RESPONSES OF NORTHERN HARRIERS TO MOBBING PASSERINES

By Keith L. Bildstein

With the exception of a few detailed investigations (Andersson 1976, Collias and Collias 1978, Curio et al. 1978, Vieth et al. 1980), most studies of avian mobbing behavior have been either manipulative (i.e. presenting potential mobbers with a variety of objects in attempts to determine proximate causation, see for example Shalter 1978) or anecdotal. In a recent review Curio (1978) listed potential functional explanations for mobbing including (1) advertising recognition of the predator's presence (see for example Smythe 1970), (2) cultural transmission leading to site avoidance by the mobbers (Sparks and Soper 1970), and (3) harrassing the predator into leaving an area. But as Curio (1978) notes, his list is not exhaustive, and in any case only two of his predictive tests, involving three hypothetical functions, are mutually exclusive. One of these mutually exclusive tests involves predictions based on the harassment of the predator and the cultural transmission of site hypotheses. While the former predicts a predator should leave the mobbing site immediately and possibly avoid it later on, the latter predicts that the mobbers will avoid the site later on as the predator is likely to return to it. Here I detail observations of passerines mobbing Northern Harriers (Circus cyaneus) and use these data to test the harrassment and cultural transmission of site hypotheses.

METHODS

Observations were made from 15 through 30 June 1979 on the Leola (Adams County) and Buena Vista (Portage County) marshes in central Wisconsin (for a description of the area see Hamerstrom 1969). During that time I watched 3 male harriers on 7 days between 4 and 10.5 h each day for a total of 54.8 h. All observations were made from a 2.4 m tower, using a $15-60 \times$ zoom telescope, tape recorder, and stop-watches. I maintained constant visual contact with the harriers except for the few instances (<1% of the time) when they perched out of sight on the ground in dense vegetation. At the time of the observations, the males were supplying food to their mates, who were either incubating eggs and/or brooding young chicks.

The times each bird spent perched, flying, and whether or not it possessed prey were recorded. I recognized 4 types of flight: (1) soaring and/or gliding, (2) transect flight, (3) quartering, and (4) border following. Soaring and gliding were defined as prolonged non-stationary, nonpowered flight. Transect flight was rather straight-line powered flight, with fewer than 5 sharp (>30°) turns per min. Quartering was powered flight to and fro over short distances, with more than 5 sharp turns per min. Border following was powered flight within 5 m of land type and/ or vegetation type edges, such as fence rows, ditches, ditch banks, or roadsides. To be certain that a bird was actively following a border and not merely flying near it by chance, I counted as border following only those instances in which the bird either doubled back and retraced its path along the border or turned at least once to follow the course of a meandering border. These flight types were quite recognizable, with shifts from one pattern to another easily discerned. When a harrier was mobbed I noted (1) its dominant flight type during the 1 min periods prior to and following the onset of the encounter, (2) the species of birds mobbing, (3) the number of individuals mobbing, and (4) the total number of times the mobbers closed to within 1 m of the harrier.

Although formal definitions of mobbing frequently include such terms as "group" (Alcock 1975), "joint assault" (Wilson 1975), and "swarm" (Heymer 1977), mobbing encounters are often initiated by single birds. Whether or not an individual manages to secure the assistance of additional mobbers by its actions (acoustical or visual), mobbing begins with the single individual (see also Kirby and Fuller 1978). Therefore I include in my analyses passerine-induced interactions involving a single mobber and a harrier.

Significance levels were found with Chi-square, Fisher's Exact, and extended median tests (Siegel 1956).

RESULTS

The 3 male harriers spent 68% of their time in flight, presumably searching for prey, which they caught on 39 occasions (Table 1). Three of the prey were small sparrows (Fringillidae), snatched as they flushed from vegetation in front of the harrier. The remainder (92%) were voles (*Microtus* spp.). The 3 harriers were mobbed 112 times (2.04 times/h) during the study by 5 species of passerines (Table 2). All mobbing flocks were monospecific, and for the sexually dimorphic species (Red-winged Blackbird, Brown-headed Cowbird, and Common Grackle) all mobbers, with the exception of 8 female Red-winged Blackbirds, were males. Mobbing encounters lasted from 2 to 105 sec and involved flocks of up to 6 individuals.

The frequency of mobbing varied with both harrier activity and whether or not the harrier possessed prey. Despite the fact that the 3 harriers were perched during almost 30% of my observation time, perched harriers were never mobbed. In contrast, flying harriers, especially those carrying prey, were mobbed frequently. Based on the expectation that the relative number of mobbing encounters observed while harriers were perched or flying should reflect the relative amount of time harriers spent in each of these activities, perched harriers were mobbed less than expected and flying harriers more than expected (Chi-square test for goodness of fit, P < .05; Fig. 1). Harriers spent too little time carrying prey to test for a significant difference then, but when they did carry prey, harriers were more than 6 times as likely to be mobbed as when they flew without prey.

	Harrier			Weighted
	1	2	3	mean
Percent of time:				
Perched	37	22	25	29
Flying without prev	62	76	73	68
Flying with prey	1.5	2.3	2.4	1.9
Number of prey captures	16	18	5	
Number of times mobbed	30	57	25	
Number of hours observed	28	20	6.8	

TABLE 1. Behavior of three male harriers in Wisconsin.

As harrier activity did not significantly affect whether there was one or more than one mobber (Fisher's Exact test, P > .50), or the number of close approaches per mobbing encounter (extended median test, P > .10), or the number of close approaches per mobber (extended median test, P > .10), I pooled these data, ignoring harrier activity, and tested for differences in single versus multi-bird mobbing encounters. The number of close approaches per mobbing encounter was greater when more than one bird mobbed (extended median test, P < .001), also the number of close approaches per bird tended to be greater in multi- than in single-bird encounters (extended median test, .10 > P > .05; Table 3).

Harriers almost always tried to avoid mobbing passerines. This was true even when there was only one mobber. Responses varied but often included rapid chattering calls of excitement (Brown and Amadon 1968), looking back over the wings at pursuing passerines, stalling and/ or rolling (especially in response to imminent stoops), increasing flight elevation, and changing flight type.

Harriers that were either quartering or border following were more

Species	Number of times mobbing	Mean number of individuals per encounter
Red-winged Blackbird (Agelaius phoeniceus)	102 (91) ¹	$1.30 \pm .81^2$
Eastern Kingbird (Tyrannus tyrannus)	4 (4)	$1.25 \pm .50$
Brown-headed Cowbird (Molothrus ater)	4 (4)	$1.00 \pm .00$
Barn Swallow (Hirundo rustica)	1(1)	1
Common Grackle (Quiscalus quiscula)	1 (1)	1

TABLE 2. Species and numbers of birds mobbing harriers.

¹ N (percent of total).

² Mean \pm SD.



FIGURE 1. Expected versus observed percent occurrence of mobbing in perched and flying male Northern Harriers (* indicates difference is significant at the .05 level using a Chi-square test for goodness of fit; N.T. indicates no test because of a small sample size).

	Harrier			
	Flying with prey	Flying with- out prey	Mean	
One bird mobbing	$4.4 \pm 7.0 \ (11)^1$	3.2 ± 3.3 (78)	3.3 ± 3.7	
More than one bird mobbing (per encounter)	8.2 ± 8.4 (6)	$9.5 \pm 7.7 (17)$	9.2 ± 8.1	
More than one bird mobbing (per bird) ²	3.1 (6)	4.2 (17)	3.9	

TABLE 3. Number of stoops directed at harriers by mobbing passerines.

¹ Number of stoops \pm SD (N).

² Derived by dividing the number of stoops per flock by the number of birds in the flock. Since the number of stoops by individual flock members is unknown, standard deviations were not computed.

likely to change their flight pattern upon being mobbed than were harriers in transect flight (Chi-square test for heterogeneity, P < .001). All harriers that were transect flying, either with (17 times) or without prey (12 times) when they were mobbed, continued in transect flight. On the other hand, in the 83 mobbings where harriers were either border following (8 times) or quartering (75 times) at the onset, most (86%) switched to transect flight and appeared to increase their flight speed following mobbing.

DISCUSSION

Most of my observations consist of a single mobber (Table 2). As it is possible that the reason individuals initiate mobbing sequences differs from the reason additional birds join ongoing interactions, I limit my initial discussion to why passerines initiate mobbing encounters.

Even when they were mobbed by single passerines, harriers quartering and following a border almost always increased their flight speed and changed to transect flight. Both responses resulted in the hawk moving away from the assailants. This type of predator response was predicted by Curio (1978) if the function of initiating a mobbing encounter was to induce the predator to "move-on," either as a result of (1) harassment by the mobbers (Curio's move-on hypothesis) or (2) the advertisement of perception of the predator by the mobbers (Curio's advertisement of perception hypothesis). This type of predator response was not predicted by Curio if the function of initiating a mobbing encounter was (3) cultural transmission leading to site avoidance by the mobbers. As Curio (1978) noted, it is not possible to discriminate between the first two hypotheses solely on the above response. But while both predict a predator should leave an area upon mobbing and possibly refrain from using the area in the future, the harassment hypothesis is supported and the perception advertisement hypothesis weakened by the fact that the mobbers I watched stooped closely on the harriers. This close, apparently aggressive approach of mobbers toward harriers seems to harass those predators, and it would certainly not be necessary for mobbers to engage in this potentially dangerous behavior (see below) if they were only attempting to inform a predator that it had been detected.

Perched harriers were never mobbed. Similarly, Hen Harriers (C. c. cyaneus) in Scotland (Watson 1977), Marsh Harriers (C. aeruginosus) in England (Hosking 1943), and Australasian Harriers (C. a. approximans) in New Zealand (Baker-Gabb 1978) all appear to be mobbed more intensely when flying than when perched. Hamerstrom (1956), working with a tame Red-tailed Hawk (Buteo jamaicensis) and holding perch site constant, noted that her bird was mobbed more frequently when it was hungry than when it was well fed. Also, although her hawk was never mobbed when it soared, it was mobbed consistently when it assumed a low, hunting flight pattern. Cade (1967) reported a similar activity-related likelihood of being mobbed for the Northern Shrike (Lanius ex-

cubitor). As passerines often mob perched individuals of other raptorial species, and as the harriers I watched usually perched above the surrounding vegetation on fence posts and were quite conspicuous there, I do not believe flying harriers were mobbed while perched harriers were not simply because flying individuals were more easily detected. Harriers hunt almost exclusively on the wing (600 of 601 observed pounces in south central Ohio, Bildstein 1978), and I believe passerine mobbing was directed at hunting rather than non-hunting harriers. Approaching and mobbing a raptor can increase a passerine's vulnerability to predation (see for example Meinertzhagen 1959, Denson 1979), in fact, several raptors appear to elicit mobbing as a hunting behavior (Smith 1969, Thurow and Black 1981). As perched harriers pose no immediate threat to prev in the vicinity, individuals mobbing at this time might increase their risk to predation with little or no immediate benefit. On the other hand, passerines harassing hunting harriers could receive an immediate benefit by forcing the harrier on.

Recent studies indicate that predators are mobbed more frequently when they possess either conspecific (Barash 1976, Kruuk 1976, Augst 1977) or heterospecific prey (Cade 1967, Augst 1977). The male harriers I watched were mobbed more frequently when they carried prey despite the fact that they were almost always (92%) carrying voles rather than passerines. Twice when a harrier without prey was mobbed, it was carrying nesting material. As mobbing birds always approached harriers to within several meters, I doubt they mistook the carried items for conspecifics. Therefore I suggest that prey-carrying harriers elicited stronger reactions than harriers without prey because the former posed a reduced threat to potential mobbers. Also, as harriers tend to return to sites of previous prey captures, it may be especially important for birds near a capture site to harass a harrier regardless of whether the prey is a conspecific.

While my observations support the harassment hypothesis with regard to the initial mobber, they do not explain the behavior of additional mobbers. If there is a risk incurred by mobbers, why do birds join ongoing mobbing encounters? Why don't they cheat? First, it may be that in some instances group efforts are substantially more effective in harassing predators and driving them from an area while group mobbers run a substantially reduced individual risk compared to single mobbers. Second, other factors, including cultural transmission of enemy recognition (Cully and Ligon 1976, Curio et al. 1978, Vieth et al. 1980) may be important. Additional field work on group mobbing is needed to resolve these questions.

SUMMARY

Northern Harriers were harassed by both single and grouped passerines. Most harriers hunting by quartering and by following borders increased their flight speed and changed to straight-line powered flight. Both responses increased the distances between the harriers and their assailants. These data support the notion that mobbing functions to harass harriers, inducing them to "move-on." Frequency of mobbing varied with both activity and whether the harrier possessed prey. Perched harriers were never mobbed. On the contrary, hunting harriers and those with prey, were mobbed frequently. These data indicate that mobbing is more likely to occur when the benefits derived from it outweigh any increase in vulnerability.

ACKNOWLEDGMENTS

I thank Eberhard Curio, Mark Fuller, Tom Grubb, Jr., J. A. Jackson, N. R. Liley, William Shields, Chris Stinson, and two anonymous reviewers for their comments on earlier drafts of the manuscript, F. and F. N. Hamerstrom for their gracious hospitality during my studies in Wisconsin, and the Wisconsin Department of Natural Resources for allowing me to work on areas they manage. The Winthrop Research Council provided financial support for my work.

LITERATURE CITED

- ALCOCK, J. 1975. Animal behavior: an evolutionary approach. Sinauer, Sunderland, Mass.
- ANDERSSON, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118:208-217.
- Augst, H.-J. 1977. Meisen (Parus) erkennen den Grad der Gerfährdung durch einen Feind. J. Ornithol. 118:301-305.
- BAKER-GABB, D. J. 1978. Aspects of the biology of the Australasian Harrier (Circus aeruginosus approximans Peale 1948). M.S. thesis, Massey University, Palmerston North, New Zealand.
- BARASH, D. P. 1976. Mobbing behavior by crows: the effect of the "crow-in-distress" model. Condor 78:120.
- BILDSTEIN, K. L. 1978. Behavioral ecology of Red-tailed Hawks, Rough-legged Hawks, Northern Harriers, American Kestrels, and other raptorial birds wintering in south central Ohio. Ph.D. diss., Ohio State University, Columbus.
- BROWN, L., AND D. AMADON. 1968. Eagles, hawks, and falcons of the world. McGraw-Hill, New York.
- CADE, T. J. 1967. Ecological and behavioral aspects of predation by the Northern Shrike. Living Bird 6:43-86.
- Collias, N. E., and E. C. Collias. 1978. Group territory, dominance, cooperative breeding in birds, and a new factor. Anim. Behav. 26:308-309.
- CULLY, J. F., JR., AND J. D. LIGON. 1976. Comparative mobbing behavior of Scrub and Mexican jays. Auk 93:116–125.
- CURIO, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. Z. Tierpsychol. 48:175-183.
 - -, Ú. ERNST, AND 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. HAMERSTROM, F. 1956. The influence of a hawk's appetite on mobbing. Condor 59:192-194.

. 1969. A harrier population study. Pp. 367-383, in J. J. Hickey (ed.), Peregrine Falcon populations; their biology and decline. Univ. Wisconsin Press, Madison.

- HEYMER, A. 1977. Ethological dictionary. Verlag Paul Parey, Berlin.
- HOSKING, E. J. 1943. Some observations on the Marsh Harrier. Br. Birds 37:2-10.
- KIRBY, R. E., AND M. R. FULLER. 1978. Observations and reinterpretation of kingfisherraptor interactions. Auk 95:598-599.

- KRUUK, H. 1976. The biological function of gulls' attraction toward predators. Anim. Behav. 24:146-153.
- MEINERTZHAGEN, R. 1959. Pirates and predators. Oliver and Boyd, London.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
- SHALTER, M. D. 1978. Studies of mobbing behavior abound. J. Ornithol. 119:462-463.
- SMITH, N. G. 1969. Provoked release of mobbing—a hunting technique of Micrastur falcons. Ibis 111:241-243.
- SMYTHE, N. 1970. On the existence of "pursuit invitation" signals in mammals. Am. Nat. 104:491-494.
- SPARKS, J., AND T. SOPER. 1970. Owls: their natural and unnatural history. David and Charles, Newton Abbot.
- THUROW, T. L., AND H. L. BLACK. 1981. Ecology and behavior of the Gymnogene. Ostrich 52:25–35.
- VIETH, W., E. CURIO, AND U. ERNST. 1980. The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: cross species tutoring and properties of learning. Anim. Behav. 28:1217–1229.
- WATSON, D. 1977. The Hen Harrier. Poyser, Berkhamsted, U.K.
- WILSON, E. O. 1975. Sociobiology: the new synthesis. Belknap, Cambridge, Mass.

Department of Biology, Winthrop College, Rock Hill, South Carolina 29733. Received 15 Mar. 1981; accepted 20 Oct. 1981.