study.

Based on these observation, I conclude that in the winter tufted titmice are not attracted to distress calls because they desire to aid the caller's escape. Rather, the response of tufted titmice to distress-call playbacks presented in this study suggests that they use distress calls as warnings of danger. Unfortunately, I had no way of assessing gain or loss in fitness related to emitting or responding to a distress call other than evidence from other studies showing that titmice remain in family groups during the winter and that other species of birds appear to benefit by learning about predators. As a result, this study lacks a rigorous coupling of the intent of the caller and the response of nearby conspecifics, and thus it fails to demonstrate convincingly that warning conspecifics is a function of distress calling, not merely a result. A calling bird may be emitting distress calls to startle the attacking predator and/or attract competing predators, functions that have been supported in other studies (Driver & Humphries 1969; Perrone 1980; Högstedt 1983), and conspecifics may merely take advantage of the situation without affecting the caller's fitness.

In all likelihood, winter distress calling simultaneously serves two or three functions. When a tufted titmouse gives a distress call, it is probably warning its kin of danger, thereby increasing its inclusive fitness, and startling its captor and attracting competing predators, thereby enhancing its chances of escape. The fact that a calling bird might be attracting both kin and predators would not necessarily mean that it would be placing its kin in jeopardy. One would assume that the incoming predators would be intent on stealing a meal, not on capturing healthy prey, and that the responding kin would be alert to danger, making them particularly difficult prey.

Although emitting a distress call while in the grasp of a predator might seem to carry little cost for the caller, this is not necessarily the case. Distress calling is only one of several behaviours to which a captured bird may resort. Feigning death is a common alternative behaviour that has been observed to result in the escape of a bullfinch, *Pyrrhula pyrrhula* (Tinbergen 1962) and an eastern chipmunk, *Tamias striatus* (personal observation) from the grasp of a house cat. By giving a distress call a bird is informing the predator that it is alive and retains enough vigour to produce a call. The chance for a surprise escape is reduced, and the calling bird may be killed more quickly by the predator.

In my view, it is only through a multifunctional approach to the question of why birds emit distress calls, including a consideration of the costs of emitting such calls, that an understanding of this behaviour will be achieved. Obviously, before any meaningful conclusions can be drawn, much more information is needed on the potential for warning kin with distress calls and on the probabilities of a bird escaping from a predator by startling its captor and/or attracting competing predators versus escaping by feigning death. If the difficulties of such quantifications can be overcome, this sort of approach should resolve not only why distress calls are given, but also why there is so much interspecific variation in the propensity of individuals to emit distress calls.

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