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Nest Predators and Breeding Birds: Do Initial Vocalizations Correlate with Predator Type and Future Defense Strategy?

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ABSTRACT — The initial vocalizations of breeding catbirds in response to predator models positioned at their nests were analyzed to determine if they were correlated with the type of later defense employed (attack model vs. no attack), intensity of defense, and type of predator model (snake vs. blue jay). Statistical differences were found in the types and numbers of vocalizations used in relation to type of nest predator and form of future defense. The data suggest that the initial catbird vocalizations may indeed encode a variety of information.

Introduction

Over 50 percent of all nesting attempts by breeding birds are terminated as a result of nest predation (1,2,3). Predators have thus exerted strong selection pressure on the evolution of such anti-predator behavior as nest concealment, distraction displays, and colonial nesting (4). There is also evidence that birds will defend their nests by active nest defense (5). In one study (6), the intensity of active nest defense was found to be related to predator type and stage of the reproductive cycle. Mounts of blue jays (*Cyanocitta cristata*) were attacked more intensely than those of snakes, and these attacks were most intense after the eggs hatched.

Physical contact between a breeding bird and nest predator is costly in terms of time and energy, and may endanger the well-being of the breeding bird. According to game theory, species have evolved mechanisms to reduce the incidence of actual fighting (7,8). Of these mechanisms, threat displays and vocalizations are especially valuable because in most contests the combatants are not evenly matched. By observing the activities of a breeding bird, a nest predator may be able to gauge whether the bird will defend its nest and the intensity with which the nest will be defended. Communication of accurate information by a breeding bird may also be used by its mate and conspecifics in coordinating nest defense.

If birds do communicate motivation and intent to others, these signals could be sound-transmitted, since birds have a fairly sophisticated system of auditory communication that is used in sexual, agonistic, and maintenance activities (9).

A number of studies have shown that mammals have developed predator-specific alarm calls which may also convey information about a predator's activities (10,11,12,13). To date, no comparable study has been performed on birds. We conducted such a study on gray catbirds (*Dumetella carolinensis*) to determine if their initial vocalizations in response to models of predators positioned at their nests accurately reflected predator type, later form of defense, and the intensity of later defense.

Methods and Materials

The study was conducted in old-field habitats in and around St. Paul, Minnesota from April through July, 1980 and 1981. The study areas were searched periodically in an effort to locate nests soon after egg laying had been initiated. For each test, a stuffed blue jay mount or a 0.75 m rubber snake model which resembled a rat snake was affixed to the nest when the female left to feed. Subsequent events at the nest were observed from a concealed position. The vocalizations of the breeding bird were recorded using a Uher 4000 Report Monitor tape recorder and a Dan Gibson P650 microphone, and were later analyzed with a Kay sonography model 6061B. In all tests, only the initial vocalizations of the returning birds were analyzed. These vocalizations were referred to as the Initial Response Repertoire (IRR). The behavioral response of the nesting bird to the predator model was also noted.

Results

Catbirds primarily used two types of vocalizations in their responses to the predator models: screams and meows. The vocalizations were similar, but meows were longer in duration.

Chi-square analyses were performed to determine if the type of predator model influenced the type of vocalizations included in the IRR. Screams and meows were examined separately and the number of birds uttering each type was compared with those not uttering it. Figure 1 illustrates the vocal responses of catbirds in relation to predator type and nest defense strategy. Ninety-two percent of the catbirds exposed to the blue jay mount gave screams, compared to 50 percent of the catbirds exposed to the snake ($\chi^2 = 11.08$; p < 0.05). The meow was significantly more likely to be included in the IRR of birds exposed to the snake model than in that of birds exposed to the jay (52% vs 4%; $\chi^2 = 11.6$; p < 0.05).

Analysis of subsequent defense activities showed that the IRRs of gray catbirds that ultimately attacked the predator models were significantly more likely to contain screams than were those unaccompanied by attack ($\chi^2 = 9.43$; p < 0.05). Meows were more likely to be included in the IRR of catbirds that did not attack the models ($\chi^2 = 4.80$; p < 0.05).

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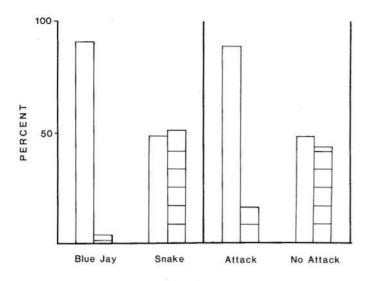


Figure 1. Proportion of gray catbirds uttering screams (clear histograms) and meows (hatched histograms) in relation to predator type and type of defense later employed.

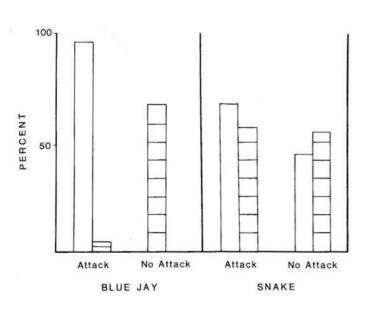


Figure 2. Proportion of gray catbirds uttering screams (clear histograms) and meows (hatched histograms) in relation to whether they attacked or did not attack each type of predator model.

The comparisons discussed above were made for both later defense strategy and predator type. The interactions between these two main factors were examined in subsequent chi-square analyses (Figure 2). Catbirds that later attacked the blue jay model were significantly more likely to include screams in their IRR than birds that did not ultimately attack the model ($\chi^2 = 2.97$; p < 0.05). The IRR of catbirds that did not attack the jay model included meows only.

The experiments with the snake model showed that these IRRs were likely to contain meows as screams regardless of whether the catbirds later attacked the snake model.

To summarize, the scream was most often included in the IRR of catbirds exposed to the jay model and in those birds that ultimately attacked the models. The meow type of vocalization was most frequently used in response to the snake model, whether it was attacked or not.

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The data suggest that the type of vocalization included in the IRR of breeding catbirds is related to both predator identify and subsequent nest defense. These data do not, however, provide information about the temporal and quantitative aspects of the vocalizations themselves. To determine whether screams of catbirds exposed to both the jay and snake models differed, sonograph tracings were made and analyzed using 2x2 analyses of variance (ANOVA).

The two main factors in the ANOVA were predator type and ultimate form of defense (fate). Seven of the eight vocal parameters studied were significantly related to the type of predator model (Table 1). Catbirds uttered four times as many vocalizations per 30-second interval in response to the jay model than they did in response to the snake model. The more frequent scream vocalizations of catbirds exposed to the jay model were about half the duration of those given in response to the snake model.

Catbirds that ultimately attacked the models uttered a significantly greater number of vocalizations/30 sec (61 and 15 per 30-second interval, respectively), and gave shorter screams with shorter intervals between notes than those catbirds that did not attack the models (Table 1).

The subeffects of the ANOVA were examined to determine the effect of predator type and defense strategy on catbird IRR patterns (Table 1). Catbirds that later attacked the blue jay model initially give significantly more vocalizations/30 sec (70/30 sec), primarily screams, than birds which did not attack the model (31/30 sec). There was less time between individual notes of screams that preceded attacks on the jay model than of screams of catbirds that did not attack the models (384.5 msec vs. 7864.8 msec). Catbirds that attacked the snake model also uttered significantly greater numbers of vocalizations/30 sec than those birds which did not later attack the snake model (27.0 vs. 11.8/30 sec). However, unlike the attacks on the jays, screams that preceded attacks on the snake model were significantly longer in duration than in catbirds that did not later attack the model (635.7 msec vs. 477.1 msec).

Initial vocalizations that preceded attacks on the jay model contained a greater number of notes, more screams, and fewer meows than those given prior to attacks on the snake model, and were shorter in duration than those given in response to the snake (285.6 vs. 635.7 msec) (Table 1).

The data indicate that vocal parameters, particularly the total number of vocalizations/30 sec, number of screams/30 sec, and the duration of screams, were related to whether a catbird later attacked the predator model. Since the intensity of the response to the model was variable, the data were analyzed with a Spearman Rank Correlation test to determine if any of eight parameters were correlated with the intensity of later nest defense (Table 2). The intensity of later nest defense was positively correlated with the total number of vocalizations/30 sec, number of screams/30 sec, and high frequency of screams in comparison to meows. Neither the duration of notes nor the duration of time between them was correlated with the levels of later aggression toward the predator models.

Discussion

The data show that the initial vocalization patterns of catbirds are related to subsequent form of nest defense, intensity of this defense, and type of predator model positioned at the nest. Birds that ultimately attacked the models and those exposed to the jay model were more likely to respond initially with screams than with meows. Differences were also found in the number of vocalizations per time interval and in such Table 1. Means and analysis of variance data on the relationship between the initial vocal responses of catbirds and the future form of nest defense employed (fate) and type of predator model.

VARIABLE	MAIN EFFECTS						SUBEFFECTS							
36		Fate	Predator				Means			F values				
	attack X	no attack X	F	Blue Jay X	Snake X	F	Snake/ attack X	Snake/ no attack X	Blue Jay/ attack X	Blue Jay/ no attack X	Attack Blue Jay vs Snake	No attack Blue Jay vs Snake	Blue Jay Attack vs No attack	Snake Attack vs No attack
	n = 51	n = 42		n = 49	n = 44		n = 10	n = 34	n = 41	n = 8				
Number of vocalization/ 30 seconds	61.4	15.4	35.2*	63.5	15.2	26.7*	27.0	11.8	70.0	31.0	54.3*	10.9*	44.5*	6.9*
Number of screams/ 30 seconds	60.1	11.0	23.1*	63.5	9.5	46.5*	20.0	6.4	70.0	31.0	67.5*	16.5*	44.5*	5.0*
Number of meows/ 30 seconds	1.4	4.3	0.4	00.0	5.8	23.4*	7.0	5.4	00.0	00.0	24.8*	14.5*	0.0	1.3
Duration of screams (msec)	343.7	406.9	9.8*	282.5	533.2	97.0*	635.7	477.1	285.6	266.5	127.6*	46.2*	0.4	26.5*
Mean duration of all vocaliza- tions (msec)	329.2	467.8	2.6	282.5	515.8	113.0*	581.6	518.1	285.6	266.5	105.7*	76.4*	0.5	4.9
Interval between notes (msec)	483.1	587.6	5.2*	1570.6	4351.0	11.0*	1059.6	5379.6	384.5	7864.8	0.1	1.5	14.1*	4.7
Low fre- quency of screams (kHz)	1.7	1.6	5.6*	1.8	1.4	25.8*	1.2	1.5	1.7	2.0	21.2*	23.6*	5.4*	4.3
High fre- quency of screams (kHz)	7.2	6.5	1.1	7.1	6.7	0.1	7.2	6.6	7.2	6.2	0.1	0.2	1.3	0.5

* Significant at p<0.05

scream-note characteristics as duration and time interval between successive notes. We found similar patterns in an earlier study of nesting robins (*Turdus migratorius*).

Most work on predator-induced vocalizations have been carried out on mammals. Vervet monkeys (*Cercopithecus aethiops*) possess a complex repertoire of predator-specific vocalizations (14,15). Like catbirds and robins, ground squirrels have a much lower diversity of alarm calls. Yet there is evidence that these species are also able to communicate predator identity (10,12). For example, California ground squirrels (*Spermophilus beecheyi*) emit "chatters" and "chats" in the presence of terrestrial predators, and "whistles" when

Table 2. Correlation coefficients of catbird vocalization characteristics and later intensity of nest defense.

Variable	Spearman Correlation Coefficient		
Number of vocalizations/30 seconds	0.58*		
Number of screams/30 seconds	0.59*		
Number of meows/30 seconds	-0.40		
Mean duration of all vocalizations	-0.19		
Duration of screams	0.26		
Interval between notes	-0.36		
Low frequency of screams	0.39		
High frequency of screams	0.52*		

* Significant at p<0.05

raptors are present. While chatters evoked by raptors and terrestrial predators were distinct from each other, those evoked by bobcats, coyotes, and dogs were indistinguishable.

Among mammals the rate of calling has been found to be related to predator type. Ground squirrels thus communicate predator identity through the use of predator-specific vocalizations, graded signals, and rates of calling (11). These findings agree with our own on catbirds. Our study goes further, however, suggesting that the initial vocalizations of catbirds can be correlated with the type and intensity of later defense.

Statistical significance of the data do not necessarily mean that animals are using vocalizations to convey information about predator identity and future patterns of defense. However, there is some evidence that this may be true. During our own experiments, we noted that the vocalizations of birds that ultimately attacked the predator models attracted other birds of both the same and different species to the general area, who in turn were agitated. Other catbirds were tolerated by the experimental birds, and may have even been involved in attacking the predator models. Catbirds that did not ultimately attack the predator models did not attract other birds to the general area of the nest. These observations suggest that nesting birds may use vocalizations as a source of information.

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