MERINO, S., AND J. POTTI. 1995. Mites and Blowflies decrease growth and survival in nestling Pied Flycatchers. Oikos 73:95–103.

MØLLER, A. P. 1989. Parasites, predators, and nest boxes: facts and artefacts in nest box studies of birds. Oikos 56:421–423.

MØLLER, A. P. 1992. Nest boxes and the scientific rigour of experimental studies. Oikos 63:309–311.

OPPLIGER, A., H. RICHNER, AND P. CHRISTE. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the Great Tit (*Parus major*). Behav. Ecol. 5:130–134.

ORELL, M., S. RYTKÖNEN, AND K. ILOMÄKI. 1993. Do Pied Flycatchers prefer nest boxes with old nest material? Ann. Zool. Fenn. 30:313–316.

POTTI, J., AND S. MERINO. 1994. Heritability estimates and maternal effects on tarsus length in Pied Flycatchers, *Ficedula hypoleuca*. Oecologia 100: 331–338.

POTTI, J., AND S. MONTALVO. 1991. Return rate, age at first breeding and natal dispersal in a Spanish population of Pied Flycatchers, *Ficedula hypoleuca*. Ardea 79:419–428.

RICHNER, H., A. OPPLIGER, AND P. CHRISTE. 1993. Effect of an ectoparasite on reproduction in Great Tits. J. Anim. Ecol. 62:703–710.

THOMPSON, C. F., AND A. J. NEILL. 1991. House Wrens do not prefer clean nestboxes. Anim. Behav. 42: 1022–1024.

The Condor 97:831–834

MOBBING OF EASTERN SCREECH-OWLS: PREDATORY CUES, RISK TO MOBBERS AND DEGREE OF THREAT[1]

FREDERICK R. GEHLBACH AND JILL S. LEVERETT[2]
Department of Biology, Baylor University, Waco, TX 76798

Key words: Cultural tutoring; Eastern Screech-Owl; kin selection; mobbing behavior; Otus asio; *predatory cues.*

Avian mobbing of raptorial birds is a common response to potential threat and may warn prey and teach naive individuals about the danger or deter predation (Altmann 1956; Vieth et al. 1980; Frankenberg 1981; Curio et al. 1978, 1983). Birds are important prey of Eastern Screech-Owls (*Otus asio*) in the spring nesting season (Van Camp and Henny 1975, Turner and Dimmick 1981, Gehlbach 1994); and frequent mobbers of the owls are those songbirds most often eaten, including permanent residents and males (Gehlbach 1994). Studies of screech-owls suggest that mobbing is most intense in the spring-early summer nesting period (Altmann 1956; McPherson and Brown 1981; Shedd 1982, 1983; Chandler and Rose 1988; Gehlbach 1994).

Eastern Screech-Owls sing two seasonally distinct songs (Hough 1960, Ritchison et al. 1988). Their monotonic trill is a nest-site advertisement and family-contact song, primarily while nesting in spring–early summer, whereas the descending trill is a territorial defense signal largely in late summer–fall (Gehlbach 1994). Mobbing songbirds orient to these songs and owl nest and roost sites (McPherson and Brown 1981, Chandler and Rose 1988, Gehlbach 1994). Mobbing is often seen near active nests, where the owls do most monotonic singing and hunting, so it may be keyed to site or song. Despite such focus, fledgling screech-owls in the nest area are seldom mobbed and then only mildly, presumably because they do not kill birds (Gehlbach 1994).

If the mobbers of Eastern Screech-Owls correctly assess risk as some European birds do (Curio et al. 1983), males and permanent residents should respond to the owls' monotonic trills more often, longer, or more intensely than its descending trills, especially in the spring near nests. Also, they should mob adult owls more than fledglings. These postulates have not been tested, and some experimental variables have been confounded in the past. Earlier investigators, for example, induced mobbing with tapes of combined songs (McPherson and Brown 1981) or did not mention the song(s) they used (Shedd 1982, 1983; Chandler and Rose 1988).

Because we conducted mobbing experiments in an area where Eastern Screech-Owls and their avian prey had been studied (Gehlbach 1994), we devised very specific tests. We wanted to know if mobbers correctly assess risks of predation by recognizing certain visual (plumage, nest-site area) and auditory (song) cues with respect to the seasonal variation in these cues. Previously, this has not been possible with any raptor, nor has mobbing been tested as regards the relative jeopardy or reproductive investment of specific mobbers

[1] Received 9 January 1995. Accepted 21 March 1995.
[2] Present address: 742 NE 15th St., Oklahoma City, OK 73104.

including male versus female Northern Cardinals (*Cardinalis cardinalis*), and the brown- versus white-crowned morphs of White-throated Sparrows (*Zonotrichia albicollis*).

STUDY SITES AND METHODS

Two study sites were located, methods tested, and experiments conducted along a path through a seminatural riparian deciduous forest (mean tree height 6 m, density 1,504/ha) in Woodway, McLennan Co., Texas, 1991–1993. Three pairs of Eastern Screech-Owls foraged and two nested in the immediate area. Study sites were 20 m from an active screech owl nest (the nest site) and 125 m away from the nearest owl nest (non-nest site). The two sites had the same species of permanent residents and continued presence of the same species of seasonal residents but not passage migrants which were a minor element in mobbing (see below).

Three trials with montonic trills and three with descending trills were conducted at each site in fall (late September–early October, deciduous trees with leaves, no nesting), again in winter (December, trees bare, no nesting), and in early spring (late February–early March; leaves appearing, earliest owls and mobbers nesting). Songs were presented randomly per site each season. Trials were at least two days apart in the hour after sunrise on clear-cloudy calm mornings over three weeks per season. A partly hidden observer sat 10 m from a gray, adult, male Eastern Screech-Owl, freeze-dried in roosting posture, fastened to an open tree limb 2 m high, 1.5 m from the trunk. Song bouts of local *O. a. hasbrouckii* were played at 85 dB (2 m) for 5 min from a tape recorder hidden below the owl on the ground.

A fourth set of three trials with each song at each site was conducted in late spring (late May–early June, leaves out, fledgling-dependency period). This time a freeze-dried, roosting, fledgling screech-owl (juvenal plumage) was fastend to an open tree limb 2 m high, 3 m from the same adult owl on the opposite side of the tree (trees different from early spring). Mobbing responses were considered specific to a particular owl if they occurred on or in its 180° portion of the tree as seen by the observer sitting equidistantly from both owls. All other parameters were the same as before except that the hidden tape player was placed halfway between the two owls.

Data were tape recorded as: (1) date, song, and site, (2) species, individuals, sexes, color morphs of birds responding, (3) individual arrival time in min after song initiation, (4) individual response duration in min, (5) individual response intensity measured as 1 = called > 3 m from owl, 2 = approached 2–3 m without vocalizing, 3 = approached 2–3 m and vocalized, 4 = approached < 2 m from owl without vocalizating, 5 = approached < 2 m and vocalized (cf. Shedd 1982). Some mobbers might have been sampled more than once, but the random presentation of songs, different tree perches, and > 8 week interval between seasonal samples should have reduced resampling and offset tendencies for habituation.

Sites, owl songs, and seasons were analyzed in three-way factorial analyses of variance (ANOVAs) using total species, total individuals, and average arrival time, response duration, and response intensity as criteria of mobbing. They were also analyzed using total species and individuals of permanent residents versus seasonal residents plus passage migrants. Fledgling versus adult owls, the two songs, and both sites, were assessed likewise. Sexes of Northern Cardinals and morphs of White-throated Sparrows plus songs, sites, and seasons (winter, early spring only for sparrows) were analyzed with the same criteria in four-way ANOVAs. Multiple means were assessed with Least Significant Differences (LSD) tests.

All data were log-transformed before analysis. The alpha level of statistical significance was $P = 0.05$; although we consider $P = 0.06$–0.10 as suggesting significance for variable interactions because of our prior knowledge of mobbing behavior in the same area (Gehlbach 1994). Summary statistics are mean differences when contrasting responses to different songs, sites, and seasons, or mean ± one standard error of the untransformed data.

RESULTS

We observed 33 episodes of mobbing in 48 trials (some trials produced no responses or data were lost due to tape recorder malfunction). Eleven species of permanent residents (PR), seasonal residents (SR), and passage migrants (PM) mobbed: *C. cardinalis* (19 times, PR), *Parus carolinensis* (16 times, PR), *Z. albicollis* (11, SR), *Parus bicolor* (7, PR), *Cyanocitta cristata* (5, PR), *Thryothorus ludovicianus* (3, PR), *Turdus migratorius* (3, SR), *Vireo griseus* (2, SR), *Picoides pubescens* (1, PR), *Icterus galbula* (1, PM), *Archilochus* sp. (1, SR).

Permanent residents outnumbered seasonal residents plus passage migrants in all trials (4.9 ± 1.4 vs 2.0 ± 0.6 individuals and 1.5 ± 0.2 vs 0.8 ± 0.1 species, respectively, $F > 2.2$, $P < 0.04$). Both groups responded most often to monotonic trills, whether measured by individuals or species ($F > 5.3$, $P < 0.03$), but may have been affected seasonally (song-by-season interaction $F > 2.9$, $P < 0.07$).

In winter White-throated Sparrows were present in flocks of 12–27 individuals versus 7–13 per species of permanent residents. Nevertheless, White-throated Sparrows participated in only 63% of mobs while present in the area (late October–late April). Despite their numbers, they averaged only 3.6 ± 1.1 individuals per mob compared to 5.3 ± 1.0 individuals of the best represented permanent resident in the same mobs (paired $t = 2.8$, two-sided $P = 0.01$).

Responses to song of all mobbers together varied seasonally as measured by species, individuals, duration, and intensity ($F > 5.3$, $P < 0.01$). Thirteen times more individuals mobbed monotonic than descending trills in winter, dropping to five times more in early spring and two more in fall. Birds mobbed monotonic trills longer and more intensely in early spring, but the mobbing of descending trills was 1.5 times longer and 1.3 times more intense in fall than in the other seasons.

Overall, monotonic trills attracted three times more species and seven times more individual mobbers than descending trills ($F > 11.5$, $P < 0.005$; Table 1). Duration of mobbing also varied with song type ($F = 5.2$, $P = 0.03$) as did mobbing intensity ($F = 12.3$, $P =$

TABLE 1. Means ± standard errors of avian mobbing criteria that distinguish seasonal and spatial features of the Eastern Screech-Owl as a predator. Data are from single-owl trials of the monotonic versus descending songs at both sites in all seasons (n = 18/song), nest versus non-nest sites using both songs in all seasons (18/site), and the three seasons using both songs and both sites (12/season, * = $P < 0.05$ in LSD tests).

Criteria	Songs		Sites		Seasons		
	Monotonic	Descending	Nest	No nest	Fall	Winter	Early spring
Species responding	2.4 ± 0.4*	0.8 ± 0.2	1.6 ± 0.3	1.5 ± 0.4	1.5 ± 0.5	1.9 ± 0.4	1.3 ± 0.4
Individuals responding	8.5 ± 2.3*	1.2 ± 0.3	5.4 ± 2.1	4.4 ± 1.6	2.6 ± 1.1	9.4 ± 3.2*	2.2 ± 0.8
Response duration	3.4 ± 0.4*	1.8 ± 0.5	3.1 ± 0.6*	2.0 ± 0.5	2.1 ± 0.9	2.8 ± 0.6	3.1 ± 0.5*
Response intensity	3.3 ± 0.4*	1.2 ± 0.3	2.3 ± 0.4	2.1 ± 0.5	2.2 ± 0.6	2.1 ± 1.9	2.9 ± 0.6*
Arrival time	1.6 ± 0.3	1.9 ± 0.8	1.0 ± 0.2	2.5 ± 0.8	2.2 ± 1.3	1.8 ± 0.4	1.4 ± 0.5

0.002). Both criteria were most responsive to monotonic trills (Table 1).

In late spring the adult owl was mobbed by 1.5 times more individuals than the fledgling (F = 10.7, P = 0.01); and, as measured by mob duration and intensity, the adult also received more attention ($F > 60.1$, $P < 0.001$). Also, mobbers were more numerous near the owl's nest site in late spring (F = 16.3, P = 0.004), but site influenced duration and intensity in all seasons ($F > 5.9$, $P < 0.04$). Generally, mobbing was longer and more intense near the owl nest (Table 1).

More male than female Northern Cardinals mobbed (1.1 ± 0.2 versus 0.5 ± 0.1; F = 14.7, P = 0.001), although this may have been seasonal (sex-by-season interaction, F = 3.2, P = 0.06). Also, males mobbed longer than females (3.8 ± 2.4 min versus 2.2 ± 2.0 min; F = 9.5, P = 0.007) with a possible seasonal difference (sex-by-season F = 3.3, P = 0.06). More white- than brown-crowned White-throated Sparrows mobbed (2.7 ± 0.5 versus 0.9 ± 0.1; F = 3.6, P = 0.002) but without differences in other criteria or song, site, and season.

Arrival time was the only insignificant criterion of mobbing, although birds tended to appear quicker in response to monotonic than descending trills, quicker near the nest site and in winter and early spring (Table 1). But arrival time was difficult to record, as some birds stayed on the periphery of mobs, indicating minor if any participation. Many peripheral individuals were female or fledgling (black-billed juvenal) Northern Cardinals and brown-crowned White-throated Sparrows, all probable subdominant flock members (Ficken et al. 1978; Gehlbach, unpubl.).

DISCUSSION

The 11 species of mobbers were among 31 noted by Gehlbach (1994) in 134 groups that mobbed Eastern Screech-Owls in the same area over a 25-year period prior to this study. Furthermore, they mobbed in the same hierarchical order (r_s = 0.70, P = 0.03). Such species-specific behavior over many generations suggests rather precise assessment of risk and hence a selective advantage to particular mobbers that adjust their degree of involvement to degree of jeopardy or perhaps reproductive investment.

Mean number of individuals per mob was also similar (6.4 versus 7.2; F = 0.3, ns). Moreover, Altmann (1956) noted a mean of 6.1 per mob of avian predators, including screech-owls, and McPherson and Brown (1981) in studying screech owls had means of 8.4 and 10.2, which are not significantly different from our value or Gehlbach's ($F < 1.8$, ns). The owls are not driven away by mobbing (McPherson and Brown 1981, Gehlbach 1994), so large numbers of mobbers would not serve the predator-displacement function sometimes ascribed to this behavior.

Instead, the risk to mobbers may be reduced by few participants. That mobbers are a select few, mostly dominant, flock members is suggested by the greater participation of male and adult Northern Cardinals and white-crowned White-throated Sparrows. As permanent residents adult cardinals should be most knowledgable about screech owls as predators, have investments in offspring and, therefore, be greater risk takers (cf. Breitwisch and Hudak 1989). Subdominants, including possible naive juveniles, remained on the periphery of mobs where they may learn through cultural transmission (Curio et al. 1978) while reducing their risk of predation.

Most mobbers were permanent residents with a greater likelihood of predation due to their relative abundance and constant presence in the avian prey community (Gehlbach 1994). Also, male Northern Cardinals were greater mobbers than females, like male Great Tits (*Parus major,* Curio et al. 1983), probably because of their dominant status (Gehlbach, unpubl. data). Since males and permanent residents do not reduce their considerable jeopardy by more mobbing (Gehlbach 1994), their fitness may be increased by tutoring relatives in the context of kin selection.

All birds mobbed monotonic trills more frequently, longer, and more intensely than descending trills, especially in spring, surely recognizing that this song signals the greatest likelihood of predation. Even seasonal species responded primarily to monotonic trills. Some White-throated Sparrows could learn this predatory

cue from direct experience, but most breed north of the Eastern Screech-Owl's range and must learn elsewhere, perhaps through interspecific associations on their winter range. Cross-cultural tutoring is possible, since White-throats mobbed more often with permanent residents than alone and with other seasonal species (82% of mobs, $\chi^2 = 4.5$, $P = 0.03$).

Although the descending trill was mobbed more intensely and longer in fall, the "correct" season for this song, it is territorial defense and cannot be associated with predation in the manner of monotonic trilling. Even so, the fall mobbing of descending trills should signal predator location and promote avoidance by songbirds, since screech owls are found as readily by means of song in fall as in other seasons. The owl's cryptic plumage suggests that song is an important signal at any season.

Precise visual signals are also important, because mobbing was directed primarily at the adult screech owl, not the fledgling, regardless of song (Chandler and Rose 1988). At the same time, proximity of the owl's nest made a difference to mobbers, who were more numerous and persisted longer and more intensely near the nest. They must determine the increased risk of predation associated with this feeding site and remember its significance. In fall and winter Eastern Screech-Owls forage more widely, as their offspring have dispersed (Gehlbach 1994), but mobbing was strongest near the owls' permanent nest site in all seasons.

Avian mobbers correctly assess the danger of predation by Eastern Screech-Owls, which changes according to predator ability and seasonal demand. They use seasonal song, age-related plumage, and nest-area cues appropriately, all three together or separately "as needed"; and mob to a degree consistent with their dominance ranking and potential reproductive investment. We suggest that avian mobbing tutors offspring and non-relatives, even seasonal species, about predatory danger and benefits relatives through kin selection.

Editorial comments on the manuscript by Millicent Ficken, Jeffery Roberts, Douglas Slack, and two anonymous reviewers are much appreciated. The study was supported by the Baylor University Honors Program and a Folmar Research Grant.

LITERATURE CITED

ALTMANN, S. A. 1956. Avian mobbing behavior and predator recognition. Condor 58:241–253.

BREITWISCH, R., AND J. HUDAK. 1989. Sex differences in risk-taking behavior in foraging flocks of House Sparrows. Auk 106:150–153.

CHANDLER, C. R., AND R. K. ROSE. 1988. Comparative analysis of the effects of visual and auditory stimuli on avian mobbing behavior. J. Field Ornithol. 59:269–277.

CURIO, E., U. ERNST, AND W. VIETH. 1978. Cultural transmission of enemy recognition: one function of mobbing. Science 202:899–901.

CURIO, E., G. KLUMP, AND K. REGELMANN. 1983. An anti-predator response in the Great Tit (*Parus major*): is it tuned to predator risk? Oecologia 60:83–88.

FICKEN, R. W., M. S. FICKEN, AND J. P. HAILMAN. 1978. Differential aggression in genetically different morphs of the White-throated Sparrow (*Zonotrichia albicollis*). Z. Tierpsychol. 46:43–57.

FRANKENBERG, E. 1981. The adaptive significance of avian mobbing. IV. "Alerting others" and "perception advertisement" in blackbirds facing an owl. Z. Tierpsychol. 55:97–118.

GEHLBACH, F. R. 1994. The Eastern Screech Owl: life history, ecology, and behavior in the suburbs and countryside. Texas A. and M. Univ. Press, College Station, TX.

HOUGH, T. 1960. Two significant calling periods of the screech owl. Auk 77:227–228.

MCPHERSON, R. J., AND R. D. BROWN. 1981. Mobbing responses of some passerines to the calls and location of the screech owl. J. Raptor Res. 15:23–30.

RITCHISON, G., P. M. CAVANAGH, J. R. BELTHOFF, AND E. J. SPARKS. 1988. The singing behavior of Eastern Screech-Owls: seasonal timing and response to playback of conspecific song. Condor 90:648–652.

SHEDD, D. H. 1982. Seasonal variation and function of mobbing and related antipredator behaviors of the American Robin (*Turdus migratorius*). Auk 99:342–346.

SHEDD, D. H. 1983. Seasonal variation in mobbing intensity in the Black-capped Chickadee. Wilson Bull. 95:343–348.

TURNER, L. J., AND R. W. DIMMICK. 1981. Seasonal prey capture by the screech owl in Tennessee. J. Tenn. Acad. Sci. 56:56–59.

VANCAMP, L. F., AND C. J. HENNY. 1975. The screech owl: its life history and population ecology in northern Ohio. N. Amer. Fauna 71.

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. Animal Behav. 28:1217–1229.