Wilson Bull., 92(3), 1980, pp. 404–408

Factors affecting the incidence of distress calls in passerines.—The response of small birds to capture by predators varies greatly, both among and within species. A captured bird may fight back, struggle to escape, give distress calls, or remain motionless and silent. It may also do some, or all of these, in sequence. Distress vocalizations, which are distinct from the mobbing and alarm calls of free birds, are typically harsh and easily located (Stefanski and Falls, Can. J. Zool. 50:1513–1525, 1972).

Norris and Stamm (Bird-Banding 36:83–88, 1965) found that in most species of small landbirds captured in mist nets, some individuals gave distress calls when handled; the percentage of callers differed widely among species. Balph (Wilson Bull. 89:325–327, 1977) reported more female Evening Grosbeaks (*Hesperiphona vespertina*) calling when handled than males. Driver and Humphries (Ibis 111:243–244, 1969) suggested that calling startles a predator into loosening its grip. Rohwer et al. (Am. Midl. Nat. 96:418–430, 1976) proposed and tested 3 more hypotheses about the functions of distress calls: (1) the call attracts helpers who attack, harrass or distract the predator enough to make it release the prey; (2) the call warns other potential prey of the location of a predator; and (3) the call attracts another predator, which may attack the first predator to kill or rob it, allowing the original prey to escape. This paper reevaluates and extends the latter work. I analyze the problem in 2 ways, dealing with both the risks and benefits of calling.

Risks of calling.—Both calling and struggling must alert a predator that its prey is still alive. Silence and motionlessness in the prey can cause the predator to loosen its grip and even put the prey down (Sargeant and Eberhardt, Am. Midl. Nat. 94:108–119, 1975), or shift its attention elsewhere and thus allow the prey to escape. For example, small birds taken from mist nets most often escape while being handled if they are still and quiet, because this behavior may lead a person to hold them loosely. Whereas active attempts to escape may succeed for prey that are nearer to their predator in size, strength or weaponry. Thus, more birds of larger and stronger species should struggle with their predator. Birds that struggle forego the benefit of feigning death and should incur no added risk by calling. Thus, a greater proportion of birds that do struggle than birds that do not should give distress calls.

Benefits of calling.—(1) *The distress call is a call for help.*—If this hypothesis is true, free birds should respond to distress calls with distraction displays, swoop dives or actual attacks directed at the predator. In fact distress calls of fledglings and juveniles of many species elicit the above responses from their parents (Stefanski and Falls, Can. J. Zool. 50:1501–1512, 1972; Curio, Anim. Behav. 23:1–115, 1975). Parents and offspring of many species stay together for a time after the juveniles fledge. Because parental defense of juveniles seems more likely than the reverse, more juveniles than adults of the same population should give distress calls.

Aside from the case of parents and offspring, we can assume helpers are either kin of the captured bird, or reciprocators. Kin selection can favor helping and the prerequisite distress calling only if kin of the captured bird are likely to be within earshot. That is, kin groups must be cohesive. Reciprocation requires cohesive groups of unrelated birds. Proof of cohesiveness requires observations of groups of marked birds of known parentage. However, kin groups in nonmigratory populations are probably more cohesive than in species that migrate at night, because the great majority of nocturnal migrants fly alone and presumably independently of their kin (Balcomb, Auk 94:479–488, 1977). Therefore, the nepotism hypothesis predicts higher proportions of callers in nonmigratory species than in nocturnal migrant species wintering in the same area, while the reciprocation hypothesis predicts no difference (Rohwer et al. 1976). Both predictions assume that the average degree of cohesiveness of winter social groups is equal in migrant and nonmigrant species.

(2) *The distress call warns other birds of the exact location of a predator.*—Birds so alerted may flee, hide, or approach the caller, but do not help the caller escape. Warned individuals may be kin of the caller or reciprocators, but can be reciprocators only if callers survive.

(3) *The distress call attracts a second predator to attack the first predator to kill or rob it, which gives the prey a chance to escape.*—This hypothesis predicts no correlation between the cohesiveness of kin or reciprocator groups and the frequency of callers. It should work best if large predators are attracted to the call.

(4) *The distress call startles the predator into loosening its grip on the prey.*—Like the predator attraction hypothesis, the startle hypothesis predicts no correlation between the cohesiveness of kin or reciprocator groups and caller frequency. To be effective, the call should be abrupt, explosive and brief. A startle effect cannot be the only function if the call is long and continuous.

Methods.—Hypotheses about risks and benefits of calling were tested with wintering birds at Point Reyes Bird Observatory (PRBO), Marin Co., California, from 15 December 1977 to 21 March 1978. Birds were captured in mist nets (N = 343) and walk-in traps baited with grain (N = 81). Included in the analysis were 11 American Robins (*Turdus migratorius*) and 27 Cedar Waxwings (*Bombycilla cedrorum*) netted in King Co., Washington, in September 1977.

I recorded the behavior of each bird as I approached the net or trap, during removal from the net or trap, and during subsequent handling. Each bird was handled in the same way in sequence: (a) held by the body and legs, with 2 fingers encircling the neck, with the palm of the same hand enclosing the torso; (b) held firmly by the legs only; and (c) released. Birds were held each way for a period varying from about 10–60 sec. For each stage of handling I recorded: (a) whether the bird called; (b) the kind of call, whether distress or other; (c) bouts of struggling, including wing flapping, squirming, biting or pecking; (d) static displays, including erection of crown feathers, partial opening of wings or spreading of tail feathers; or (e) silence and motionlessness.

Distress calls of 1 hand-held Varied Thrush (*Ixoreus naevius*) and 1 Brown Towhee (*Pipilo fuscus*) were played back from a Sony TC-11OB portable tape recorder, with frequency response range 50–10,000 Hz. I chose these species for their loud voices. I matched playback volume to the natural level or slightly louder. Each original cut was duplicated several times in sequence to produce a continuous playback of about 5 min duration. Playbacks were transmitted through the hand-held recorder in 7 cases and through an amplifier in 8 cases. In the latter playbacks a mounted Sharp-shinned Hawk (*Accipiter striatus*) was placed next to the amplifier and I sat 5–20 m away. All playbacks took place within 11 km of the recording site at PRBO, in sites occupied by the species whose calls were used. For each playback I noted (a) all bird vocalizations, by species and call type, within about 50 m of the tape player during the playback and in the 5 min interval preceding and 10 min interval following the playback, and (b) the tendency of birds to approach the source of the call, depart or remain stationary in the same interval. Playbacks lasted 30 sec–5 min, sometimes with pauses. Status of birds as migrant or resident was determined from a 12-year summary of seasonal distribution and abundance prepared from PRBO banding records.

Results.—(1) *Frequency of calling in relation to body size and struggling.*—Struggler frequency and body size were compared with Spearman rank correlation tests. All species with 8 or more individuals represented were included in the analysis (Table 1). For 7 species of nocturnal migrants the frequency of strugglers within a species correlated positively with body size ($P < 0.05$), as predicted. Among 7 nonmigrant species size and struggler frequency were uncorrelated ($P > 0.50$).

The frequency of calling in relation to struggling was recorded for the birds listed in Table 1 and for 92 birds of 26 other species as well, totalling 378. Thirty-seven percent of 284

TABLE 1

STRUGGLING FREQUENCY AND CALLING FREQUENCY IN NONMIGRANT AND NOCTURNAL MIGRANT SPECIES CAPTURED IN TRAPS AND MIST NETS[a]

Species	Mean weight (g)[b]	N	Struggling frequency (%)	Calling frequency (%)
Nonmigrants				
Robin	80	11	91	85
Song Sparrow	19	8(7)	100	0
Oregon Junco	17	21	64	0
Wrentit	13	24(2)	88	8
Pine Siskin	11	8	25	0
Chestnut-backed Chickadee	9	36	94	44
Bushtit	5	23	78	70
Nocturnal migrants				
Varied Thrush	76	11	91	57
Fox Sparrow (*Passerella iliaca*)	33	14(9)	79	0
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	31	28(25)	86	11
Hermit Thrush (*Catharus guttatus*)	23	10	90	10
Townsend's Warbler	9	9	67	0
Ruby-crowned Kinglet	5	29	38	17
Golden-crowned Kinglet	5	54	53	17

[a] Mist net captures in parentheses.
[b] Weights are of lean birds (little or no fat in the furculum) at time of capture.

strugglers and 9% of 94 nonstrugglers called. Thus, a significantly greater proportion of strugglers than nonstrugglers called ($\chi^2 = 45.16$, df = 1, $P < 0.01$), as predicted. Of the 110 callers, 101 struggled, 6 gave static displays interpretable as threat displays and 3 Ruby-crowned Kinglets (*Regulus calendula*) remained still. Thus, in every species except this kinglet, all or nearly all, callers struggled, as predicted.

Four Golden-crowned Kinglets (*Regulus satrapa*) were captured more than once. Two were silent in each of 2 and 3 captures, respectively. One called once in 2 captures and 1 called once in 4 captures, and thus they varied in behavior.

(2) *Nepotism versus reciprocation.*—Both the warning and call-for-help hypotheses assume the existence of stable social groups. The nepotism model predicts that the proportion of callers in a population should increase with the proportion of related individuals in the group. This proportion should be larger, on the average, in nonmigratory species than in nocturnal migrants. Because almost all callers struggle and struggler frequency increases with body size among nocturnal migrants, species of similar size should be compared. Three such comparisons were possible between nonmigrant and migrant species.

The sedentary Bushtit (*Psaltriparus minimus*) showed a significantly higher proportion of callers than either of 2 migratory species, the Golden-crowned Kinglet ($\chi^2 = 15.27$, df = 1, $P < 0.01$) and Ruby-crowned Kinglet ($\chi^2 = 9.77$, df = 1, $P < 0.01$). The sedentary Chestnut-backed Chickadee (*Parus rufescens*) called more than Townsend's Warbler (*Dendroica townsendi*), a nocturnal migrant, though the difference was not significant ($\chi^2 = 2.47$, df = 1, NS). The American Robin, nonmigratory in western Washington, called more than the

Varied Thrush, a nocturnal migrant ($\chi^2 = 5.54$, df = 1, $P < 0.05$). All 3 cases support the nepotism model.

(3) *Call-for-help hypothesis.*—Because parental defense of juveniles seems more likely than the reverse, more juveniles than adults should give distress calls. This held true for the 2 species examined. Significantly more juveniles than adults called among House Finches (*Carpodacus mexicanus*) ($\chi^2 = 10.78$, df = 1, $P < 0.01$) and Cedar Waxwings ($\chi^2 = 9.95$, df = 1, $P < 0.01$). Ten percent of 215 adult and 25% of 67 juvenile House Finches called (data from S. A. Rohwer, Univ. Washington). One of 5 adult and 18 of 22 juvenile waxwings called. One adult waxwing was captured and mouthed by a cat until the cat was forced to release it. The bird was silent and still while held by the cat.

Responses of small birds to playbacks of distress calls of Varied Thrush and Brown Towhee in January, February and March 1978 were similar in all 15 experiments. Playbacks failed to attract conspecifics. Birds of all species either continued with previous activity, e.g., singing or feeding, or became quieter during playbacks. There were 2 exceptions, both using a hand-held recorder and no stuffed hawk. Two Scrub Jays (*Aphelocoma coerulescens*) approached the speaker, calling loudly during a playback. Once 2 Wrentits (*Chamaea fasciata*) and a Bewick's Wren (*Thryomanes bewickii*) approached 1 min after a playback had stopped.

(4) *Warning hypothesis.*—Distress calls indicate the exact location of a predator and small birds can use this information for their own protection. The warning hypothesis predicts that more birds with kin within earshot than birds without kin nearby will call and is supported by the data from the Bushtit, kinglets, Chestnut-backed Chickadee, Townsend's Warbler, American Robin and Varied Thrush.

(5) *Predator attraction hypothesis.*—This hypothesis assumes that distress calls attract predators of small birds and perhaps larger, second-order predators as well. Playbacks confirmed this. Of 7 trials with a hand-held recorder, playbacks attracted a Cooper's Hawk (*Accipiter cooperii*) once, 2 Sharp-shinned Hawks once (the first bird to arrive chased the second one), and Great Horned Owls (*Bubo virginianus*) twice, once in mid-afternoon and once at dusk. Of 8 trials using a stuffed Sharp-shinned Hawk, playbacks attracted a Cooper's Hawk once and a Sharp-shinned Hawk once. In 4 of 5 cases the accipiters appeared within 10 sec of the onset of the playbacks, approached to within 10 m or less of the speaker, perched overhead in vegetation and peered in the direction of the sound source and at the observer who sat nearby. The Great Horned Owls appeared within 30 sec and 3 min of the start of the playbacks and approached to within 15 and 6 m, respectively.

(6) *Startle hypothesis.*—This hypothesis assumes that the distress call surprises the predator by its sudden and explosive occurrence. If the call continues, its later portions cannot be startling and must serve another purpose, if any. Of 110 birds that called, 59% continued to call through more than 1 stage of handling. For these birds the startle hypothesis seems inadequate.

Discussion.—Nearly all captured birds that gave distress calls struggled in the hand. Among nocturnal migrants larger species struggled more often than smaller species, and this suggests that the propensity to struggle increases with physical strength. Differences in tendency to struggle among individuals of a species may also be based on differences in strength, perhaps due to hormone levels or general health. The lack of correlation of size and struggler frequency among 7 nonmigrant species is unexplained.

Birds more likely to be within earshot of kin, called more than species of similar size who were probably not with kin. This result supports the nepotism hypothesis, which construes the call as a warning, a cry for help, or both. Rohwer et al. (1976) also found callers to be more common in nonmigrant than nocturnal migrant species. In the present study 3 of 7 nonmigrant species, Pine Siskin (*Spinus pinus*), Oregon Junco (*Junco hyemalis oreganus*) and Song Sparrow (*Melospiza melodia*), yielded no callers. This can be taken either as evidence that these 3 species do not have cohesive kin groups or as evidence against the

nepotism hypothesis. One should avoid assumptions about kinship and stability of social groups unless observing marked birds of known parentage.

Distress calls of fledglings and juveniles of some species attract their parents, who attack or distract the predator. This confirms the nepotism model for this case. Accordingly, more juveniles than adults of 2 species (House Finch and Cedar Waxwing) gave distress calls when handled. However, for 2 species of wintering birds playbacks of distress calls failed to elicit responses that could lead to helping. They did attract predators of birds, usually within a few seconds of the start of the playback. Such rapid arrival could find a captured bird still sufficiently unharmed that it could escape during a struggle between predators. Bent (U. S. Natl. Mus. Bull. 170, 1938) described an instance in which the scream of a meadowlark (*Sturnella* sp.) caught by a Prairie Falcon (*Falco mexicanus*) seemed to attract a Golden Eagle (*Aquila chrysaetos*), and when the eagle approached, the falcon released its prey, who then flew away.

Whether a distress call can startle a predator is unclear. Observations of captures by natural predators are needed. Naive predators should be the most susceptible because the behavior is new to them. The protracted calling of many captured birds implies that startling is not the sole function of the call.

Except in the case of parental defense of juveniles, altruism may be entirely absent from the distress call phenomenon in birds. The altruistic basis of calling (i.e., the risk incurred by the caller) is to alert the predator that the prey is still alive. However, nearly all captured birds that call also struggle, and the struggle itself suffices to tell the predator the condition of the prey. Thus, as long as a bird struggles it can call at no added risk to itself.

There are also 2 unexplained results. First, because silence confers no identifiable benefit on strugglers, it is odd that only 37% of strugglers called. Perhaps such birds were silent because their kin were absent, though this point is untestable without direct knowledge of kinship. Second, 2 Golden-crowned Kinglets differed in behavior between captures, sometimes calling and other times not. This suggests that calling frequencies may be affected by the capture and handling techniques, including the following. (1) The conditions of capture and handling are not consistent, e.g., length of time a bird spends in the net or trap and amount of time taken to remove a bird vary. Birds confined or handled for long periods may tire and switch to a different behavior. Perrone and Paulson (Condor, 81:423-424, 1979) found differences between observers in the incidence of distress calls of mist-netted birds, apparently due to differences in handling methods. (2) Mist nets and traps are not natural predators and may induce abnormal responses, e.g., a few birds caught in nets gave distress calls as I approached them and before I began to untangle them. This situation of being caught and yet not caught must have few parallels in nature. (3) Birds may habituate to capture by human and not regard it as predation. Balph (1977) reported that Evening Grosbeaks are less likely to call in successive recaptures than when first handled.

In conclusion, this work shows that outside the nesting season at PRBO, distress calls do not summon help or even attract small birds, but warning occurs inevitably and predator attraction often occurs. The swift approach of accipiters to the source of the call may explain why small birds do not approach—it is dangerous for them to do so. The predator attraction and startle hypotheses are not incompatible with the warning and call-for-help hypotheses. Studies must be done to assess their relative importance for individual species and different seasons.

Acknowledgments.—I thank the staff and volunteers of the Point Reyes Bird Observatory for their help, especially Bruce Sorrie. Julienne Lemoine taught me to tape-record bird calls. Anne Clark, Steven Fretwell, Gordon Orians, Dennis Paulson, Sievert Rohwer and Raymond Stefanski provided valuable reviews of the manuscript.—MICHAEL PERRONE, JR., *Zoology Dept., Univ. Washington, Seattle Washington 98195.* (Present address: *HDR Sciences, 804 Anacapa St., Santa Barbara, California 93101.*) *Accepted 15 Feb. 1979.*