SEASONAL VARIATION AND FUNCTION OF MOBBING AND RELATED ANTIPREDATOR BEHAVIORS OF THE AMERICAN ROBIN (TURDUS MIGRATORIUS)

Douglas H. Shedd¹

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14850 USA

ABSTRACT.—American Robins (*Turdus migratorius*) displayed four classes of approach to a Screech Owl (*Otus asio*): silent approach, vocal approach, mobbing, and attacking. Mobbing and attacking were confined to the breeding season. Mobbing first appeared in March and reached a maximum duration per mobbing bird in May and a maximum frequency in June. Mobbing and attacking were most often performed by pairs of robins or by single birds. These responses were directed at a Screech Owl located on the territory of the pair or individual. Silent approach and vocal approach occurred at all times of the year. During the breeding season, birds approached a Screech Owl located on a territory other than their own, observed the owl being mobbed, but joined in mobbing only if the owl flew. Outside the breeding season, robins gathered in large mobile flocks. Birds in such flocks sometimes approached a Screech Owl but did not mob.

I suggest that the contexts in which these responses occurred indicate that mobbing and attacking are beneficial for robins only when birds are confined to territories or home ranges. The presence of young on territories further increases the amount of parental mobbing. *Received 20 August 1980, accepted 4 November 1981.*

MANY species of birds, in diverse orders, are known to exhibit mobbing behavior. The widespread occurrence of this behavior is somewhat surprising, for it often involves an animal seeking out a potentially dangerous predator and performing conspicuous displays near it. That mobbing may be risky is confirmed by reports of mobbing birds being captured by predators (Hartley 1950, Cade 1967, Denson 1979). As a result, the adaptive significance of mobbing has remained largely an enigma, although many hypotheses have been advanced (Marler 1956; Humphries and Driver 1967; Curio 1975, 1978; Cully and Ligon 1976).

Certain aspects of the behavior, however, do suggest possible functions. An association between the breeding season and an increased tendency to mob has been reported in a number of species (Bolles 1890, Altmann 1956, Curio 1975). In some cases actual possession of a nest is necessary for mobbing to occur (Horn 1968). This relationship between mobbing and reproduction indicates that mobbing may be a particularly advantageous response to predators during the breeding season, possibly even serving mainly as a nest-defense mechanism.

The objectives of this study were (1) to test for a breeding season-mobbing association in the American Robin (*Turdus migratorius*), and (2) to investigate the adaptive significance of this association, if it were found.

Methods

From 1 June 1974 through 31 August 1976, field trials were performed on a regular weekly basis. The procedure during these trials was planned to simulate a natural mobbing episode. A mounted Screech Owl (*Otus asio*) was placed in a conspicuous location 2 m from the ground. A recorded Screech Owl call was then played by means of a cassette tape recorder with the speaker located 10 cm from the mounted specimen. The taped calls were played on either a Norelco Tape Cassette Carry-Corder "150" (Model E13302P) or a Panasonic AC/Battery Portable Cassette Recorder RQ-209AS. All trials were observed from concealed positions 10 m from the mount.

Comparative tests showed no significant difference between the response to a stuffed specimen and taped call and the response to a captive live owl and taped call. Observations of birds mobbing wild owls further confirmed the adequacy of the test situation. Using a similar experimental design, Curio (1975) found no difference between the response directed at stuffed specimens and live predators.

¹ Present address: Department of Biology, Randolph-Macon Woman's College, Lynchburg, Virginia 24503 USA.

icant numbers from 1 March through 15 November; a few individuals were present throughout the winter						
Month	Total trials	Successful trials	Total birds	Percentage of successful trials	AMM/B	Average number of birds/success- ful trial
January	35	0	0	0.0	0.0	0.0
February	18	0	0	0.0	0.0	0.0
March	37	2	3	5.4	1.0	1.5
April	59	7	11	11.9	3.2	1.6
May	103	24	36	23.3	5.9	1.5
June	134	44	67	32.8	5.0	1.5
July	151	36	65	23.8	4.1	1.8
August	172	15	15	8.7	2.7	1.0
September	91	0	0	0.0	0.0	0.0
October	95	0	0	0.0	0.0	0.0
November	54	0	0	0.0	0.0	0.0
December	29	0	0	0.0	0.0	0.0

TABLE 1. Percentage of successful trials, average minutes of mobbing/bird (AMM/B), and average number of birds/successful trial for each month (Ithaca, New York). Robins were present on study sites in signif-

Data for many variables were collected during each trial; variables that proved useful include the number of individuals mobbing, the presence or absence of vocalizations and displays, the number of attacks on the predator mount, and the total minutes of mobbing performed by each bird.

Data from the study period were totaled and then treated as a single 12-month series. For each month, the average number of minutes of mobbing per bird (AMM/B) was calculated by summing the minutes of mobbing and dividing by the total number of mobbing birds. Also calculated for each month were the percentage of successful trials (trials that resulted in mobbing) and the average number of mobbing birds per successful trial.

Means for each month were tested for statistical probability of equality using a single classification ANOVA, with means weighted according to the reciprocal of the variance of the samples from which they were drawn. This adjustment results in an approximate test of equality of means when variances are heterogeneous (Snedecor 1956, Sokal and Rohlf 1969).

The fieldwork for this research was carried out in the vicinity of Ithaca, New York. During December and January 1976, trials were also performed at various locations in Florida. The New York study sites consisted mostly of deciduous woodland where beech (Fagus grandifolia) and sugar maple (Acer saccharum) predominate. Floodplains dominated by Fraxinus species and large areas of old field habitat were also sampled. Robins were common in all of these areas from early March until late October, with breeding densities averaging 5-8 pairs/ha.

Testing in Florida was done at Merritt Island National Wildlife Refuge and on Sanibel Island. Both areas contained extensive regions of coastal palmetto (Sabal palmetto) thickets. Robins were abundant in both localities, drawn in part by the fruiting palmetto. Where flocks were present, densities exceeded 1,000 birds/ha. Screech Owls were found at both Florida study sites.

Mobbing behavior is only one phase in a continuum of behavioral responses to a predator that range from fleeing to attacking (Simmons 1952). Although responses intergrade continuously, it is useful to categorize them for purposes of data collection. In this study positive responses (i.e. responses involving movement toward the predator) were divided into four classes:

Silent approach.-In many trials in which either the mounted owl or a captive owl was used, birds were observed locating the owl and then silently observing it for several minutes without vocalizing. Eventually, these birds flew off, usually leaving the vicinity of the owl.

Vocal approach.—Birds vocally approaching a predator gave alarm calls typical of mobbing birds but remained several meters away and exhibited few, if any, of the visual displays typical of mobbing. Such birds seemed to experience little risk of capture.

Mobbing.—Mobbing birds approached a predator closely (within 1 m) and performed a combination of visual displays and vocalizations. Visual displays typical of mobbing consist of intention movements to approach or flee, such as wing-flicking, tail-wagging, and nervous hopping. Mobbing vocalizations are loud and high-pitched. Generally calls are of 0.1 s or less in duration and of a narrow range of frequencies; this combination presumably makes the calls easy to locate (Marler 1959). Both visual displays and vocalizations are frequently repeated during mobbing.

Attacking.-Mobbing birds sometimes suddenly

TABLE 2. Attacks by Robins at study sites in Ithaca,New York. Attacks occurred only from Aprilthrough August.

Month	Total trials	Trials with attacks	Total attacks	Average number of attacks/ trials with attacks
April	59	3	5	1.7
May	103	6	81	13.5
June	134	7	14	2.0
July	151	5	8	1.6
August	172	6	12	2.0

ceased mobbing and pressed an attack directly on the predator. Such attacks consisted of short dashing flights, culminating in strikes on the predator, usually about the head or neck.

RESULTS

Robins were present in Ithaca in significant numbers from early March until middle November (with isolated individuals lingering through the winter), but mobbing was confined to the sampling period extending from March through August (with a single exception noted below). Monthly averages for the AMM/ B index rose during this time from a minimum of 1.0 min of mobbing/bird in March to a maximum of 5.9 in May and then declined to 2.7 in August (P < 0.05, F = 14.759). The average amount of mobbing performed by each bird increased with the advance of the breeding season until May and then declined (Table 1).

The percentage of trials that was successful in producing mobbing among robins rose from a low of 5.4% in March to a peak in June of 32.8%. The percentage then declined to 8.7% in August (Table 1).

During the 6 months in which mobbing was observed, there was no significant change in the number of birds responding during each successful trial (Table 1). Trials in July averaged 1.8 birds/successful trial for a maximum, while in August a minimum of 1.0 was reached (P < 0.05, F = 0.439).

Other responses that were closely related to mobbing also varied seasonally. Robins were observed attacking the owl mount only during the breeding season (Table 2). The number of attacks was highest in May. Attacks were in-

TABLE 3. A	Average number	r of Robins/trial displa	ying
silent or	vocal approach	(SVA/ST) for each mo	nth.
Total tri	als: TT; trials wit	th silent or vocal appro	ach:
ST.		•••	

	Adu	Adult-plumaged birds			Immature- plumaged birds	
Month	TT	ST	SVA/ST	ST	SVA/ST	
New York						
January	35	0	0.0	_	_	
February	18	0	0.0			
March	37	7	2.9	_	_	
April	59	12	1.8		_	
May	103	17	1.5			
June	134	18	1.9	2	1.0	
July	151	32	3.1	35	3.5	
August	172	40	3.4	45	8.0	
September	91	12	3.6	12	5.3	
October	95	24	8.3	—	_	
November	54	1	1.0		_	
December	29	0	0.0			
Florida						
December	57	15	17.9		_	
January	35	11	35.2			

corporated into the general mobbing activities of the birds and consisted of swooping flights toward the mounted owl (usually directly at the head), followed by an abrupt retreat. Only one attack was observed that was not preceded by preliminary displays of mobbing. Robins mobbing wild owls attacked them in a similar fashion.

The behaviors of silent and vocal approach were more common in Ithaca outside the breeding season (Table 3). At the Florida study sites, large numbers of robins were exposed to the owl mount and taped call. None of these birds was observed to mob, although some displayed silent or vocal approach.

Silent approach was typical of immature robins, which were first observed responding in June (Table 3). These birds always arrived after adult birds were mobbing and may have been attracted by the adults' alarm calls rather than by the owl call. By July many immatures were attracted, and most continued to display silent approach. In August the number of immature robins attracted outnumbered adults. At this time immatures responded directly to the owl call and displayed vocal approach. Immature robins were observed to mob on only two occasions (22 July 1974, 11 August 1976).

Discussion

Seasonal variation in mobbing.—Several studies of mobbing behavior have noted an association between this behavior and reproductive activity (Edwards et al. 1949, Root 1969, Curio 1975). In the present study, a peak in mobbing activity occurred in May and June (Table 1), markedly overlapping with the interval of 2 May through 23 June when 70% of the hatching and fledging of young could be expected (Howell 1942). The willingness of robins to mob during the breeding season probably stems from at least two factors: (1) birds are territorial at this time and lack the option of easy relocation away from predators on their territories, and (2) birds are likely to have eggs or young on their territories.

Restriction to a small home range or territory may be an important factor influencing the performance of mobbing. The single instance of postreproductive mobbing by robins observed in this study occurred on one of the New York study sites in January. Two robins, confined to a sumac (*Rhus typhina*) thicket by heavy snows, mobbed vigorously when exposed to the mounted owl and taped call. This was in marked contrast to the response typical of robins outside the breeding season (see below).

The relationship between mobbing and territoriality is further demonstrated by a consideration of Table 1, which indicates that, although the percentage of trials successful in stimulating mobbing increased greatly from March until June, the number of birds mobbing during a successful trial did not vary significantly during this period, always being less than an average of two birds. The territorial distribution of the mobbing birds made it apparent that they were individuals maintaining territories where the Screech Owl was located.

Just as maintenance of a territory seems to have the effect of increasing the intensity of mobbing, a breeding bird's genetic investment in young is likely to have a similar effect. The risk entailed by a mobbing bird would be counterbalanced by an increase in fitness through kin selection if mobbing reduced mortality in that bird's young. If this were true, mobbing intensity would increase as the eggnest unit grew older and parental investment increased. This was observed to occur by Howell (1942) and is suggested by the AMM/B index (Table 1). Mobbing seems to follow a pattern of development during the breeding season similar to that observed in antipredator behaviors such as distraction displays and reactivity to distress calls (Stefanski and Falls 1972, Barash 1975).

The manner in which mobbing may function to reduce predation remains open to debate. Because mobbing by robins is sometimes interspersed with direct attacks on the predator (Table 2), and because mobbing displays are often virtually identical to displays used during territorial encounters with conspecifics, it is likely that mobbing functions in this species to drive predators away. Certainly the advantage inherent in driving a Screech Owl away from a territory is evident from a consideration of the owl's diet, which during the spring may consist predominately of small and mediumsized birds (Allen 1924, Stewart 1969, Van Camp and Henny 1975).

Silent and vocal approaches.—Silent and vocal approaches seem to occur in situations in which the risk of mobbing is greater than any benefits that might result. Silent approach is a low-risk behavior allowing birds to locate and then avoid a predator. Vocal approach may discourage a predator from further hunting without the risk of the close approach necessary for mobbing (see "Perception Advertisement" *in* Curio 1978).

Silent and vocal approaches appear in two contexts: (1) Breeding birds show these responses when locating predators not on their own territories. Observations of the mobbing of live owls revealed that birds from distant territories were often attracted to a mobbing pair but joined in mobbing only if the owl was forced into flight by the mobbers. A similar observation has been made of colonially nesting gulls by Kruuk (1976). (2) Birds show these responses when they abandon territories at the close of the breeding season. All of the birds attracted to the mounted owl and taped call from September until November in New York were such birds (with the single exception of the mobbing pair noted above). Similar responses were obtained in Florida during December and January. The factor most responsible for the cessation of mobbing at the end of the breeding season and the substitution of silent or vocal approaches appears to be the movement of territorial birds into highly mobile nonbreeding flocks. Robins in such flocks would seem to have little to gain by mobbing; it is presumably more adaptive for them to locate a predator and then avoid further contact with it.

The numerous theories currently being proposed as to the function of mobbing have been synthesized by Curio (1978) into nine hypotheses with resultant predictions of prey and predator behavior. Of these hypotheses, some variation of Curio's "Moving on" model seems most consistent with my results. Other factors, however, may be operating concurrently. For example, Curio et al. (1978) suggest the possibility of cultural transmission of information about predators. Such an hypothesis is supported by observations in this study indicating that immature robins respond initially to calls of mobbing adults and closely observe these adults. Because many factors may be operating to cause mobbing, it is useful to keep in mind that many of the proposed hypotheses are not mutually exclusive. Also, given the frequent occurrence of mobbing among groups of unrelated birds (and mammals), it would be unrealistic to hope for an explanation of the function of mobbing that would apply to all species in all situations.

Acknowledgments

This paper is based on a portion of a Ph.D. dissertation submitted to Cornell University. Financial support for this research was provided by the Frank M. Chapman Fund, the Section of Ecology and Systematics, the Peregrine Fund, and a Randolph-Macon Woman's College Humanities Grant. I owe a special debt of gratitude to T. J. Cade for suggesting this research topic and for providing equipment, advice, financial support, and editorial assistance. P. Marks and D. Q. Thompson were also very helpful in many aspects of my research. J. A. Wiens, T. Michalik, W. A. Coulter, and several anonymous reviewers made many valuable comments. Above all, I thank my wife Barbara for her unceasing encouragement and support.

LITERATURE CITED

- ALLEN, A. A. 1924. A contribution to the life history and economic status of the Screech Owl. Auk 41: 1–16.
- ALTMANN, S. A. 1956. Avian mobbing behavior and predator recognition. Condor 58: 241–253.
- BARASH, D. P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the Alpine Accentor. Wilson Bull. 87: 367–372.
- BOLLES, F. 1890. Barred Owls in captivity. Auk 7: 101–114.
- CADE, T. J. 1967. Ecological and behavioral aspects of predation by the Northern Shrike. Living Bird 6: 43–86.

- CULLY, J. F., & J. D. LIGON. 1976. Comparative mobbing behavior of Scrub and Mexican jays. Auk 93: 116–125.
- CURIO, E. 1975. The functional organization of antipredator behaviour in the Pied Flycatcher: a study of avian visual perception. Anim. Behav. 23: 1–115.
- . 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. Z. Tierpsychol. 47: 175–183.
- ——, U. ERNST, & W. VIETH. 1978. The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. Z. Tierpsychol. 48: 184–202.
- DENSON, R. D. 1979. Owl predation on a mobbing Crow. Wilson Bull. 91: 133.
- Edwards, G., E. Hosking, & S. Smith. 1949. Reactions of some passerine birds to a stuffed Cuckoo. Brit. Birds 42: 13–19.
- HARTLEY, P. H. T. 1950. An experimental analysis of interspecific recognition. Symp. Soc. Exp. Biol. 4: 313–336.
- HORN, H. S. 1968. The adaptive significance of colonial nesting in Brewer's Blackbirds (*Euphagus cyanocephalus*). Ecology 49: 682–694.
- HOWELL, J. C. 1942. Notes on the nesting habits of the American Robin. Amer. Midl. Natur. 28: 529–603.
- HUMPHRIES, D. A., & P. M. DRIVER. 1967. Erratic displays as a device against predators. Science 156: 1767–1768.
- KRUUK, H. 1976. The biological function of gulls' attraction toward predators. Anim. Behav. 24: 146–153.
- MARLER, P. 1956. Behaviour of the Chaffinch, Fringilla coelebs. Behav. Suppl. 5: 1–184.
- Root, R. 1969. The behavior and reproductive success of the Blue-gray Gnatcatcher. Condor 71: 16–31.
- SIMMONS, K. E. L. 1952. The nature of predator reactions in breeding birds. Behaviour 4: 161–171.
- SNEDECOR, G. W. 1956. Statistical methods. Ames, Iowa, Iowa State College Press.
- SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman.
- STEFANSKI, R. A., & J. B. FALLS. 1972. A study of distress calls of Song, Swamp, and Whitethroated sparrows (Aves: Fringillidae). I. Intraspecific responses and functions. Can. J. Zool. 50: 1501–1512.
- STEWART, P. A. 1969. Prey in two Screech Owl nests. Auk 86: 141.
- VAN CAMP, L. F., & C. J. HENNY. 1975. The Screech Owl: its life history and population ecology in northern Ohio. North American Fauna No. 71.