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COMPARATIVE ANALYSIS OF THE EFFECTS OF VISUAL AND AUDITORY STIMULI ON AVIAN MOBBING BEHAVIOR

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Abstract.—Both visual and auditory stimuli elicit avian mobbing behavior, but there is little comparative information on their isolated and additive effects. Using three combinations of two experimental stimuli (mount and tape of an Eastern Screech-Owl, *Otus asio*) we tested the effects of stimuli on the frequency, intensity, and duration of avian mobbing behavior. Of 169 mount-only trials, only 11 (6.5%) were successful in attracting birds. Tape-only ($n = 169$) and mount-and-tape ($n = 170$) were equally successful in attracting birds (approximately 85% of all trials), but mount-and-tape trials were more likely to initiate mobbing behavior. Birds responding to mount-and-tape trials mobbed more intensely and for longer periods of time than those responding to tape-only trials. All stimuli showed similar increases in effectiveness during the summer months. These results suggest that the presence of an auditory stimulus dramatically increases the probability of an owl being detected by potential mobbers. A visual stimulus, however, provides a focus for antipredator responses and results in maximal mobbing behavior. Mobbing may be a more important force in selecting for cryptic diurnal behavior in owls than previously thought.

ANÁLISIS COMPARATIVO DEL EFECTO DE ESTÍMULOS VISUALES Y AUDITIVOS EN CONDUCTA DE TUMULTOS EN AVES

Resumen.—Tanto estímulos visuales como auditivos producen conducta de tumultos (mobbing) en aves. Muy poca información existe en el efecto de estos estímulos aislados o su efecto sumativo. Utilizando un espécimen montado de buho (*Otus asio*) y una grabación de su voz, se diseño un experimento en donde se estudio el efecto de los estímulos previamente mencionados en la frecuencia, intensidad y duración de la conducta de tumultos. En 169 presentaciones del buho montado, en tan solo 11 (6.5%) las aves respondieron a la presencia de este. La grabación de la voz del buho ($n = 169$) y el conjunto del buho montado-grabación ($n = 170$) tuvieron virtualmente el mismo éxito en producir un tumulto de aves (85% de las veces). Sin embargo la combinación tendió a ser más llamativa. La combinación de estímulos trajo como consecuencia una respuesta más extensa y por un mayor periodo de tiempo. Todos los estímulos mostraron un patrón de incremento similar durante los meses de verano. Estos resultados sugieren que la presencia de un estímulo auditivo puede aumentar la probabilidad de que un depredador, como un buho, pueda ser detectado por otras aves. Sin embargo, un estímulo visual provee de un foco particular para respuestas anti-depredadoras y resulta en comportamiento de tumulto en su máxima expresión. Los tumultos que forman aves, a depredadores como buhos, podría ser un factor de selección natural en la conducta críptica que muestran estas aves durante las horas de luz.

Avian mobbing, the corporate vocal and physical display by small birds toward a larger potential predator, is an antipredator response elicited by a remarkable array of stimuli. Typical objects of avian mobbing include hawks (Bildstein 1982, Smith 1969), owls (Altmann 1956, Hartley 1950), shrikes (Curio 1963), corvids (Buitron 1983), snakes (Bourne 1977), large

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mammals (Buitron 1983), and humans (Blancher and Robertson 1982, Shields 1984). Most research on avian mobbing has focused primarily on the importance of visual cues in the recognition and response to these predators (e.g., Curio 1963, 1975; Hartley 1950; Hinde 1954). However, even in the absence of any visual stimulus, the call notes of many predators are sufficient to trigger mobbing behavior (McPherson and Brown 1981, Miller 1952, Smith 1969).

Despite the role of both visual and auditory stimuli in eliciting mobbing responses, there is little comparative information on the isolated and additive effects of these stimuli on mobbing behavior. Mobbing studies have used either visual (e.g., Altmann 1956, Curio 1975, Shields 1984), auditory (McPherson and Brown 1981), or a simultaneous combination of these stimuli (Shedd 1982, 1983) without conducting between-stimuli comparisons. Our study was undertaken to test the effects of visual and auditory stimuli on avian mobbing, using three combinations of two experimental stimuli. Our objective was to determine whether the frequency, intensity, and duration of mobbing varied as a function of the stimulus.

MATERIALS AND METHODS

Field experiments were conducted in forested habitats weekly from January 1983 through February 1984, except in December 1983 when no experiments were conducted because of poor weather. The three primary study areas were the Great Dismal Swamp National Wildlife Refuge in southeastern Virginia and adjacent North Carolina (267 trials); Newport News Park, Newport News, Virginia (87 trials); and Powdermill Nature Reserve, field station for the Carnegie Museum of Natural History, Westmoreland County, Pennsylvania (67 trials). All remaining trials were conducted at secondary locations in Virginia ($n = 76$) and Florida ($n = 11$). Because of the possible problem of birds habituating or becoming sensitized to the experimental stimuli (which alters normal mobbing responses; Knight and Temple 1986, Shalter 1978b), the mobbing experiments were conducted at many sites within the study areas. No more than one trial was conducted at any one site. Although the use of a specific site for more than one experiment was avoided, the primary study areas were large enough (800–40,000 ha) to allow repeated use.

Mobbing behavior was initiated using three combinations of two experimental stimuli. These stimuli were a taxidermy mount of a red-phase Eastern Screech-Owl (*Otus asio*) displayed on a wooden pole 2-m in length and a 10-min tape-recording of an Eastern Screech-Owl (taken from Wetmore 1965) played on a General Electric model 3-5120B portable cassette recorder. The two stimuli were presented in experimental trials at randomly chosen locations as mount-only, tape-only, or mount-and-tape combined. In mount-only trials, the pole holding the mount was placed in a realistic but clearly visible location. During tape-only trials, the tape recorder was placed in an inconspicuous location at ground level in order to minimize visibility of the recorder without restricting the bird's ability to approach the stimulus (i.e., thick vegetation was avoided). In mount-and-tape trials, the recorder was placed at the base of the pole holding the mount. There was no discernible effect on normal mobbing behavior as a result of the physical separation of the visual and auditory stimuli in mount-and-tape trials. All trials lasted for 10 min, as timed by a Cronus digital chronometer.

These stimuli could have been presented at known nest sites (as opposed to randomly chosen locations), to ensure equal detectability of stimuli. However, stimuli presented at nest sites are almost certain to be detected and mobbed (Curio 1975; Shalter 1978a,b; Shields 1984) and thus no inferences can be made concerning the frequency at which these stimuli are normally detected and approached away from nest sites or outside the breeding season. Because mobbing is by definition not limited to nest defense (Hartley 1950), and mobbing in many species does in fact occur at all seasons (e.g., Altmann 1956, Shedd 1983), we specifically sought to quantify the detectability of, and response to, stimuli under conditions not limited to nest defense.

Before each trial, the location, date, and time of day were recorded; observations were made from an inconspicuous location approximately 20 m from the stimulus. All birds that responded were identified according to species and, where possible, their sex and age were recorded. Three variables were recorded for each bird: latency of response (time elapsed from initiation of trial until the bird was observed responding), duration of response, and intensity of the response. Intensity was rated on a scale of 1–5 (modified from Shedd 1982) to express a continuum of possible antipredator responses. The ratings were defined as follows: 1—silent approach, in which birds approached the stimulus but gave no call notes or mobbing displays (such as wing and tail flitting); 2—vocal approach, in which only call notes were given; 3—low-intensity mobbing, in which call notes and displays were given sporadically and the stimulus was approached no closer than 2 m; 4—high-intensity mobbing, in which call notes and displays were given steadily and the stimulus was approached within 2 m; and 5—actual physical attack upon the stimulus. Although the difference between ratings of three and four is subjective, we feel it is biologically justified and a useful distinction.

RESULTS

Of the 508 trials, 303 (59.6%) elicited a response (of any rating) by at least one bird (Table 1). Overall, these 303 trials resulted in responses by 2121 birds representing 85 species (93% passerines). Although a comparative analysis of behavioral differences among the responding species is of interest, the more general question of responses to stimuli is considered here.

The frequency of antipredator responses differed significantly among the three treatments (Table 1). Mount-only trials were notably ineffective in attracting birds and failed to elicit mobbing behavior (ratings of three or greater). Tape-only and mount-and-tape trials were equally effective

TABLE 1. Frequency (and percent) of mount-only, tape-only, and mount-and-tape trials resulting in antipredator responses by small birds and the number of species and individuals attracted by each treatment.

Trial	*n*	Frequency of response		Species (individuals)
		All responses[a]	Mobbing responses[b]	
Mount-only	169	11 (6.5%)	0 (0.0%)	8 (18)
Tape-only	169	144 (85.2%)	59 (34.9%)	69 (998)
Mount-and-tape	170	148 (87.1%)	91 (53.5%)	75 (1105)
	508	303 (59.6%)	150 (29.5%)	85 (2121)

[a] Trials resulting in a response of any rating by at least one individual.

[b] Trials resulting in at least one bird receiving a rating of 3 or greater.

in eliciting responses ($G = 0.023$, df = 1, NS), but mount-and-tape trials were significantly more likely to initiate mobbing behavior ($G = 6.67$, df = 1, $P < 0.01$).

The differences among the stimuli in their ability to elicit antipredator responses were reflected in the number of species and individuals attracted (Table 1). Because only 18 birds (representing eight species) responded in mount-only trials, that sample size was insufficient to include in further analysis. Tape-only and mount-and-tape trials, however, attracted both large numbers of species and individuals. There was a high degree of similarity between the species responding to tape-only trials and those responding to mount-and-tape trials (Jacard's index of similarity = 0.778). Thus, any observed effects of stimuli should not be the result of each stimulus attracting different species of birds.

The distribution of ratings among those birds responding to tape-only trials differed significantly from that of birds responding to mount-and-tape trials (Kolmogorov-Smirnov two-sample test, $D = 0.198$, $P < 0.01$). Birds responding to the tape-only received a preponderance of ratings one and two; those at mount-and-tape trials received more ratings of three and four (Table 2). Note, however, that the auditory stimulus alone was able to elicit intense mobbing responses. Mount-and-tape trials elicited responses of significantly greater mean duration (ANOVA, $F = 9.99$, $P < 0.01$) than did tape-only trials (Table 2).

Clearly, the frequency, intensity, and duration of avian mobbing differed among the three treatments. However, these aspects of mobbing also varied seasonally. Both tape-only and mount-and-tape trials elicited higher frequencies of antipredator responses during the summer months (Fig. 1). In fact, the percentage of tape-only trials resulting in mobbing in a given month was significantly correlated with that of mount-and-tape trials ($r_s = 0.809$, $P < 0.01$). Tape-only and mount-and-tape trials also showed significantly correlated patterns of seasonal variation in both rating ($r_s = 0.923$, $P < 0.001$) and duration ($r_s = 0.727$, $P < 0.01$) of response (Fig. 2). Thus, despite differences in the absolute frequency, intensity, and duration of the responses they elicit, tape-only and mount-

TABLE 2. Frequency distribution of ratings and mean duration of responses for birds responding to mount-only, tape-only, and mount-and-tape trials.

Trial	n	Frequency of ratings[a] 1	2	3	4	Duration (min) $\bar{x}$ ± SE	Range
Mount-only	18	8	10	0	0	1.57 ± 0.20	0.53–3.29
Tape-only	998	358	471	115	54	3.73 ± 0.09	0.09–9.83
Mount-and-tape	1105	261	438	231	175	4.17 ± 0.07	0.07–9.80

[a] Ratings: 1—silent approach, 2—vocal approach, 3—low-intensity mobbing, 4—high-intensity mobbing. Ratings of 5 were not observed.

and-tape trials showed correlated patterns of seasonal variation in these variables.

DISCUSSION

The stimuli used to elicit mobbing behavior clearly had differential effects on mobbing responses. One conspicuous result was the low frequency at which mount-only trials elicited antipredator responses. This result is in striking contrast to most studies, in which some form of visual stimulus was used with success. These visual stimuli have often been decidedly unlifelike (e.g., Altmann 1956) or abstract (e.g., Curio 1975) and yet they were successful in eliciting mobbing behavior. Thus, the mounted screech-owl used in this study should have been sufficiently realistic to allow its recognition by nearby birds.

We believe the poor response to the mount-only stimulus is most easily explained by the circumstances surrounding its use. Most studies have presented a visual stimulus either at a nest site (e.g., Curio 1975; Shalter 1978a,b; Shields 1984) or in laboratory enclosures (e.g., Cully and Ligon 1976, Curio et al. 1978, Frankenberg 1981), where detection of the stimulus was almost certain to occur. In our study, however, we specifically sought to quantify the effects of stimuli in situations where detection of the stimulus was not guaranteed. In this case, a silent mount placed randomly in forest habitat would be difficult to detect due both to its unpredictable location and the nature of its cryptic plumage. The natural inconspicuousness of an owl sitting silently in the woods is, we believe, the most likely explanation for the ineffectiveness of the mount-only stimulus.

The similarity of tape-only and mount-and-tape trials in their ability to attract birds is not unexpected given the ineffectiveness of the mount as a stimulus, because if the mount is not seen initially, birds are cued primarily by the auditory stimulus. In fact, individuals of 52 species were recorded as being the first bird to respond at tape-only and mount-and-tape trials (i.e., definitely were responding to the stimulus and not to the calls of other mobbers), indicating that auditory recognition of predators is widespread in birds (McPherson and Brown 1981, Miller 1952). There has been surprisingly little research on the mechanism of auditory rec-

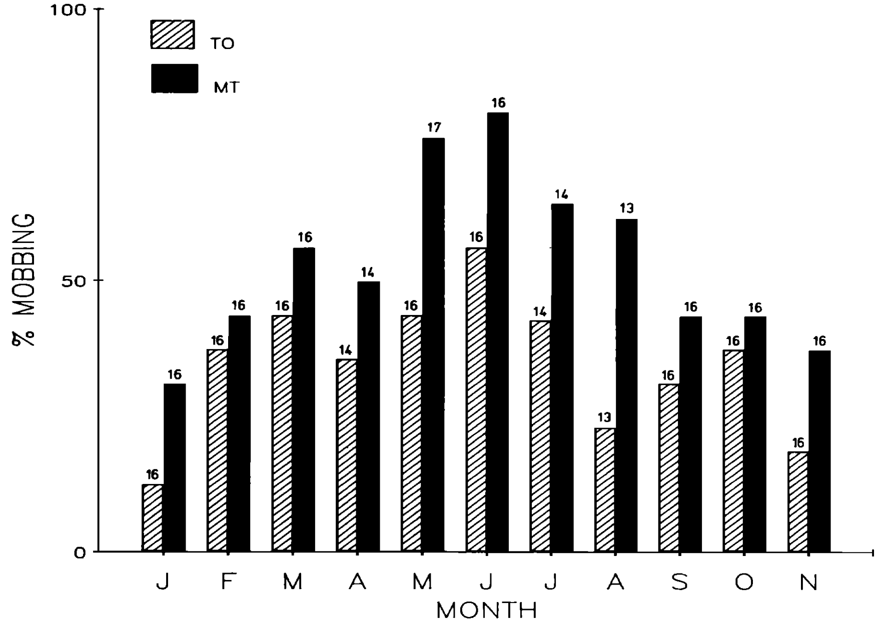

FIGURE 1. Percent frequency of tape-only (TO) and mount-and-tape (MT) trials resulting in mobbing behavior (ratings of 3 or greater) during each month of study. Numbers above bars indicate the monthly sample sizes. The percentage of tape-only trials resulting in mobbing in a given month is significantly correlated with that of mount-and-tape trials.

ognition of predators since Miller's (1952) report. It is unclear to what degree auditory recognition is innate or a result of experience with calling predators (as Shalter, 1978a, suggested was sometimes necessary for successful visual recognition). Curio (1963) provided evidence that response to calling owls is learned. Cully and Ligon (1976), however, found differences in the innate ability of species to recognize predators visually and it is possible that there are similar differences in auditory recognition. We observed that juvenile birds in late summer often responded to the auditory stimulus without the company of an adult, suggesting that auditory recognition of predators is established by an early age. The exact nature of auditory recognition of predators is a fruitful area for future research.

Although tape-only and mount-and-tape trials were equally likely to attract birds, mobbing occurred more frequently at mount-and-tape trials, individual birds tended to receive higher ratings, and birds responded for longer periods of time (Table 2). After an initial attraction to the auditory stimulus, birds responding to mount-and-tape trials clearly focused on the mount for subsequent mobbing behavior; this increased both the rating and duration of the antipredator responses. This dichotomy between the

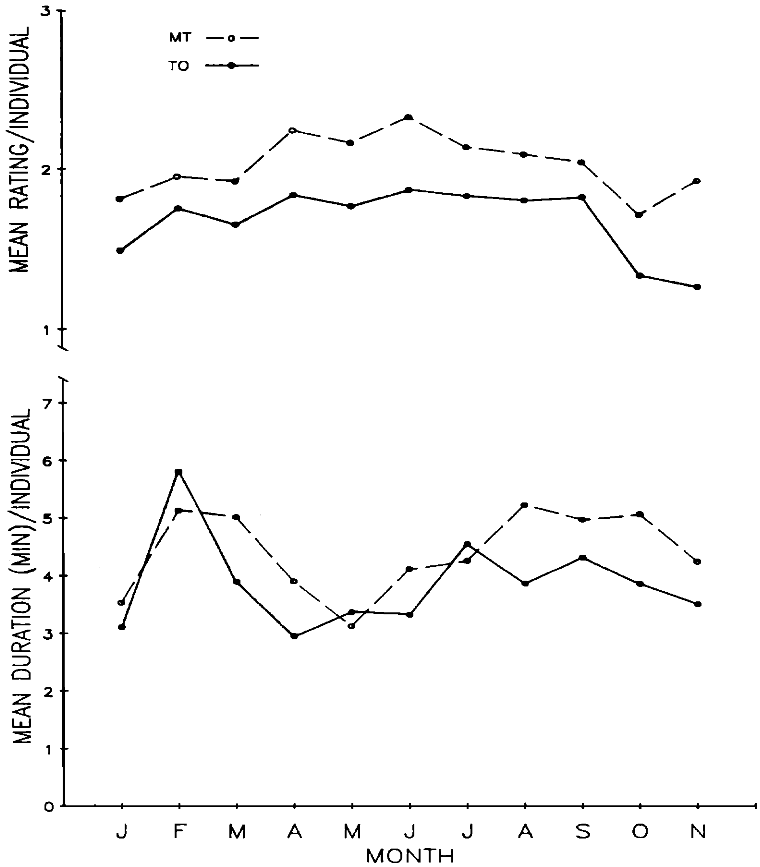

FIGURE 2. Mean rating and duration of antipredator responses by birds responding to tape-only (TO) and mount-and-tape (MT) trials during each month of study (ratings: 1—silent approach, 2—vocal approach, 3—low-intensity mobbing, and 4—high-intensity mobbing). Patterns of seasonal variation in response to tape-only and mount-and-tape trials are significantly correlated.

aural detection and visual release of behavior has been reported in other contexts (Murray and Gill 1976) and may be characteristic of many behavioral interactions involving both auditory and visual components. Increased response at mount-and-tape trials is also consistent with the additive effects of increasing number of stimuli (Curio 1963, 1975; Hartley 1950; Hinde 1954). The risk associated with mobbing a predator that cannot be visually located (as in tape-only trials) may have contributed to the weaker and briefer responses toward the tape-only stimulus. Given the risky nature of mobbing behavior (Denson 1979, England 1986, Myers 1978), it is reasonable to expect that birds will mob most intensely when the predator is clearly visible and has lost the advantage of surprise.

Seasonal variation in antipredator responses was similar for tape-only and mount-and-tape trials. Curio (1975) reported that increased mobbing responses during the breeding season in Pied Flycatchers (*Ficedula hypoleuca*) were not affected by a change of visual stimuli (owl vs. shrike), but we know of no similar comparisons between visual and auditory stimuli. The observed seasonal variation in mobbing, of considerable interest itself, is discussed elsewhere (Altmann 1956; Curio 1975; Shedd 1982, 1983; Shields 1984).

Finally, we can speculate on the significance of these results for the behavior of owls. Our results suggest that owls perched silently at a day roost are detected and harassed rarely by mobbing birds. A calling owl, however, will almost certainly attract potential mobbers (approximately 85% of trials in this study). Because owls that are detected by birds usually are mobbed relentlessly, and presumably suffer reduced hunting success or increased risk of predation, mobbing behavior may be an important force in selecting for cryptic diurnal behavior (e.g., silence, well concealed day roosts, etc.) in some owls. Conversely, mobbing may encourage owls to restrict conspicuous behavior, such as calling, to nocturnal hours. If these suggestions are correct, mobbing may actually reinforce nocturnal behavior in predators such as screech-owls and thereby reduce the probability of future encounters between a mobber and its potential predator.

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