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VULNERABILITY OF BOT FLY *(Cuterebra)* INFECTED *Peromyscus maniculatus* TO SHORTTAIL WEASEL PREDATION IN THE LABORATORY

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Abstract: In the laboratory, *Peromyscus* bearing a single *Cuterebra* larva are no more vulnerable to weasel predation than are uninfected control mice, and may be taken less often under certain conditions. Mice bearing two or more larvae appear to be more vulnerable than either controls or singly infected mice. Their increased vulnerability probably results from their failure to use arboreal pathways. Decreased activity may be responsible for the relative advantage of singly infected mice. Previous reports of higher survivorship among mice with a single bot parasite than among uninfected mice, and of lower survivorship among multiply infected mice, may result in part from differential predation rates.

INTRODUCTION

Rodent bot flies of the family Cuterebridae are relatively common parasites of small rodents in temperate and tropical North America. Their larvae, encapsulated under the skin on various parts of the host, are relatively large, and would appear to have an adverse effect on mobility and survival of the host. Laboratory experiments with *Cuterebra* have revealed significant changes in activity patterns of parasitized eastern Chipmunks[3] and Deermice,[35,36] but the ecological significance of such changes have not been ascertained. If *Cuterebra* are well adapted parasites, as suggested by a number of authors,[5,8,15,38] their effects upon host behavior, appearance, and vulnerability to predation should be minimal, or at least if changes are apparent, their presence should have minimal effects upon host mortality.

Many reports are contrary to these expectations. Pearson and Pearson[31] reported *Cuterebra* integument in owl pellets in Pennsylvania, and Scott and Snead[32] observed *Cuterebra* and *Peromyscus* remains in scats of cat and red fox. In neither case, however, were any comparisons made between predation rates on infected and healthy rodents. Although predation is not necessarily implicated, several authors have reported significantly lower survival rates among *Cuterebra* infected mice, especially those with multiple infections.[29,38] Others[7,10,32,33] have suggested that the "obvious locomotory awkwardness" of hosts might decrease their effectiveness in escaping predators.

In contrast, some studies[14,38] have demonstrated significantly higher survival among rodents infected with a single bot larva. Getz[13] reported a slight, but not significant increase in survival of infected *Microtus pennsylvanicus*, but did not consider severity of infection in his comparisons. Hunter *et al.*[19] explained this apparent increase in survival as an artifact due to more resident than transient mice being infected. Thus the residents, which remain on a study plot longer, inflate survival estimates for infected mice.

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The question of susceptibility to predation, however, still requires an answer.

A number of authors [1,20,21,22,23,24,28] have utilized controlled laboratory experiments to study behavioral aspects of predation. In this study, healthy and *Cuterebra* infected *Peromyscus maniculatus* were exposed to shorttail weasel *(Mustela erminea)* predation using laboratory methods similar to those of Metzgar[28] and Jamison[20]. *Peromyscus* comprise a considerable proportion of the natural diet of the shorttail weasel, [2,16] and the results presented here should help to clarify the effects of weasel predation on survival of singly and multiply infected rodents in field situations.

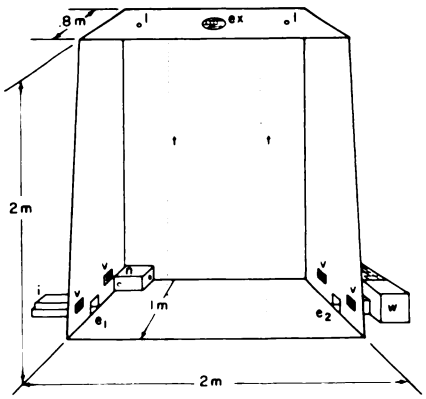

FIGURE 1. Arena used in weasel predation studies: e^1 = mouse entrance, e^2 = weasel entrance, ex = air exhaust vent, i = mouse injector, l = light fixtures, t = t-bar supports for plexiglass front panels, v = air input vents, w = weasel cage and access tunnel.

MATERIALS AND METHODS

Two plywood and plexiglass predation arenas, previously designed and constructed for similar purposes, were utilized for this study. The floor, three sides, and top of each were of 0.95 cm plywood with external framing, and the front consisted of three removable plexiglass panels (66 x 200 x 0.7 cm thick) supported by metal t-bar framing (Figure 1). Each arena was two meters wide, one meter deep at the bottom, and two meters high. The fronts sloped back slightly, and the depth was 80 cm at the top. Access ports (8 x 8 cm) for mouse and weasel were centered at floor level on opposite sides of the arenas, and entrance of the experimental animals was controlled by remotely operated sliding or rotating panels. Each arena was actively ventilated through a screened ceiling exhaust port (6.5 cm diam.) connected to a remote fan by corregated plastic conduit (10 cm diam.). Air entered via four adjustable screened vents located slightly above floor level. A mouse nest box was provided in each arena; on the floor in one, and elevated one meter above the floor in the other.

The floor of each arena was covered with approximately 2 cm of wood shavings, and a few dried leaves were scattered over the litter. Ground-level complexity was provided by randomly placing stones (0.25 to 2.5 kg) on the floor of one arena and by adding horizontal sticks and log fragments to the other. Vertical or "arboreal" structure was constructed by erecting an interlaced network of leafless sticks and branches from the floor to the ceiling of each arena. The density of the "structure" was adjusted to provide maximum complexity consistent with ease of observation under low light intensity. The structure of each arena was changed periodically, although not between every pair of trials, to prevent the weasels from becoming too familiar with the environment.

Two laboratory-born shorttail weasels, one male and one female, were maintained in holding cages consisting of wire runways (1.25 cm^2 mesh; 23 x 40 x 19 cm high) attached to wooden nest boxes (2.5 cm white pine; 23 x 35 x 19 cm high). Weasels had free access to the wire runways via a 5 cm diam. hole in the nest box. Water was available at all times, and each weasel was fed one laboratory mouse per day. Remains of

the previous day's meal were removed at each feeding.

Each weasel's cage was connected to a predation arena by a rectangular wooden tunnel (10 x 12 cm high x 40 cm long). Access to this tunnel was prevented by a sliding panel at the end nearest the cage. Access to the predation arena was controlled by a silent, rotating panel that the investigator operated with a string and pulley system from behind a camouflage screen. Weasels were not allowed into the tunnel or the predation arena except during experiments. Weasels were deprived of food for 10 to 12 hours prior to each experiment to help insure similar motivational state for all tests. The sliding panel in the access tunnel was removed shortly before each trial, allowing the weasel to enter the tunnel but not the predation arena.

A removable mouse "injector" was attached to the opposite side of each arena. It consisted of a 6.5 cm^2 x 13 cm long plywood tunnel with a sliding panel door at the end nearest the arena. The opposite end consisted of a square plunger that could slide the full length of the tunnel and gently inject the mouse into the arena. Both sliding door and plunger were operated remotely via a silent string and pulley system.

All *Peromyscus* utilized for predation experiments were first generation laboratory-born mice. They thus had no previous experience with either the predator *(M. erminea)* or the parasite *(C. approximata).* A paired test design was used for all time comparisons. Statistical procedures and tables used in analyses were taken from Siegel[34]. The Wilcoxon Matched-pairs Signed-ranks Test or the Mann-Whitney U Test were used for comparison of time parameters, and the Fisher Exact Probability Test was used to compare distributions of action patterns between groups. Two-tailed statistical comparisons were utilized, rather than assigning one-tailed alternative hypotheses, because of Lincicome's[26] "Goodness of Parasitism" hypothesis and the conflicting reports of survival of parasitized mice.

Mice were matched for sex, age, and weight, and sibling pairs were used whenever possible. One mouse of each pair was infected orally and/or nasally with freshly hatched *Cuterebra* larvae. Dosage varied from one to six larvae, depending upon larval viability and the level of infection desired. Among a total of 22 infected mice, 17 harbored a single bot, four carried two larvae each, and one mouse had three larvae. During the course of infection the mice of each pair were housed individually in adjacent plastic mouse cages (28 x 18 x 13 cm high) with wire tops. Wood chips were provided as litter, and Purina Lab Chow and water were available *ad libitum.*

Experimental trials were performed when *Cuterebra* infections reached 22 or 23 days of age, approximately one to two days prior to the time the larvae were expected to exit from the host. Control and experimental mice were both run in the same arena with the same weasel, but on subsequent nights. The order of testing was reversed for each new trial pair. The standard procedure was to acclimate each mouse to the test arena for one night (approx 20 hrs) prior to the experiment. Mice were removed from the enclosures shortly before nightfall on the evening of the test and were returned to their original cages until 15 min. before the experiment began. They were then placed into the mouse injector tunnels and attached to the arena for the remaining 15 min. The laboratory remained darkened during all preparations.

During the experiments light was provided by two 25 watt red light bulbs mounted on the ceiling of each arena.

Light intensity was varied with a dimmer rheostat to attain the lowest illumination consistent with observation by the investigator. All other lights were extinguished by a timer switch at least an hour prior to experimental runs. During each trial the primary investigator and one or two additional observers were concealed behind a camouflage screen and viewed the trial through rectangular slits in the blind.

Mouse behavior: Mice generally paused for a brief bout of grooming behavior immediately after entering the arena, and activity patterns during the ensuing five minutes were interrupted periodically by similar grooming bouts. Duration of these bouts varied from mouse to mouse and from time to time in a single mouse, but times were not recorded. Though mice had been acclimated to the predation arena before the trial period, short forays about the enclosure comprised a considerable proportion of their activity prior to the introduction of the weasel. This behavior, apparently exploratory in nature, also varied from mouse to mouse. Sixteen of 44 mice remained on the floor of the arena, and 11 of these 16 continued intermittant exploration until the weasel entered. Two of the remaining five terrestrial mice (both multiply infected) entered the nest box and remained there until the weasel caught them. The other three moved slowly into a corner or to a log or rock and sat motionless, except for short bouts of grooming.

Among the 28 mice that climbed above the floor, only one (a control) entered the elevated nest box. Movement appeared less intense along arboreal pathways than on the floor, probably because the mice were more restricted in the pathways available. Mice were more apt to select a protected spot and sit motionless or groom.

Mice generally noticed the weasel as soon as it entered the arena. Only three of 44 mice failed to do so, and all but one observed the predator before it saw them. Generally, a mouse's initial reaction to the presence of a weasel was to "freeze" as described by Eisenberg.[11] Mice watched the weasel intently, following its progress with minute head movements. They appeared to be aware of the weasel's orientation and of where its attention was directed. Most mice (19 of 25) that moved while the weasel was searching the arena did so only when the weasel was looking or moving away from them, and froze when the weasel turned in their direction. In 36 of 44 cases mice remained motionless if the weasel approached slowly. If the weasel sprinted toward or lunged at the mouse, it generally fled (38 of 44). Under laboratory conditions, however, every mouse tested was caught and killed by a weasel.

Single bot infections: Peromyscus infected with a single *Cuterebra* larva were no more susceptible to predation than were healthy mice. Median time to capture, i.e., time from introduction of the weasel to final capture of the mouse, was longer for infected mice (60.0 sec) than for healthy mice (30.8 sec; Table 1). This difference was not significant ($P >> .05$), but stronger trends were observed when total time to capture was partitioned into search and chase times.

The median search time required for a weasel to locate an infected mouse was 60.0 sec, compared with a median of 28.9 sec for locating healthy mice ($P = .098$; Table 1). Subjective evaluation by the observers revealed little difference between control and experimental mice in their ability to climb and take advantage of vertical habitat structure. On two occasions infected mice appeared to lose their balance momentarily while climbing and seemed awkward in regaining their

TABLE 1. Comparisons of weasel predation among 17 pairs of healthy and singly infected mice.

	Control mice	Singly infected mice	Significance of difference
Median time to capture (sec)[a]	30.8	60.0	P >>.05[b]
Median search time (sec)	28.9	60.0	P = .098[b]
Median chase time (sec)	1.9	1.9	P>>>.05[b]
Number of escapes	5	6	P > .99[c]
Number of mice terrestrial/arboreal	5/12	4/13	P > .99[c]
Number of mice stationary/moving	5/12	8/9	P = .482[c]
Number of mice bolting/freezing	2/15	5/12	P = .398[c]

[a] Times reported here are *median* values; thus, the sum of search time and chase time need not equal total time to capture.

[b] Wilcoxon matched-pairs signed-rank test, 2-tailed.

[c] Fisher exact probability test, 2-tailed.

position. This also was observed in one control mouse. Both groups of mice, however, utilized arboreal pathways equally (P > .99; Table 1); 70.6% of the control mice and 76.5% of the experimentally infected mice were above the floor of the arena when the weasel entered. A single control mouse entered the nest box in the arena and was caught by the weasel while inside. No singly infected mouse entered a nest box during test runs. No significant difference was observed between groups in their tendency to move about while the weasel was searching the arena (P = .482) or in their tendency to bolt as the weasel approached (P = .398).

Control and experimental mice did not differ significantly in chase times by weasels (median = 1.9 sec for both groups; P>>.05). Temporary escapes were observed in both groups of mice (Table 1); five among controls and six among experimentals (P > .99). No mice escaped more than once.

Multiple bot infections: Only five trials were performed on mice with multiple infections. Four mice bore two larvae each, and one mouse had a triple infection. Multiply infected *Peromyscus* appeared to be more vulnerable to mustelid predators than either control or singly infected mice (Table 2), but the small sample size prevented statistical confirmation. The weasels appeared to be less motivated during these later studies, and the variability between tests increased dramatically. Median time to capture was 121.2 sec for controls and 54.7 sec for infected mice (P>>.125). Median search time

TABLE 2. Comparisons of weasel predation among 5 pairs of healthy and multiply infected mice.

	Control mice	Multiply infected mice	Significance of difference
Median time to capture (sec) a	121.2	54.7	P >>>.125 [b]
Median search time (sec)	120.0	52.5	P>>>.125 [b]
Median chase time (sec)	2.6	1.1	P >.125 [b]
Number of escapes	2	0	P = .444 [c]
Number of mice terrestrial/arboreal	2/3	5/0	P = .167 [c]
Number of mice stationary/moving	3/2	3/2	—
Number of mice bolting/freezing	1/4	0/5	P >.99 [c]

[a] Times reported here are *median* values; thus, the sum of search time and chase time need not equal total time to capture.

[b] Wilcoxon matched-pairs signed-rank test, 2-tailed.

[c] Fisher exact probability test, 2-tailed.

for healthy mice (120.0 sec) exceeded that for experimentals (52.2 sec), and infected mice appeared more susceptible to capture than controls (median chase times were 1.1 sec and 2.6 sec, respectively; P > .125). These trends comprised a complete reversal of those observed in singly infected mice.

Each trial began with the reintroduction of the test mouse to the arena. The sliding panel in the mouse injector was opened and the mouse was gently inserted into the arena using the plunger in the injector. Each mouse was observed during a five minute acclimation period before the weasel entered the arena. The weasel was then allowed to enter the arena via the rotating panel in its access tunnel. Weasels were not actively injected, but readily entered the enclosure when the panel was opened.

Two stop watches were started when the weasel entered. One watch was stopped when the weasel had located the mouse and began chasing it. The second watch was turned off when the mouse was captured. Three time parameters were thus recorded: (a) total time to capture, (b) search time, and (c) chase time (c = a - b). In addition, an "escape" was scored whenever a continuous chase was interrupted, even momentarily, and the weasel had to resume searching for the mouse. The weasel was promptly returned to its holding cage after each trial. The investigator and all observers then left the darkened laboratory and composed a single verbal

and diagramatic description of their observations. Behaviors of both mouse and weasel were described during the search, chase, and capture sequence. When two pairs of mice were being tested concurrently, a second trial was then performed in the other arena using identical procedures.

RESULTS

Weasel behavior: Shorttail weasels used in this study were aggressive and readily entered the predation arenas as soon as access was provided. Both weasels were agile climbers and were able to move along arboreal pathways with little difficulty. Weasels evidently employed both sight and smell in hunting for prey. They commonly perched on elevated vantage points (rocks, logs, or branches) and peered intently about the enclosure, often assuming an upright posture. While moving along the ground they generally quested to both sides with their noses on or near the substrate. In following arboreal pathways they regularly "tested" several alternative pathways by smell before selecting a route. In a number of cases it was evident that the weasels were tracking mice olfactorily, since they followed the exact route earlier utilized by the mouse. Short diversions from the "proper" path were abandoned, and the weasel would return to the last choice point before proceeding further.

Weasel behavior varied greatly once a prey was detected. In arboreal situations slow, stealthy approaches were most common, although rapid sprints were also observed, especially if the mouse began to move. On the ground, or where firm footing was available, sprints were the rule rather than the exception.

Once a chase was initiated, either by a mouse bolting from the approaching weasel or by a lunge or sprint of the predator, it was rapid, continuous, and often circuitous. Momentary escapes were noted on 13 occasions (in 44 trials), but the weasel generally relocated the mouse and resumed the chase within one to two seconds. Unless the mouse was caught on the first lunge the chase almost always (95% of the time) ensued on the floor of the arena, even when initiated arboreally. Once on the floor, mice were never able to regain an arboreal escape route before being caught.

Weasel capturing and killing behavior is remarkably stereotypic. Behavioral patterns observed and described here for *M. erminea* are virtually identical with those described by Heidt[17] for *M. nivalis.* Initial capture consisted of locking the mouse in a sustained bite; usually on or near the mouse's neck, but other sites were used opportunistically. The weasel then rolled to its side and curled its body around the mouse, using all four feet to control its struggles. Once this was accomplished, the original grip was released and a new purchase was sought in the occipital area of the mouse's skull. A single bite in that region generally killed the mouse. Unless a better grip on the skull was required to kill the mouse, the weasel never released this grip until well after the mouse ceased to struggle.

The occipital grip was often maintained even after the mouse was dead and the weasel began to move about the arena. At this point the stereotypic behavior pattern was broken. Weasels often dropped the mouse and resumed investigation of the habitat or moved to the entrance of the tunnel linked to its holding cage. Once the connecting panel was opened the weasel often entered its cage voluntarily, and was equally likely to carry the mouse or to leave it behind.

No significant differences were noted between control mouse and infected mouse behavior while a weasel

was in the arena. Both groups were equally likely ($P > .999$) to creep to "safer" or more remote locations while the weasel was present. Once the weasel approached closely, both groups of mice were equally likely to initiate a chase by bolting ($P > .999$). Subjectively, mice with two or more larvae appeared to be more awkward than singly infected or healthy mice. No multiply infected mice used arboreal pathways, but two control mice were above floor level when the weasel entered the arena. This trend was not significant when paired comparisons were made ($P = .167$; Table 2), but was significant when controls were pooled to increase sample size ($n = 22$, $P = .020$). Two of five infected mice entered the nest box (ground level) and were caught by the weasel while inside. The other three trials were performed in the arena with the elevated nest box. None of the control mice utilized nest boxes while being observed.

General comparisons: Median search time required to locate arboreal control mice (106.8 sec) was longer than that required to locate terrestrial control mice (8.7 sec, $P > .02$; Table 3). Chase times and number of escapes of arboreal and terrestrial mice did not differ significantly (Table 3). Mice with one bot were significantly more arboreal than were multiply infected mice (13 of 17 *vs* 0 of 5; $P = .0096$, Fisher exact probability Test, 2-Tailed). However, there was no difference in their tendency to "creep" (8 of 17 *vs* 3 of 5; $P > .99$, Fisher test, 2-Tailed) or in their tendency to "bolt" from the weasel (5 of 17 *vs* 0 of 5; $P = .470$, Fisher test, 2-Tailed).

DISCUSSION

Peromyscus maniculatus infected with single *C. approximata* larvae did not appear to be any more vulnerable to shorttail weasel predation than did uninfected control mice. The median time required to catch a mouse, once detected, was identical for singly infected and control mice. On the other hand, weasels apparently took longer to locate singly infected mice than healthy mice. This appeared to give singly infected *Peromyscus* a slight advantage over healthy individuals subjected to weasel predation. In contrast,

TABLE 3. Comparisons of weasel predation among control mice exhibiting different behavioral patterns.

	Behavioral pattern	Significance probability of difference
Median search time:	Arboreal = 106.8 sec Terrestrial = 8.7 sec	$P < .02$ [a]
Median chase time:	Arboreal = 1.9 sec Terrestrial = 2.1 sec	$P >> .10$ [a]
Number of escapes:	Arboreal = 6 in 15 Terrestrial = 1 in 7	$P = .486$ [b]
Median search time:	Moving = 28.9 sec Stationary = 110.2 sec	$P >> .10$ [a]

[a] Mann-Whitney U Test, 2-tailed.

[b] Fisher Exact Probability Test, 2-tailed.

mice bearing more than one *Cuterebra* larva may have been more susceptible to predation than either singly infected or control mice. Although the small sample size prevented statistical confirmation, multiply infected mice appeared to be more easily detected and more easily caught than paired control mice.

There appears to be no simple, single hypothesis to explain the differences among healthy, singly infected, and multiply infected *Peromyscus* in their vulnerability to weasel predation. In this experiment weasels appeared to locate their prey primarily by sight and smell, and generally investigated terrestrial portions of the habitat prior to climbing above the ground. Mice bearing multiple bot larvae were probably more susceptible to weasels because they failed to use arboreal pathways. Singly infected mice used arboreal pathways extensively, as did healthy mice, and therefore were less readily detected by weasels than heavily infected individuals. In addition, odors from the exudate (host tissue fluid and larval excrement) of larval respiratory pores may have been stronger in the case of multiple infections than in single infections. Though mice with multiple bots were less active and may have been more difficult to detect visually, their restriction to terrestrial habitat, possibly with a stronger odor, may be sufficient to explain why they were more vulnerable to weasel predation than healthy or singly infected mice.

Why singly infected mice appeared to be less readily detected by weasels than were healthy mice is more difficult to explain. Singly infected mice also were significantly less active than healthy individuals.[35,36] Infected mice may have left fewer scent trails than uninfected mice, though warble pore exudates probably increased their odor. This might have given them an advantage, especially in three-dimensional arboreal situations where the probability of a weasel crossing their trail is reduced. Decreased activity also would reduce the chances of visual detection of infected mice.

The artificial habitat constraints in this study resulted in extremely intense predation pressure. Weasels were conditioned to expect prey every time they entered the predation arena, and every mouse tested was eventually detected and killed by a weasel. In natural situations, where weasels must expend more time and effort in locating and capturing prey, the differences in time parameters observed here may be even more pronounced. Mice restricted to movement along the ground might be more easily detected by weasels than those using arboreal pathways. In addition, they also would be more vulnerable to other predators such as shrews and snakes. If infected mice are less active than healthy mice and subsequently move about less, weasels and other terrestrial predators would be less likely to detect their scent trails, especially those of arboreal, singly infected mice.

Whether the same susceptibility pattern would pertain in relation to avian predators is uncertain. *Peromyscus* are primarily crepuscular-nocturnal in their activity.[12,25,35,36] Owls are undoubtedly their primary avian predators, and *Peromyscus* are common fare for many owl species.[9,27] Owls hunt their prey by sound as well as sight.[4,30] Decreased activity by infected mice would decrease their exposure to avian predators, but awkwardness resulting from bot larvae may significantly increase the amount of noise they make. In addition, many small owls may readily take arboreal prey,[4] and the use of arboreal pathways may not confer an advantage in those cases.

The mice tested in this study were carrying large, fully developed bot larvae, and were probably suffering the

maximum physical handicap incurred during the course of infection. Changes in mouse activity patterns are evident early in the infection,[35,36] but the stage at which the physical burden of growing larvae becomes significant is questionable. It does appear, however, that the time span involved is sufficient to cause noticeable changes in mortality of field populations. Patterns in vulnerability to weasel predation observed in this study parallel reported trends in natural mortality of several *Cuterebra* infected small rodent populations.[13,14,38] The increased survivorship of mice infected with a single bot may result from differential predation rates. This conclusion does not refute the hypothesis of Hunter *et al.*[19] (see above), but offers a supplemental explanation that also accounts for increased mortality among multiply infected hosts. Hunter concluded there was no evidence for bot flies (directly) causing significant deermouse mortality, and this observation is supported by several laboratory studies.[6,18,35,36] In addition, it is unlikely that infected mice are more apt to emigrate from study plots than healthy mice.[19,38] The observed increase in mortality of multiply infected mice probably results from predation.

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