DISTRESS CALLS IN THE ACORN WOODPECKER[1]

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Abstract. Acorn Woodpeckers live in extremely stable kin groups. Nonetheless, only 59.9% of birds caught in roosting aggregations gave distress calls or fear screams. Distress calling was highly repeatable among individuals and apparently heritable. However, the incidence of distress calling did not vary seasonally or according to age, sex, or status. Also, with two marginally significant exceptions, distress calls did not vary consistently with group characteristics or with the composition of roosting aggregations. Screams did not attract conspecifics, but sometimes attracted large mammalian predators. These results fail to support Rohwer's (1975) "calling for help" hypothesis and instead are consistent with Högstedt's (1983) "predator attraction" hypothesis that distress calls function to attract secondary predators that will distract or dispute the original predator, thereby inadvertently allowing the caller to escape.

Key words: Acorn Woodpecker; distress calls; Melanerpes formicivorus; *predator attraction; screams.*

INTRODUCTION

Distress calls or fear screams are given when animals are in considerable danger or after they have been captured. They are loud, conspicuous, and common among birds, but their function remains unclear. The incidence of fear screams within a species can vary according to a variety of factors including age, sex, and season (Stefanski and Falls 1972a, 1972b; Balph 1977) and can also be influenced by handling effects (Perrone and Paulson 1979). However, most attempts to explain the function of fear screams have ignored such variation and focused on interspecific differences (Norris and Stamm 1965, Rohwer 1975, Rohwer et al. 1976, Perrone 1980, Högstedt 1983).

Four hypotheses have been proposed to explain distress screams: (1) The "predator startle" hypothesis: screams startle predators into inadvertently allowing captured individuals to escape. (2) The "kin selection" hypothesis: screams warn kin of imminent danger. (3) The "calling for help" hypothesis: screams are calls for help directed at kin or reciprocal altruists, either related or not. (4) The "predator attraction" hypothesis: screams are an attempt to attract other predators that, in their attempt to pirate the prey,

may either distract or fight the primary predator and allow the caller to escape inadvertently.

Recent authors have generally dismissed the first two hypotheses. With respect to the predator startle hypothesis (1), originally proposed by Driver and Humphries (1969), Perrone (1980) pointed out that screaming following capture unambiguously informs a predator that the caller is still alive. This knowledge is likely to increase the predator's vigilance against allowing the prey to escape rather than startle predators into loosening their grip (see also Högstedt 1983). The kin selection hypothesis (2) has been discounted based on the observation that conspecifics generally ignore distress screams instead of seeking cover (Perrone 1980) and on the logical grounds that a successful predator is unlikely to be harmful to individuals other than its captured prey (Högstedt 1983).

The calling for help hypothesis (3), proposed by Rohwer (1975) and Rohwer et al. (1976), is supported primarily by comparative evidence that permanent residents (who are more likely to live near kin) scream more than winter residents and that diurnal migrants (who are more likely to be in kin groups) scream more than nocturnal migrants. Rohwer (1975) further noted an inverse correlation between the incidence of distress calling and male winter plumage variability, a relationship consistent with the altruism hypothesis assuming that winter plumage

variability facilitates the signaling of social dominance status among strangers.

Recent work by Perrone (1980) and Högstedt (1983) has garnered considerable support for the predator attraction hypothesis (4). Evidence supporting this hypothesis includes the observation that screams frequently attract other predators, that screaming is more common in prey species that are large in relation to their main predators, and that screaming is more common among species living in densely vegetated habitats where potential pirates are more likely to detect feeding opportunities based on acoustic, rather than visual, cues.

Here we examine the incidence and heritability of distress calls in the cooperatively breeding Acorn Woodpecker (*Melanerpes formicivorus*). In California this species lives in extended family groups consisting of closely related multiple breeders of both sexes (cobreeders) along with their offspring (nonbreeding helpers) from prior years (Koenig and Mumme 1987). Consequently, Acorn Woodpeckers offer a unique opportunity to examine the pattern of distress calling under differing social circumstances within a single population.

We examined the pattern of distress calling with the goal of testing the calling for help and predator attraction hypotheses. The calling for help hypothesis predicts that screams should attract conspecifics. In addition, the following observations would be consistent with this hypothesis: (a) Distress calls should be very common, since Acorn Woodpeckers live in extremely stable kin groups (Koenig and Mumme 1987). (b) Birds should call more during the post-breeding season when the most young, inexperienced birds are present. (c) Younger and more vulnerable birds should call more than less vulnerable birds. (d) Birds should call more vigorously when they either belong to a larger social unit or when a higher proportion of their social unit can come to their aid.

In contrast, the predator attraction hypothesis predicts that screams should attract predators potentially capable of scaring or disputing the original (primary) predator. This hypothesis makes no a priori prediction concerning the pattern of distress calls according to age, sex, status, or group composition. However, since Acorn Woodpeckers live in open habitat, a relatively low incidence of distress screams would be consistent with this hypothesis.

METHODS

During the course of a long-term study of the Acorn Woodpecker at Hastings Reservation, Monterey County, California, we captured 189 individuals for which we subsequently obtained information on distress screams. Captures were made between March 1982 and March 1989. Some individuals were captured and scored more than once, yielding a total sample of 227 captures. Most frequently, birds were "ambushed" at communal roost holes. This was done by blocking holes before dawn and then capturing roosting birds either as they exited the cavity by themselves or by manually pulling them out of previously opened holes. In all, birds were captured in 80 different ambushes. These ambushes, although unnatural events, are probably mimicked in nature by predators that attempt to enter or destroy roost cavities at night and capture one or more roosting individuals.

Birds were kept in closed bags until shortly after dawn, at which time they were weighed, banded, and bled. Thus, although the length of time individual birds were handled was reasonably constant, the length of time birds were held prior to handling varied arbitrarily among individuals. Although this protocol may have increased the variation in the incidence of distress calls (Perrone and Paulson 1979), there is no reason to expect that the incidence was biased in any particular direction.

Like other distress screams, those of Acorn Woodpeckers are shrill, piercing vocalizations given with considerable vigor while the bird pecks and squirms (see Högstedt 1983). We scored birds while handling them for their distress calls on a scale of 0 (no distress calls given) to 3 (distress calls given almost continuously). For analysis, we used either this scale or the percentage of individuals that gave any distress calls at all (score ≥ 1).

Heritability is the proportion of total phenotypic variance that can be attributed to additive genetic variance and is directly proportional to the rate at which selection can produce evolutionary change (Boag and van Noordwijk 1987). Within a population, distress screams must therefore be significantly heritable in order to currently evolve in response to ecological or social factors.

Repeatability, which provides an upper limit to heritability, was measured among individuals

TABLE 1. Estimated heritability of distress calls given by Acorn Woodpeckers.

	Correlation or regression coefficient $\pm$ SE[a]	P-value	Estimated heritability	n[b]
Offspring–father	0.31 ± 0.21	0.15	0.62 ± 0.42	27
Offspring–mother	0.43 ± 0.33	0.21	0.87 ± 0.65	15
Offspring–midparent	0.93 ± 0.48	0.09	0.93 ± 0.48	11
Correlation among broods (F-ratio = 3.15; r^2 = 0.59)	0.39	0.005	0.79	14, 43

[a] Regressions of brood means on mean score for cobreeders of the appropriate sex.
[b] For offspring-parent regressions, sample size is the total number of broods. For correlation among broodmates, sample size is the number of broods followed by the total number of individuals.

captured more than once by dividing the among-groups variance by the combined among-groups and within-groups variance (Lessells and Boag 1987). Heritability was estimated as follows: First, we determined the presumed parents and brood-mates of each individual. "Presumed parents" refer to the cobreeders present when the individual hatched, and broodmates refer to all individuals sharing the same or a bisexual subset of those cobreeders as parents; exact parentage was rarely known (e.g., see Mumme et al. 1985). Cobreeders are virtually always closely related in the Hastings population (Koenig and Mumme 1987) and thus such individuals constitute either parents or closely related uncles/aunts. Similarly, broodmates include a combination of full siblings, half siblings, and closely related cousins. These definitions are made necessary by the polygynandrous mating system of this population and complicate, but do not invalidate, the standard procedures for estimating heritability. For additional information concerning the mating system of Acorn Woodpeckers at Hastings and for our methods of classifying individuals as breeders or nonbreeders, see Koenig et al. (1984).

Next we determined the mean distress call scores (DCS) by averaging scores for multiple captures of the same individual. DCS for birds sharing the same set of cobreeders as presumed parents were averaged to yield a mean DCS for broods. Brood means were regressed on the mean DCS for all male cobreeders for which we had distress calls (offspring–father regression), all female cobreeders (offspring–mother regression), and the average of the two (offspring–midparent regression). As an additional estimate, the intraclass correlation coefficient of DCS for siblings was determined by ANOVA. Heritability is estimated as the offspring–midparent regression coefficient, twice the offspring–parent regression

coefficients, and twice the intraclass correlation among siblings (Boag and van Noordwijk 1987).

We also investigated whether there was a consistent pattern in the incidence of distress calls as a function of the the age, sex, or status of individuals, group composition, or composition of the roosting aggregation. We looked for seasonal variation by dividing the year into three seasons: winter (1 October–30 March), breeding (1 April–30 June), and post-breeding (1 July–30 September).

RESULTS

REPEATABILITY AND HERITABILITY

Two or more independent measures of distress calls were obtained on 31 individuals. The number of scores per individual ranged from 2–4 ($\bar{x}$ = 2.3). Repeatability, r, based on the distress call scores, was 0.778 ($F_{30,38} = 8.67$; $P < 0.001$).

Estimates of heritability varied from 0.62 to 0.93 (Table 1). However, sample sizes were small and the only estimate significantly different from zero was the 0.79 value based on the resemblance of broodmates. This latter procedure yields an upper limit on heritability because of the shared environment among broodmates (Boag and van Noordwijk 1987). These data suggest that there is a strong additive genetic component to the incidence of distress calling in Acorn Woodpeckers amounting to between 62 and 78% (based on the repeatability value) of the total phenotypic variance in this trait.

One potential confounding factor in these estimates of heritability could be a tendency for the distress calls of birds captured and processed at the same time to resemble each other for reasons other than consanguinity. Birds were typically processed within hearing distance of one another; thus, this would be true if giving distress

calls was contagious. We tested for such an effect in three ways. First, we categorized birds based on the order in which they were processed following individual ambushes. Then we tested for ordering effects on distress calling by performing a Kruskal-Wallis ANOVA on DCS using processing order (first, second, third, fourth, and fifth plus all subsequent individuals) as categories. No significant ordering effect was found ($\chi^2 = 3.1$, df = 4, $P > 0.5$).

This analysis suggests no significant overall ordering effect but does not directly address the possibility of DCS being contagious. To do this, we first looked for how distress calling was distributed within groups of birds caught together at ambushes; to simplify the analysis, only the 27 sets of two birds caught together were used. If distress calling is contagious, both birds should tend to either give distress calls or not to give distress calls more frequently than expected, depending on whether the first bird to be processed did or did not call. Contrary to this prediction, there was no significant difference ($\chi^2 = 0.2$; ns) between the observed and expected number of sets of birds for which zero, one, and both birds gave distress calls assuming a binomial distribution and an expected probability for distress calling of 59.9% (see below).

Finally, we examined the calling behavior of the second bird to be processed in all ambushes involving two or more birds to see whether it depended on the behavior of the first bird to be processed. The second bird screamed in 10 of 21 (48%) cases when the first bird did not scream and 19 of 34 (56%) cases when the first bird screamed; this difference is not significant ($\chi^2 = 0.1$; ns).

These results suggest that there are neither ordering effects nor any obvious contagious behavior influencing distress screaming in this population. However, in the absence of cross-fostering experiments it is not possible to eliminate various potential effects of shared environment on heritability estimates (Boag and van Noordwijk 1987). Thus, the values derived here can only be considered upper estimates.

EFFECT OF DISTRESS CALLS

Distress calls were given by 59.9% of the 227 captured individuals. Such calls never attracted conspecifics. However, on two occasions we were approached by large mammalian predators that were attracted to distress calls. One of these was a bobcat (*Lynx rufus*) attracted to a calling bird being transferred by us to a holding bag at the roost cavity 8 m up in a tree. The second involved a grey fox (*Urocyon cinereoargenteus*) attracted to a bird screaming while being processed on the ground. The bobcat climbed up into the tree but left quickly after discovering the equally startled senior author; the fox remained in the area and approached whenever the captured bird screamed.

We never inadvertently released captured birds, even in the two cases described above. However, the possibility that natural predators will sometimes release birds that have attracted a secondary predator with their screams was confirmed when one of us (MTS) observed a Cooper's Hawk (*Accipiter cooperii*) capture an Acorn Woodpecker, who screamed briefly. Upon noticing the human observer several seconds later, the hawk released the woodpecker and flew off. The woodpecker, still able to fly, followed.

CONTEXT OF DISTRESS CALLING

Neither the mean DCS nor the incidence of distress calling varied significantly with age, sex and status, or season (Table 2). The mean DCS of individuals caught in individual ambushes did not correlate significantly with the number of birds caught, the number of group members *not* caught, the proportion of a group captured, total group size, or number of birds caught in any sex or status subclass with the exception of the number of females (Table 3). Birds had higher DCS when more females were captured in the ambush.

We further investigated the pattern of distress calling by asking whether birds of a particular sex/status category were more or less likely to call depending on whether no birds of the same or another sex/status category were caught or whether at least one such bird was captured. Only cases in which at least one bird of the target sex/status category was present were included. Of the eight comparisons (Table 4), only one was significant: nonbreeders are more likely to give distress calls when no breeders are captured in the ambush than when at least one breeder is captured.

DISCUSSION

Although sample sizes are small, the high repeatability and significant heritability estimated from the resemblance of broodmates support Norris and Stamms (1965) suggestion that dis-

TABLE 2. Incidence of distress calls as a function of age, sex and status, and season.[a]

	Mean (±SD) score	Percent giving distress calls	n birds	χ^2	df
Age					
First-year	1.22 ± 1.19	61.0	159	0.1	1
Adult	1.26 ± 1.22	57.9	57		
Sex and status					
Breeder males	1.12 ± 1.19	54.3	94		
Breeder females	1.40 ± 1.12	71.2	52	4.5	3
Nonbreeder males	1.33 ± 1.23	62.8	43		
Nonbreeder females	1.13 ± 1.19	55.3	38		
Season					
Winter	1.19 ± 1.15	60.0	140		
Breeding	1.34 ± 1.18	64.2	53	1.1	2
Post-breeding	1.21 ± 1.32	52.9	34		

[a] Percent of birds giving distress calls in the different categories tested by χ^2; all $P > 0.10$.

tress calls have a significant additive genetic component detectable despite the noise introduced by differences in handling (see Perrone and Paulson 1979). This suggests that natural selection currently has the opportunity to alter the incidence of this trait within the population depending on the costs and benefits associated with giving distress screams under particular circumstances.

The results generally support the hypothesis that distress calls are an attempt to attract secondary predators or pirates who may scare or disturb the primary predator into inadvertently allowing the caller to escape. Evidence concordant with this view, and contradictory to the calling for help hypothesis, include the following observations:

(1) Predators are attracted to distress calls (Perrone 1980, Högstedt 1983). We recorded two species of large mammals being attracted to screaming Acorn Woodpeckers. The frequency of such attraction was not high. However, given the apparently dire straits of the caller, even the rare attraction of secondary predators might yield significant selective benefits as long as they occasionally yield an opportunity for the caller to escape. This was observed once when one of us inadvertently scared away a Cooper's Hawk, allowing the Acorn Woodpecker it had just captured to escape. Distress calls did not attract conspecifics.

(2) The overall frequency that captured birds gave distress calls, 59.9%, places Acorn Woodpeckers 12th among the 29 species listed in Rohwer et al. (1976). Given that Acorn Woodpecker

groups at Hastings are certainly more stable and of higher average kinship than any of the species considered by Rohwer et al. (1976), this relatively low incidence is not consistent with the hypothesis that they are calls for help directed toward kin or other group members. It is, however, consistent with the prediction of the predator attraction hypothesis that the incidence of distress screams should be relatively low in species living in open habitats, such as that used by Acorn Woodpeckers in our study site.

(3) With two marginally significant exceptions discussed below, distress calling was generally independent of age, sex and status, group composition, or the birds caught or not caught within a group relative to group composition (Tables 2–4).

The two significant results reported in Tables 3 and 4 provide the only possible support for the

TABLE 3. Spearman rank correlations of distress calls (mean score among all birds caught in an ambush) with characteristics of the group and the roosting aggregation.

Variable	r_s	n ambushes
n birds caught in ambush	−0.04	80
n group members not caught	−0.05	78
Percent of group caught	0.00	78
Total group size	−0.06	79
n breeders caught	−0.01	77
n nonbreeders caught	0.04	77
n males caught	−0.18	78
n females caught	0.24[a]	77

[a] = $P < 0.05$ (two-tailed); other $P > 0.05$.

TABLE 4. Distress calls as a function of the sex and status of birds caught and not caught in roosting aggregations.[a]

Sex and status		Percent of A giving distress calls when at least one (additional) B was present and		
Bird A	Bird B	Not caught (n)	≥1 caught (n)	χ^2 (df = 1)
Males	Male	57.1 (14)	54.7 (86)	0.0
Males	Female	39.3 (28)	61.7 (81)	3.4
Females	Male	86.7 (15)	61.5 (65)	2.4
Females	Female	73.3 (15)	65.5 (55)	0.1
Breeders	Breeder	57.1 (14)	60.7 (122)	0.0
Breeders	Nonbreeder	75.0 (12)	66.0 (47)	0.1
Nonbreeders	Breeder	86.7 (15)	53.3 (45)	4.0[b]
Nonbreeders	Nonbreeder	71.4 (7)	62.0 (50)	0.0

[a] χ^2 value corrected by Yate's method.
[b] = $P < 0.05$; other $P > 0.05$.

calling for help hypothesis found here. First, birds gave stronger distress calls when more females were captured (Table 3). The significance of this result is unclear, but females are subordinate to males within groups (MacRoberts and MacRoberts 1976) and thus it could conceivably reflect a tendency for subordinates to scream more for help when more such individuals are captured together. Second, nonbreeders were more likely to give distress calls when no breeder was caught than when one or more breeders were caught with them (Table 4). Nonbreeders are generally younger and less experienced than breeders (Koenig and Mumme 1987), and thus this result is predicted by the hypothesis that screams are given by young, inexperienced birds in an attempt to attract parents who may help to defend them (Stefanski and Falls 1972a). However, as noted above, no such defense was noted in this study. Further, as pointed out by Högstedt (1983), this cannot explain the existence of distress screams in adults during most of the year. Finally, given the number of statistical tests performed, it is plausible that the two marginally significant results we found may be purely attributable to chance.

In conclusion, these results provide considerable evidence against the hypothesis that distress screams are calls for help from conspecifics, closely related or not. In contrast, our findings are generally consistent with the hypothesis that their function is primarily to attract secondary predators whose presence may lead to the inadvertent escape of the caller. At least in the Acorn Woodpecker, distress calls appear to be an example of interspecies communication that has evolved as a last-ditch ploy by apparently doomed individuals to outwit, and even potentially to destroy, their captors.

Why is there so much variability among individuals in their propensity to give distress screams? Possibly the selective benefits of distress calling are slight and are balanced against the costs associated with having a captured individual let the primary predator know it is still alive. If so, does the population consist of an evolutionary stable equilibrium of callers and non-callers or are non-calling lineages at a selective disadvantage? Answering such questions will require considerable additional study of this striking phenomenon.

ACKNOWLEDGMENTS

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