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RESPONSES OF WHITE-FOOTED MICE AND MEADOW VOLES TO FLYOVERS OF AN AERIAL PREDATOR SILHOUETTE¹

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Abstract. The response of white-footed mice and meadow voles to a stylized hawk model pulled overhead was studied. Behavior such as looking up and following the path of the model, immobility, and/or entering a nest can was observed and statistically analyzed. Overall responsiveness peaked as the model passed directly overhead. Stationary models elicited fewer instances of immobility than moving models while significantly increasing the number of white-footed mice that entered nest cans. Meadow voles were more likely to move about the 36 x 20 x 15 cm cage, but not into nest cans, during stop-go flyovers than during non-stop flyovers.

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Data of small mammal's behavior in response to avian predator silhouettes are scarce. There is field evidence that diurnally active small mammals living in social groups recognize and respond to aerial predators with alarm calls. These calls alert group members to potential danger (Linsdale 1946 cited in Carl 1971, and King 1955), but the cues to which these animals attend are uncertain. Experiments with Lodgepole chipmunks, *Eutamias speciosus*, (Muller-Schwarze and Muller-Schwarze 1971) and two species of British voles, *Microtus agrestis* and *Clethrionomys britannicus*, (Fentress 1968) demonstrate that with these species, responsiveness to aerial models is independent of model configuration; geometric figures and models of predator

silhouettes elicited similar responses. In two experiments using live predators (owls), Norway rats, *Rattus norvegicus*, (Spiegel *et al* 1974) and white-footed mice, *Peromyscus leucopus*, (Lay 1974) failed to respond to an owl until after it had struck. Both of these experiments, which were conducted at night, involved placing the test animals in enclosures only briefly before testing. Metzgar (white-footed mice, 1967) and Ambrose (meadow voles, 1972) have found that small mammals unfamiliar with an area were more vulnerable to owl predation. Their results suggest that the lack of responsiveness on the part of the test animals in the two experiments mentioned above may have been an experimental artifact rather than the lack of a predator recognition and avoidance system; further study is warranted.

The 24 hour activity pattern of *Microtus* appears to be quite variable, with several investigators reporting vole activity throughout a 24 hour cycle while others report a basically diurnal

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pattern (Wiegert 1961). Meadow voles are active for at least part of the day and are preyed on by several diurnally active hawks (Craighead and Craighead 1956). Similarly, members of the genus *Peromyscus*, normally active only at night (Falls 1968), are also taken by several diurnally active hawks (Craighead and Craighead 1956) and are therefore susceptible to diurnal aerial predation. Our experiment was designed to test for reactions to such a diurnal predator.

We used a stylized hawk model (Figure 1) because previous experimenters

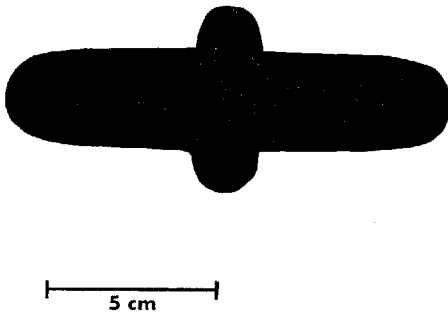


FIGURE 1. Silhouette of the stylized hawk model.

have found that various configurational stimuli did not differently activate the small mammals they tested. The model was cardboard, painted flat black, and measured 5.5 x 13.0 cm. The two-headed model configuration we chose enabled us to easily reverse the direction of flight of the model without changing its configuration. In addition to testing for a general responsiveness to an aerial model, we wished to determine if different kinds of aerial stimuli produced different responses in white-footed mice and meadow voles, and hypothesized that movement might be an important cue in predator recognition. Vestal (1973) reported that *Peromyscus* he tested appeared to be very responsive to movement. He felt that the increased sensitivity found when measuring visual acuity in two *Peromyscus* species using the optokinetic rather than simultaneous discrimination method was probably due to increased attentiveness on the part of the mice to moving stimuli. Therefore, we decided

to test if changes in either the speed or direction of the model had any effect on small mammal responses. We did this by flying the stylized hawk model over the mice and voles in two distinct flight patterns: a non-stop flight pattern and a stop-go flight pattern. We chose these flight patterns for two reasons: 1) both flight patterns roughly approximate those used by several diurnally active hawks and 2) the non-stop flight pattern involves directional changes while holding speed constant, while the stop-go flight pattern involves speed changes while holding direction constant.

MATERIALS AND METHODS

Subjects used were 32 wild white-footed mice and 31 meadow voles trapped in Delaware, Fairfield, and Franklin Counties, Ohio and included adults and juveniles of both sexes. Mice were placed in individual 36 x 20 x 15 cm hardware cloth cages equipped with a water bottle and nest can. Crushed sycamore leaves (white-footed mice) and cut grass (meadow voles) were provided for bedding and cover. Food and water were provided *ad libitum*. Subjects were kept on a 12:12 light-dark cycle for 4 to 7 days before testing. This holding period was incorporated to allow the test animals time to familiarize themselves with and adjust to their new environment (Ambrose 1972). Each subject was tested once with a non-stop flight pattern and once with a stop-go flight pattern. In addition, a control test consisting of a mock run in which all experimental conditions were simulated, with the exception of attaching the silhouette to wire, was employed to establish a base-line response. Subjects were tested individually and received one flight pattern or control test per day for 3 consecutive days. Flight patterns and the control test were presented in random order. Tests were conducted indoors in a runway lined with white cloth, measuring 3.3 m long, .95 m wide, and 1.3 m high. During flyovers the model was hand pulled along a monofilament line 1.4 m above the test cage. Continuous monitoring assured that, when moving, model speed was $.2 \pm .02$ m/sec (3.6 diameters/sec) for both flight patterns. The stop-go flight pattern consisted of three 5 sec flights interrupted by two 15 sec stationary periods, together making up one complete flyover. The non-stop-flight pattern consisted of three complete uninterrupted 15 sec flyovers separated by two 5 sec intervals during which time the model was out of sight of the test mouse: the direction of flight on the second flyover was opposite the direction of the first and third flyovers. With both flight patterns the model was in sight for a total of 45 sec.

Upon being placed in its cage on the test runway, the mouse was ejected if necessary from its nest can with the use of a plunger that forced the can's contents out onto the cage floor. The plunger was then retracted, reopening the nest

can. This process was repeated twice if necessary. If the mouse persisted in immediately reentering the can a third time, it was again pushed from the can and the plunger left extended, thus closing the can and preventing re-entry. If a mouse remained in a *behavioral freeze* upon being pushed from its nest, we delayed presentation of the model for up to 10 min, waiting for the mouse to commence normal movements. We define a *behavioral freeze* as the lack of any head, body, or limb movement for two or more sec. Flyovers and control tests were initiated following a 1 min freeze-free period.

Mice and voles were observed through a one-way glass from a distance of 0.5 m for 1 min prior to, during, and for 5 min after the flyover. We noted the time and duration of movements, lookups, can entries, and freezes, and considered each of these behavioral patterns a reaction to the model. The mice probably reacted in other ways as well, and our estimates of mouse responses to flyovers are likely to be conservative. Data were analyzed using chi-square tests for independence, Fisher's exact tests, and binomial tests (Sokal and Rohlf 1969).

RESULTS

Mice and voles whose behavior required us to close their nest cans during tests usually attempted can entry or remained behaviorally frozen on the floor or walls of the cage while those whose cans remained open appeared less disturbed. To avoid confusing reactions to the experimental situation with reactions to the model, we restricted our analysis to those tests in which the mouse or vole was stationary and the can open prior to the flight pattern or control period. We define stationary as the lack of locomotory but not head, body, and/or other limb movement for 10 or more seconds.

We found no significant differences in the reactions of male, female, or juvenile mice or voles; nor were any trends apparent. Consequently, we analyzed our data without regard to age or sex of the test animal.

Responses of white-footed mice. Mice responded during 96% of the stop-go flyovers and during 86% of the non-stop flyovers (Table 1). Looking up was the most frequent response. With non-stop flyovers 84% of the mice looked up at least once while during stop-go flyovers 92% of the mice looked up. During 13 test flights mice froze on 25 separate occasions. Only three of the behavioral freezes lasted for longer than 6 sec. Behavioral freezes appeared to represent

TABLE 1
*White-footed mice responding to aerial model flyover.**

Type of flyover	Responses			Positive Response**
	Lookup	Can entry	Freeze	
STOP-GO (n=24)				
1st move.	17	4	8	29
1st hover	29	26	13	31
2nd move.	85	0	29	94
2nd hover	20	41	6	47
3rd move.	40	0	10	40
NON-STOP (n=22)				
1st	77	18	27	86
2nd	86	7	20	100
3rd	75	8	15	92
Control (n=24)	0	17	0	17

*Percentages are based on the number of mice that remain in the cage outside their nest can.

**We considered lookup, can entry, or freeze a positive response.

startle reactions; once the model was viewed for a few seconds, the mice came out of their freeze and remained stationary in that location while continuing to look up, or began grooming, moving about the cage, or entered their nest can. The majority (84%) of the behavioral freezes occurred while the model was in motion; several mice froze for short periods during each of the three flyovers in a non-stop test. Two of these freezes were followed by entries when the model overhead entered a 15 sec stationary period. No mice froze during any of the control tests.

More mice (14 of 24) entered their cans during the stop-go flyovers than during the non-stop flyovers (6 of 22; $P < 0.05$). There was no significant increase in the number of can entries during non-stop flyovers compared with control tests (4 of 24; $P > 0.30$). Of those entering their cans during the stop-go flyovers, significantly more than expected ($P < 0.05$) did so during the stationary portion of the flight pattern. Four of the six mice that entered their cans during the non-stop flight pattern did so on the first flyover. Two-thirds of the mice that entered cans during a non-stop flyover and

half the mice that entered cans during a stop-go flyover did so after the model had passed directly overhead. The mice that entered their cans during a flyover (40%) moved to the can opening and looked out of, but did not leave the can during the 5 min period after the flyover.

Of the mice not entering their cans during the flyover, 35% did so during the 5 sec following the flyover, while 23% of those remaining did so during the next 295 sec. Entries that occurred at up to 5 sec after the flyover differed from those occurring later. The former were usually rapid darts into the can; the latter were preceded by slower movements. Similarly, while 77% of the mice entering within 5 sec of the flyover remained in their cans for at least 5 min following the flyover, only 17% of those entering later did so. This percentage compares with the 75% that remained in their cans through that some period after entering during the flyover. The number of mice that began moving, but did not enter their cans, did not increase significantly above the control level (4 of 24) during either stop-go (6 of 24; $P > 0.20$) or non-stop flyovers (5 of 22; $P > 0.25$).

Responses of meadow voles. More than 75% of the voles reacted to the model during at least one portion of the stop-go flyover, while all of the voles reacted to at least one flyover of the nonstop flight pattern (Table 2). During seven test flights seven different voles froze while the model was in sight. Of these only one vole was immobile after the model had been out of sight for more than 5 sec. As was the case with the white-footed mice, the freezes appeared to be startle reactions with 6 of them (86%) occurring while the model was moving overhead. Two voles entered their cans immediately following their freeze. One did so when the model was stationary overhead while the other did so during the 5 sec period between non-stop flyovers. No voles froze during any of the control tests.

The number of voles entering cans did not increase significantly above the control level (3 of 24) during either stop-go (6 of 23; $P > 0.20$) or non-stop flyovers (4 of 24; $P > 0.50$). Half the voles that entered cans during either stop-go or non-stop flyovers did so after the model

TABLE 2
*Meadow voles responding to aerial model flyovers.**

Type of flyover	Responses			Positive Response**
	Can Lookup entry	Freeze		
STOP-GO (n=23)				
1st move.	34	4	4	39
1st hover	32	9	0	41
2nd move.	65	0	5	65
2nd hover	45	15	5	50
3rd move.	38	0	6	44
NON-STOP (n=24)				
1st	75	8	8	79
2nd	48	10	10	57
3rd	83	0	11	88
Control (n=24)	0	13	0	13

*Percentages are based on the number of voles that remain in the cage outside their nest can.

**We considered lookup, can entry, or freeze a positive response.

had passed directly overhead, and 55% of the voles entering cans during the flyover remained in the can for at least 5 min following the flyover. Voles that did not enter their cans during the flyover (14) did so during the 5 min following the flyover, but only 2 of these (14%) did so within 5 sec of the flyover. Voles entering their cans after the flyover (64%) remained in the can during the 5 min following the flyover. Significantly more voles began moving, but did not enter their cans, during stop-go flyovers (14 of 23) than during non-stop flyovers (3 of 24; $P < 0.001$) or control tests (1 of 24; $P < 0.0001$).

DISCUSSION

Our results show that white-footed mice and meadow voles responded to relatively small aerial silhouettes. As our model was stylized and did not depict any particular species of hawk, it is unlikely that the responses we observed are limited to specific silhouette configurations.

Results from our non-stop flight pattern tests indicated that at least during short sequences of repeated flyovers white-footed mice and meadow voles continue to look up during successive flyovers. At the same time, the number of mice that froze or entered their cans in

response to flyovers decreased following the initial non-stop flyover. These findings agree with those of Melzack (1961), who found that Mallard ducks continued to respond with "non-emotional orienting responses" toward hawk and goose models after 2000 flyovers, long after the fear responses to the models had ceased. He concluded that the "habituation of fear responses" to aerial models is due to the replacement of emotional fear responses with non-emotional orientating responses. The sharp decline in the percentage of meadow voles looking up during the second flyover of the non-stop flight pattern indicates that a change in the direction of an aerial silhouette may influence the voles' responsiveness to that silhouette.

Stop-go flight pattern tests showed that white-footed mice were more likely to enter their nest cans when the model was motionless than when the model was moving overhead. With meadow voles, stationary individuals were more likely to begin moving about their cage (but not into their nest cans) during a stop-go flyover than during a non-stop flyover or control test. Hawks are able to detect moving prey more easily than stationary prey (Cushing 1938, Ingles 1940, and Snyder 1974), and it may be that their hovering behavior, which is energetically costly, serves to enhance prey movement and hence vulnerability. It should be pointed out, however, that while our models were motionless when hovering, hawks often flap their wings when hovering and may in fact be more conspicuous to their prey when hovering than when soaring (Brown and Amadon 1968).

Though we had anticipated immediate responses to the model, most of the initial responses occurred after the model had passed directly overhead. During tests in which the stop-go flight pattern was used there was a peak in responses during the second period of movement at which time the model was close to or directly overhead.

While there were conspicuous differences in the responsiveness of the two species (white-footed mice are more likely to freeze and enter their cans than are meadow voles), mouse and vole responsiveness is remarkably similar overall. In both species, freezing and look-

ups appear more likely during periods of model movement, especially when the model was overhead and individuals were more likely to move into their cans (the white-footed mice) or about their cages (the meadow voles) during stop-go flyovers than during non-stop flyovers and control tests. Our results indicate that both white-footed mice and meadow voles responded differently to aerial silhouettes depending on where the model was and whether it was moving or stationary.

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