

RESPONSES OF CAPTIVE MEADOW VOLES TO FLYOVERS OF A NORTHERN HARRIER AND AN AMERICAN KESTREL¹

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ABSTRACT. Meadow voles responded to harrier and kestrel flyovers by looking-up and tracking the flight path of the bird, by entering into behavioral freezes, or by running into their nest cans. Voles responded more frequently when they could see, as well as hear, the bird overhead. When they could see the bird overhead, voles responded more frequently to the harrier than to the kestrel. Shifts in the flight pattern of the harrier did not significantly influence vole responses. Responses of voles to aerial predators may be linked to vole selection of areas with heavy protective cover.

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INTRODUCTION

The reactions of avian prey to the silhouettes of avian predators are well documented (Melzack 1961, Martin and Melvin 1964, Muller-Schwarze and Muller-Schwarze 1970). Results differ but generally indicate that depending on the prey species, the factors of size, speed, and/or configuration of the model, as well as prey familiarity with the silhouette influence the prey's reaction (Schleidt 1961). Similar data for small mammals are scarce. Experiments with hoary marmots (*Marmota caligata*; Noyes and Holmes 1979), lodgepole chipmunks (*Eutamias speciosus*; Muller-Schwarze and Muller-Schwarze 1971), and 2 species of British voles (*Microtus agrestis* and *Clethrionomys britannicus*; Fentress 1968) show that responsiveness to aerial models is not necessarily dependent on model configuration. But meadow voles (*Microtus pennsylvanicus*) responded differently to aerial models depending on whether the model was moving or stationary and on whether it was directly overhead

(Bildstein and Althoff 1979). Here we present data on the responses of captive meadow voles to controlled flyovers of a live American kestrel (*Falco sparverius*) and a live northern harrier (*Circus cyaneus*). The kestrel is a small falcon with a wing span of 51–62 cm. The harrier is a medium-sized hawk with a wing span of 102–137 cm (Heintzelman 1975). Both species prey on meadow voles (Craighead and Craighead 1956, Bildstein 1978), and the distributions of the 3 species overlap throughout much of North America.

Harriers hunt by flying low over open country and often fly over their prey before seeing it. When this happens, they turn and circle back before pouncing (Bildstein 1978). In an attempt to duplicate this behavior in the lab, our male harrier was trained to circle once over the vole before flying out of sight. In addition both the kestrel and harrier were taught to fly in a straight line, directly over the vole. Besides testing for differences in vole responsiveness to the 2 avian predators and to the different flight patterns, we also tested for changes in responsiveness when voles could hear but not see the flying hawk or falcon.

METHODS AND MATERIALS

Thirty-eight adult meadow voles were trapped from fields hunted by harriers and kestrels in Frank-

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lin, Ross, and Pickaway Counties, Ohio. Voles were housed individually in $36 \times 20 \times 15$ cm hardware cloth cages equipped with nest cans. Food and water were provided *ad libitum*, and cut grass was provided for bedding and cover. Voles were kept on a 12L:12D (light-dark) schedule for 4–9 days before testing. This holding period allowed the voles time to adjust to their new surroundings (Ambrose 1972). A single male harrier and a single female kestrel, collected as nestlings, were trained using falconry techniques (Woodford 1966) to fly for a food reward over an indoor runway at heights of from 1.8 to 2.2 m. The runway, which was lined with white cloth, was open at the top and measured 3.3 m long, 1.0 m wide, and 1.3 m high.

Each vole was tested one time with a straight harrier flyover, a straight kestrel flyover, a harrier "noise-over," a kestrel "noise-over," and a harrier "circle-over." Noise-over flights, in which an opaque partition separated the flying bird from the view of the vole, tested vole responsiveness to sounds generated by flapping wings in the absence of visual stimuli. Tape recordings of flyovers and noise-overs indicated the opaque wall attenuated less than 4% of the noise generated by the flying hawk and kestrel. During a "circle-over," the male harrier flew half-way along the runway and then circled once over the vole before continuing its flight down the runway. In several circle-overs when the harrier turned on a long radius it was momentarily out-of-sight of the vole. An additional control test in which all experimental conditions were simulated, with the exception of a flying predator, was used to establish a base-line response. Voles were tested individually on 6 consecutive days. The order of presentation of stimuli and the control test was random.

Voles were observed through a one-way glass from a distance of 0.5 m. During the course of the flyover, we noted whether the vole, confined to its cage, looked-up to watch the predator, entered a behavioral freeze, moved about the cage, or entered its nest can. After being placed in its cage in the center of the test runway, the vole was ejected from its nest can, if necessary. If, during a presentation, the vole persisted in reentering its can, we deleted that vole's responses from our analysis. If a vole remained in a "behavioral freeze" upon being pushed from its can, we delayed presentation for up to 10 min. We define a behavioral freeze as the lack of any head, body or limb movement for 2 s. Flyovers and control tests were started following a 1 min freeze-free period. To avoid confusing reactions to the experimental situation with reactions to the birds, we restricted our analysis to tests in which the vole was stationary and the can was open prior to the flight pattern or control test. We continued to collect data until we had at least 24 acceptable tests for each situation and compared the first 24 acceptable tests for each.

Data were analyzed using Chi-square tests for heterogeneity and Fisher's exact tests (Sokal and Rohlf 1969).

RESULTS

Voles responded to harrier and kestrel flights by looking-up and tracking the course of the flying bird until it flew out of sight, by running into their nest can, and by entering into a behavioral freeze. Voles responded more frequently to both harrier and kestrel noise-overs than to control tests, but the differences were not significant (Fisher's Exact $P = 0.12$, for harriers; $P = 0.21$, for kestrels), nor was the increase significant when harrier and kestrel noise-overs were combined and compared with controls ($P = 0.11$; table 1). However, voles responded 2-3 times more frequently when they could see, as well as hear, the hawk or falcon fly over ($\chi^2 = 14.1$, $P < 0.005$, for harriers; $\chi^2 = 10.5$, $P < 0.01$, for kestrels). In response to harrier flyovers, voles looked up and entered their nest cans more frequently than during control tests. For kestrel flyovers there was an increase in all 3 response types, though not all differences were significant (table 1).

Voles responded more frequently to straight harrier flyovers than to straight kestrel flyovers ($\chi^2 = 4.5$, $P < 0.05$). Although voles responded to harrier circle-overs more frequently than they did to straight flyovers, the difference was not significant (Fisher's Exact test, $P = 0.20$). Similarly, while the number of voles entering their nest can during harrier circle-overs was greater than the number that entered during straight flyovers, the difference was not significant ($\chi^2 = 0.8$, $P > 0.20$).

DISCUSSION

As a number of avian predators select active over inactive prey (Bildstein and Forsythe 1979), an immobility response (freezing and watching the hawk or falcon) should render the vole less susceptible to avian predation, as should cover-seeking behavior such as can entry. While looking-up and following the path of the predator differs from the above 2 responses in that it is not an avoidance response, such aware-

TABLE 1

Number of meadow voles responding to flyovers of a northern harrier and an American kestrel.

| Type of flyover | N | Response* | | | Total responding** N(%) |
|---------------------|----|-----------------|--------------|----------------------|----------------------------|
| | | Look-up N(%) | Can entry | Behavioral freeze | |
| Northern harrier | | | | | |
| Straight noise-over | 24 | 4(17) | 2(8) | 0 | 6(25) |
| Straight flyover | 24 | 12(50) | 7(29) | 0 | 19(79) |
| Circle flyover | 24 | 10(42) | 10(42) | 2(8) | 22(92) |
| American kestrel | | | | | |
| Straight noise-over | 24 | 5(21) | 0 | 0 | 5(21) |
| Straight flyover | 24 | 7(29) | 3(13) | 2(8) | 12(50) |
| Control | 24 | 0 | 2(8) | 0 | 2(8) |

*See text for a description of responses.

**Response includes a look-up, can entry, and/or behavioral freeze.

ness behavior probably acts to inform the vole of the predator's location. Therefore we consider all 3 responses to be anti-predatory behavior.

Overall, the results show that meadow voles respond more frequently when they can see, as well as hear, a harrier or kestrel flying overhead; that voles respond more frequently to flyovers of harriers than to kestrels; and that shifts in the flight pattern of harriers do not significantly influence vole anti-predator responses. The first result suggests that noise alone is not responsible for vole responses to flyovers, while the second suggests that size is important. Harriers are considerably larger than kestrels and tests with models (Fentress 1968) indicated larger model size increased response strength in 2 species of British voles. Similarly, in previous tests we conducted using a small (5.5 × 13.0 cm) stylized hawk model (pulled overhead at approximately the same height the hawk and falcon flew over, Bildstein and Althoff 1979), voles responded less strongly to the model than they did to the larger hawk and falcon used here. Why a shift in the harrier flight pattern was less influential is not so clear, although results of tests with models were also similar. In these tests, moving models

produced higher response rates than stationary models, but changes in the direction of moving models did not (Bildstein and Althoff 1979). Thus it appears that size and movement per se, rather than directional changes in the predator's flight pattern, are important cues.

Even during harrier circle-overs, when voles were most responsive to flyovers, only half of the voles froze or fled into their nest cans. The remaining 42% that responded only looked up at the hawk, and 8% did not respond at all. Results of tests with silhouettes (Bildstein and Althoff 1979) also show that voles often failed to respond to silhouettes. In the same series of tests with models, white footed mice (*Peromyscus leucopus*) were significantly more responsive under all test conditions.

We believe this limited behavioral responsiveness of voles is related to their association with dense vegetative cover which affords protection from aerial predation (Birney et al. 1976). For example, Getz (1970) reported that predation by crows contributed significantly to a vole decline in an area where protective vegetative cover had been removed, and Ambrose (1972) noted that *Microtus* released into experimental environments "sought cover immediately upon release." We suggest

this ecological response to heavy cover probably precludes the necessity for a strong behavioral response to aerial predators. Unlike *Peromyscus*, which are not dependent on vegetative runways for movement, and are more responsive to aerial models (Bildstein and Althoff 1979), *Microtus* are usually under protective cover and don't see aerial predators, and thus have not developed precise aerial predator detection capabilities.

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