MOBBING OF EASTERN SCREECH-OWLS: PREDATORY CUES, RISK TO MOBBERS AND DEGREE OF THREAT¹

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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 (Altman 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 (Altman 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.

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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 monotonous 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 out, fledgling-dependency period). This time a partly hidden observer sat 10 m from a gray, adult 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, fledging-dependency period). This time a freeze-dried, roosting, fledging screech-owl (juvenile plumage) was fastened 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 vocalizing, 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 (ANOVA) 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 bicolour (7, PR), Cyanocitta cristata (5, PR), Thryothorus ludovicianus (3, PR), Turdus migratorius (3, SR), Vireo gilvus (2, SR), Picosites pubescens (1, PR), Icterus galbula (1, PM), Archilochus sp. (1, SR).

Permanent residents outnumbered seasonal residents plus passage migrants in all trials \( (4.9 ± 1.4 \text{ vs } 2.0 ± 0.6 \text{ individuals and } 1.5 ± 0.2 \text{ vs } 0.8 ± 0.1 \text{ species, respectively, } F > 2.2, P < 0.04) \). 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 \( (F > 11.5, P < 0.005; \text{Table 1}) \). Duration of mobbing also varied with song type \( (F = 5.2, P = 0.03) \) as did mobbing intensity \( (F = 12.3, P = \ldots) \).
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).

<table>
<thead>
<tr>
<th>Criteria</th>
<th>Songs</th>
<th>Sites</th>
<th>Seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Monotonic</td>
<td>Descending</td>
<td>Fall</td>
</tr>
<tr>
<td>Species responding</td>
<td>2.4 ± 0.4*</td>
<td>0.8 ± 0.2</td>
<td>1.6 ± 0.3</td>
</tr>
<tr>
<td>Individuals</td>
<td>8.5 ± 2.3*</td>
<td>1.2 ± 0.3</td>
<td>5.4 ± 2.1</td>
</tr>
<tr>
<td>Response duration</td>
<td>3.4 ± 0.4*</td>
<td>1.8 ± 0.5</td>
<td>3.1 ± 0.6*</td>
</tr>
<tr>
<td>Response intensity</td>
<td>3.3 ± 0.4*</td>
<td>1.2 ± 0.3</td>
<td>2.3 ± 0.4</td>
</tr>
<tr>
<td>Arrival time</td>
<td>1.6 ± 0.3</td>
<td>1.9 ± 0.8</td>
<td>1.0 ± 0.2</td>
</tr>
</tbody>
</table>

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 juvenile) 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 = 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 knowable 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 else-
where, perhaps through interspecific associations on
the winter range. Cross-cultural tutoring is possible,
since White-throats mobbed more often with perma-
nent residents than alone and with other seasonal spe-
cies (82% of mobs, \( \chi^2 = 4.5, P = 0.03 \)).

Although the descending trill was mobbed more in-
tensely 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 sig-
nal 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 remem-
ber its significance. In fall and winter Eastern Screech-
Owls forage more widely, as their offspring have dis-
persed (Gehlbach 1994), but mobbing was strongest
near the owls' permanent nest site in all seasons.

Avian mobbers correctly assess the danger of pre-
dation by Eastern Screech-Owls, which changes ac-
cording 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 invest-
ment. We suggest that avian mobbing tutors offspring
and non-relatives, even seasonal species, about pre-
datory danger and benefits relatives through kin selec-
tion.

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