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Abstract: Peromyscus maniculatus subjected to bot fly (Cuterebra) parasitism in the laboratory showed significant changes in amount and temporal distribution of several activity patterns. Strenuous activities, such as running in an exercise wheel or stereotypic somersaulting, declined while less strenuous activities associated with maintenance behaviors increased. Diurnal response to handling and disturbance declined significantly in infected mice. The temporal distribution of nocturnal activity was altered, and may affect vulnerability of infected mice to small predators. Most changes persisted for at least a week postinfection.

INTRODUCTION

Parasites often debilitate or induce significant changes in the behavior of their hosts. Modification of intermediate host behavior by immature parasites with complex life cycles is common.[14] Increased vulnerability of the intermediate host, and its consequent consumption by a predator, may be required for completion of the parasite life cycle. However, well adapted parasites with more direct, simple life cycles should avoid harming the host.[18] Significant changes in activity patterns might still occur, but these should not normally increase host mortality. The rodent bot flies, family Cuterebridae, undergo a simple, direct life cycle and belong to this group of parasites.

A number of authors [7,9,10,19] have commented on the apparent locomotory awkwardness of small rodents infected with Cuterebra. Hirth[13] reported that infected mice were lethargic and more easily handled, and Wecker[25] hypothesized reduced movement and migration of infected mice to explain the increased survivorship that he observed. Others have pointed out that physical disability probably is restricted to near the end of infection or the time of larval emergence[6,21] and this disability is noticeably more severe in multiple infections.[10] Brown[5] observed little evidence of awkwardness in Peromyscus boylei with dorsally located bots, and Clough[8] observed no decrease in swimming ability nor in survival time in cold water of Microtus pennsylvanicus infected with Cuterebra.

Dunaway et al.[10] concluded that activity of Peromyscus did not seem to be affected by Cuterebra parasitism. Home range sizes of infected M. pennsylvanicus did not differ significantly from those of healthy voles,[11] but parasitized Peromyscus may be captured more often than healthy mice.[12,15] Hunter et al. observed no difference in movement patterns between infected and uninfected Peromyscus maniculatus.

In laboratory studies of eastern chipmunks (Tamias striatus) infected with from two to six Cuterebra emasculator, Bennett[4] observed decreased running activity of the hosts at the time the larvae exited. However, his observations were restricted to second instar and later infections. His control

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data consisted of either continued observations after the exit of larvae in the case of natural infections, or observations prior to surgical implantation of second instar larvae into the host. In the former case control data did not eliminate the possibility of prolonged postinfection effects on activity. In the latter case the effects of "postoperative shock" could not be isolated from parasite induced effects.

In this study, activity patterns of *P. maniculatus* were observed prior to, during, and following laboratory infections with *C. approximata*. The hosts were infected in essentially a "natural" manner. Variations in activity resulting from sources other than parasitism were minimized, and were accounted for by concurrent observations of control animals.

MATERIALS AND METHODS

Only *P. maniculatus* older than 48 days were used in activity studies. All were first-generation laboratory-born offspring of wild caught parents. Prior to the experiment they were maintained individually in plastic mouse cages (approx. 28 x 18 x 13 cm high) with wire tops. Wood shavings were provided as bedding and Purina Lab Chow and water were available *ad libitum*. Mice were transferred individually into activity cages for the duration of the experiment.

The activity cages (Figure 1) were constructed of 2 cm x 15.25 cm softwood with 1.25 cm² wire mesh floor and top. The floor was supported by slots in the sides of the cage, so that the bottom was approximately 3.75 cm above the substrate. The wire mesh top was hinged to provide access to the interior of the cage. Water was provided *ad libitum* from a calibrated glass fountain located opposite the food vessel. An activity wheel was housed in a separate chamber, with access
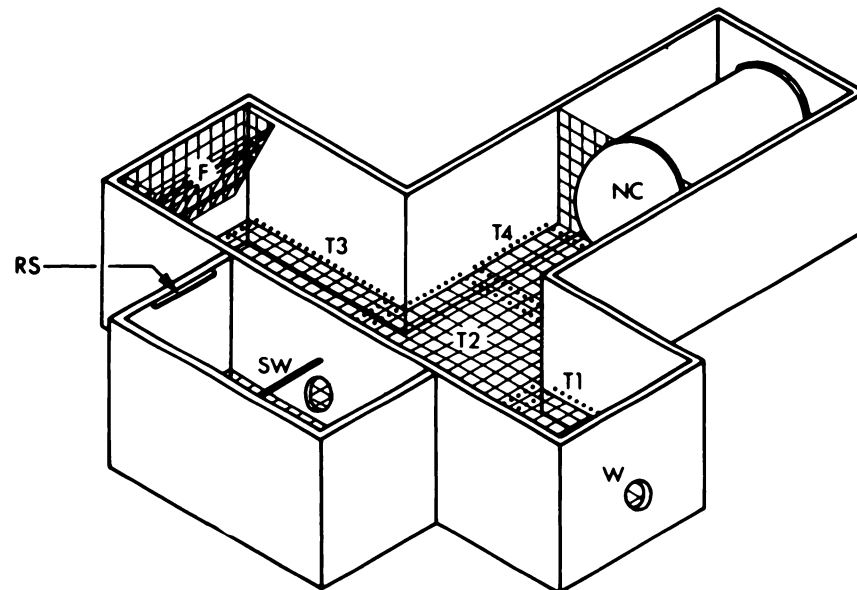

FIGURE 1. Mouse cage used in activity studies (exercise wheel and cover removed). Dotted lines represent outlines of treadles, T1 = water treadle, T2 = center treadle, T3 = food treadle, T4 = nest entrance treadle, F = food rack, NC = nest container, RS = reed switch for exercise wheel, SW = shaft for exercise wheel, W = aperture for water fountain.

provided by a 3.9 cm diam. hole in the wood partition. A nest box was located at the opposite extremity from the exercise wheel and consisted of a steel beverage can with one end removed. A small amount of cotton was provided as bedding.

Wire mesh treadles were supported above the floor of each cage (Figure 1). One was located immediately below the food vessel, one beneath the water fountain, one at the entrance to the nest can, and one at the center of the activity cage. Each treadle was connected to a microswitch by a short, sheet metal lever, so that the switch closed whenever a mouse stepped upon the treadle. A small bar magnet was affixed to each exercise wheel, and a magnet activated reed switch was attached nearby to the wall of the cage. The reed switch closed with each revolution of the wheel. All switches (five in each cage) were wired to an Esterline-Angus 20 channel event recorder located in an adjacent room. Because the number of channels monitored (5 switches x 8 cages = 40 channels) exceeded the capacity of the event recorder, the eight mice were divided into two groups of four. Each group of four mice was monitored on alternate days and activity data for all eight mice were summarized over two day intervals.

A noise generator was placed among the activity cages in an attempt to drown out auditory cues that might stimulate similar activity patterns among the mice. It consisted of an activity wheel driven by a small electric motor. A series of spring loaded levers vibrating against the wheel provided a relatively loud, constant "chatter", the total effect simulating the noises of the treadles, microswitches, and exercise wheels in the activity cages.

Mice were maintained in the activity cages for an acclimation period of one week prior to the experiment. During this period the complete system was operated to refine the electrical and mechanical linkages, data collection, and data interpretation, but the data collected were discarded. Once the main experiment was begun, each one-minute segment of event recorder tape was examined, and activity for that interval was assigned to one of three general categories. Whenever any pen showed a continuous thick trace, indicating rapid deflections of the pen, that one-minute interval was recorded as representing "strenuous" or "running" activity. Any interval when separate pen deflections were discernible was termed a "low level" activity period, and those intervals during which no pen deflections occurred were recorded as "no detectable" activity.

Following acclimation and prior to infection, 10 days of baseline data were collected on each mouse. Two mice of each sex were then selected randomly, and each was infected nasally with a single freshly hatched bot larva. The larvae were transferred from an egg mass to the nostril of the host with a fine camel hair brush. Noninfected control mice were similarly treated, except that they received no bot larva. Thereafter, all mice were examined daily for evidence of successful bot infection. If a bot had not cut a respiratory pore through the skin of an infected mouse by the 10th day of infection, the infection was considered unsuccessful and the mouse was infected a second time. If a mouse had to be infected a second time its activity record and that of one control mouse were shifted ten days to synchronize the period of infection with those of other mice before the data were analyzed.

The preinfection activity patterns observed varied greatly, both between mice and within a single mouse from one day to the next. Changes in activi-

ty patterns during the course of the experiment were consequently standardized to minimize the effects of between mouse differences. Means were calculated from the first 10 days of activity data for each mouse. For all following days, changes in activity of each mouse were expressed as deviations in minutes from the calculated mean for that individual prior to infection.

The time series data resulting from these activity observations suffer a shortcoming common in behavioral studies. Because the observations were taken on the same mice, from day to day, the observations were not independent. They thus fail to satisfy a critical assumption explicit in most statistical tests. For want of a better small-sample procedure, conventional analyses were used, with the realization that the calculated significance probabilities may be slightly in error. The activity distributions of infected and control mice were tested for significance of difference using the Wilcoxon Matched-pairs Signed-ranks test.[20] The mean value for all experimental mice versus that for all control mice over a two day period constituted a pair. The comparisons were made within preinfection, third instar, and postinfection time blocks. They also were made using data from the whole infection period and from the infection plus postinfection periods. The number of observations within the first and second larval instars were too few to allow similar within block analyses.

The total distribution of mouse activity within each 24 hr period was further divided into two time blocks. Because *Peromyscus* are primarily nocturnal or crepuscular, activity from one hour prior to "lights-out" to one hour after "lights-on" was used as a measure of "normal" activity. The distribution of this nocturnal activity was compared (1) between control and experimental groups and (2) within each group between the preinfection interval and six day time blocks during and after infection. The mice in this experiment also showed a period of diurnal activity in response to disturbance and handling during daily feeding and maintenance. This activity was termed "disturbance response". The total minutes of activity during this period were summed as a measure of a mouse's reaction to disturbance. Comparisons were made between groups and time periods using the mean deviations procedure described above.

RESULTS

Direct observations of mice during daylight hours aided in interpretation

TABLE 1. Nocturnal activity of mice for 10 days prior to infection. Presented as means ± SE in minutes per day. Means are derived from 5 observations per mouse.

Mouse No.	Sex	Total activity	Running activity	Low level activity	Proportion of active time spent running
1	F	454.4 ± 29.5	209.6 ± 23.2	244.8 ± 15.3	0.458 ± 0.029
2	F	578.8 ± 48.9	428.6 ± 46.6	150.2 ± 9.6	0.734 ± 0.023
3	M	222.0 ± 15.0	27.0 ± 4.0	195.0 ± 13.9	0.122 ± 0.016
4	M	299.6 ± 50.8	188.4 ± 49.2	111.2 ± 6.5	0.565 ± 0.101
5	M	438.0 ± 29.4	294.0 ± 36.8	144.0 ± 20.6	0.664 ± 0.058
6	M	260.4 ± 23.7	50.0 ± 8.3	210.4 ± 22.1	0.193 ± 0.029
7	F	467.0 ± 40.4	278.4 ± 33.2	188.6 ± 9.5	0.590 ± 0.022
8	F	265.4 ± 23.0	44.6 ± 6.0	220.8 ± 18.7	0.166 ± 0.018
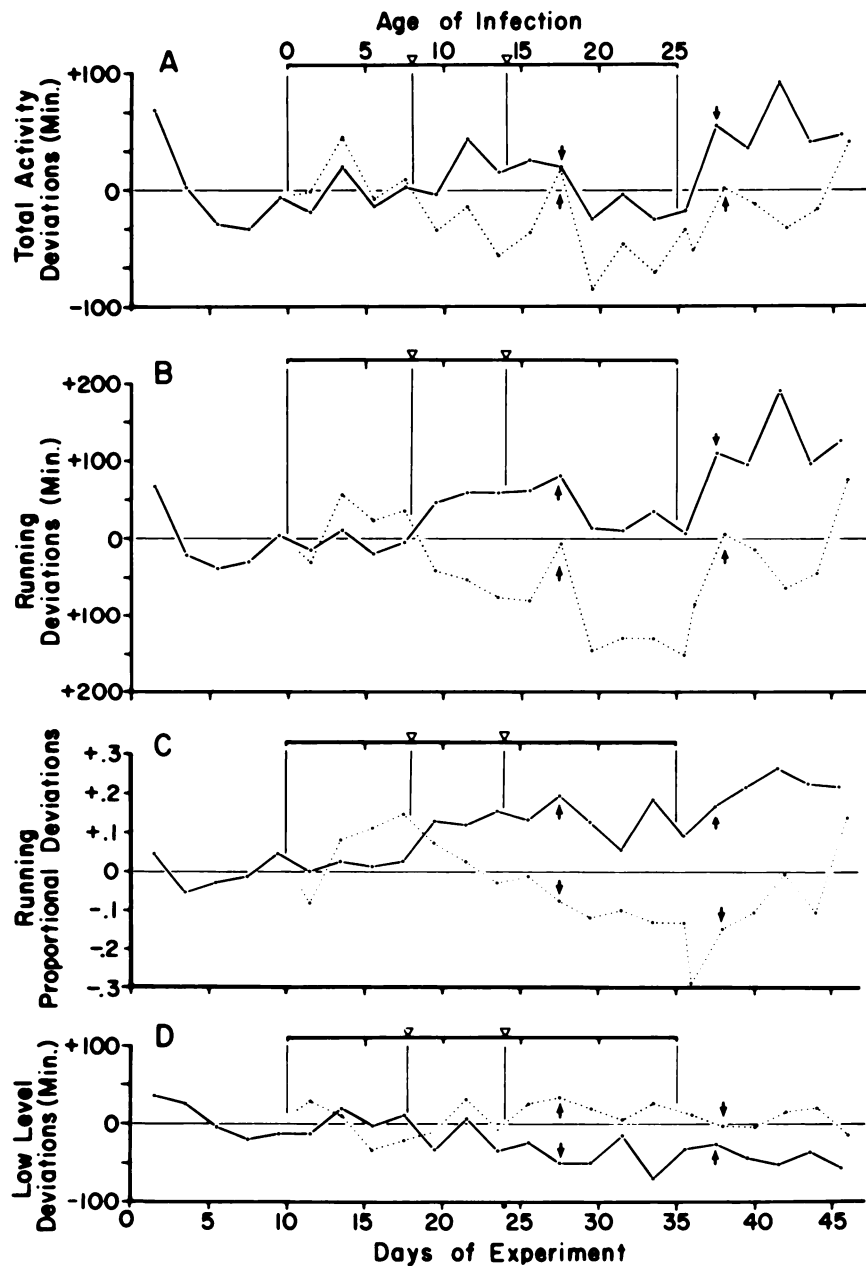
FIGURE 2. Activity trends in *Cuterebra* infected (dotted lines) and control (solid lines) *Peromyscus maniculatus*, presented as deviations from daily activity means for ten days prior to infection. Triangle pointers on upper scale represent larval molts. Arrows indicate data points reflecting introduction of adjacent weasel colony (see text). *A*. Total activity, *B*. Running activity, *C*. Proportion of active time spent running, *D*. Low level activity.

of event recorder records. Patterns described as "running" activity included several types of strenuous exercise: running in the exercise wheel, somersaulting, and other rapid stereotypic movements within the main activity cage. "Low level" activity included "maintenance" behaviors such as feeding, watering, and grooming, as well as "investigatory" behavior and other slow movement patterns.

One major artifact appeared in all activity trends observed. On the 38th day of the experiment a colony of shorttail and longtail weasels was moved into the room adjacent to the activity experiment. The two rooms shared a common door and ventilation system, and olfactory and/or auditory stimuli generated by the weasels induced several days of intensified behavior by the mice. The point at which the weasels were introduced is indicated by arrows in Figure 2. The increased activity is reflected at two points in the chronology of the experiment because the infections of two mice were out of synchrony with the rest. The data for those mice and an equal number of controls were shifted by 10 days so that the periods of infection corresponded for data analysis. Consequently, the weasel induced activity changes were partially masked because they were averaged with "normal" activity for other mice.

Control and experimental mice did not differ significantly in their activity during the preinfection period. During early infection, infected mice appeared to be slightly more active than control mice. Subsequently, however, total activity for infected mice declined significantly below that of control mice (P < .01; Figure 2A). This difference persisted for 12 days after larvae left the hosts, but the activity curves for the two groups showed strong evidence of convergence when the experiment was terminated on the 12th day postinfection. During the second and third larval instars (days 8-25 of the infection) and the first 12 days postinfection, declines in total activity of experimental mice averaged 83.4 min./day below the activity deviations of controls (P < .01). These differences were also significant within third instar and postinfection periods considered individually (P < .05).

When total activity trends were factored into running and low level activity, deviations in running time paralleled those observed for total activity quite closely. During the first larval instar infected mice spent slightly more time running than did control animals (Figure 2B, mean difference between groups = 28.5 min./day). Subsequently, running activity declined in experimental mice, and during the second and third instars and for 12 days postinfection, running was significantly lower in infected animals than in controls (P < .01; mean difference between groups = 143.0 min./day). Running activity of infected mice also was significantly lower (P < .05) within the third instar and the postinfection periods. The two running curves also showed evidence of convergence at the end of the experiment.

Deviations in the *proportion* of active time spent running (Figure 2C) paralleled those for *total* running time. Deviations in running time thus resulted from changes in relative time allocations to different activity patterns as well as from declines in activity as a whole. Prior to infection, the two groups of mice did not differ significantly. During the first larval instar, infected mice spent a greater proportion of their time running, though the limited number of observations prevented demonstrating a significant difference. The overall trend during the experiment revealed that infected mice spent a significantly lower proportion of their time running than did controls (P < .01; mean difference between groups = 0.213).
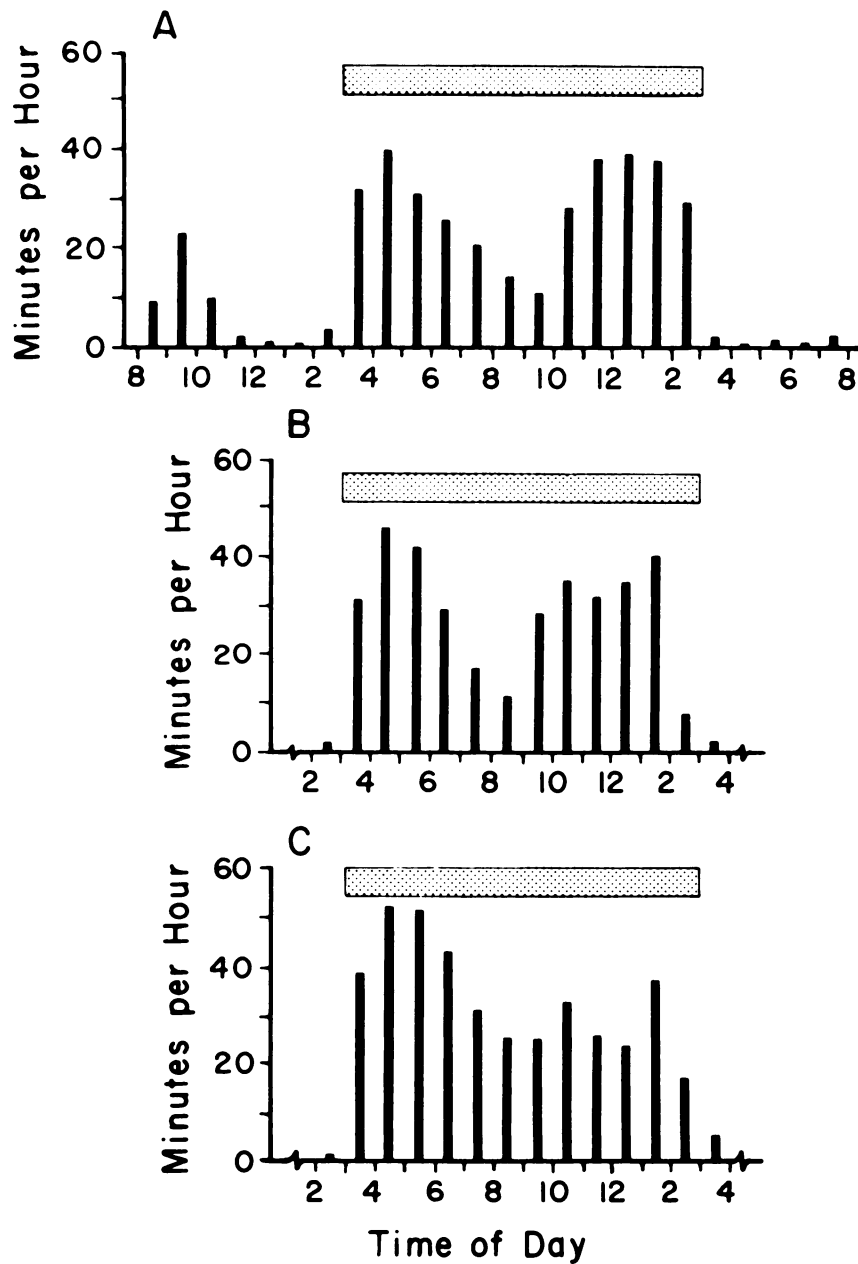
FIGURE 3. Temporal distribution of total activity for four *Peromyscus* experimentally infected with *Cuterebra*. Stippled bars represent hours of darkness. *A*. Mean distribution of daily activity for 10 days prior to infection. Diurnal peak (8-11 A.M.) reflects response to handling and data collection *B*. Mean distribution of nocturnal activity for days 13-18 of infection. *C*. Mean distribution of nocturnal activity for days 7-13 postinfection.

Significant differences (P < .05) also were observed within the third instar period and during the first 12 days postinfection. The experimental and control curves showed strong indication of convergence when the experiment was terminated.

Trends in low level activity were reversed from those for total running and proportional running activity. During the first eight days of infection, experimental mice were initially slightly more, then slightly less active at low levels than were control mice (Figure 2D). During the second and third larval instars and postinfection, experimental mice showed significantly more low level activity than did controls (P < .01; mean difference between groups = 47.7 min./day). These differences were also significant within the third instar and the postinfection period (P < .05). Low level activity curves showed very little evidence of convergence when the experiment was terminated.

The temporal distribution of nocturnal activity prior to the infection period did not differ significantly between experimental and control groups. Nocturnal activity was initiated immediately following lights-off and was distinctly bimodal in distribution (Figure 3A). The first peak occurred within two hours and tapered off smoothly over the next five hours. The second peak was more symmetrical, encompassed the five hours prior to lights-on, and declined sharply when the lights came on.

Temporal distribution of nocturnal activity within the control group did not differ greatly when the preinfection data were compared with subsequent time blocks for the same mice. Among the experimental mice, however, noticeable differences in temporal patterns appeared during days 13-18 and days 19-24 of the infection, and during days 7-12 postinfection.

During infection the early peak of nocturnal activity became more symmetrical and dropped off more sharply within the ensuing two hours (Figure 3B). The second period of high activity became more uniform and dropped off sharply an hour prior to lights-on. During the first several days postinfection, infected mice were the least active of any time during the experiment. What little activity did occur, however, was distributed almost identically with that observed during the preinfection period. During the final six days of the experiment (days 7-12 postinfection) experimental mice became more active. The initial peak of activity persisted, but subsequent activity was sustained at a higher level throughout the night, more or less masking the second peak (Figure 3C). Some evidence of bimodality did remain later in the night, and activity did not drop off so sharply prior to lights-on.

The "disturbance response" of infected mice declined an average of 11.5 min. below that of controls when the infection and postinfection periods were combined (P < .01). This difference was also significant within the total infection period alone (P < .01), but no statistical significance could be demonstrated within shorter time blocks. The disturbance responses of the two groups also showed evidence of convergence when the experiment was terminated.

DISCUSSION

This study revealed significant changes in behavioral patterns of *Peromyscus* infected with *Cuterebra*. The time periods involved for the first and the second larval instars were short, and the numbers of observations were too few for significant differences to be demonstrated. However, the temporal relationships observed among (1) changes in host activity, (2) stages of larval development, and (3) previously

described signs of bot fly parasitism (see below) strongly suggest that changes observed during these periods were meaningful.

Various authors [1,2,3,16,17] have described wheezing, sneezing, and other signs of irritation during the first instar of some *Cuterebra* infections. *C. approximata* larvae are generally in the nasal or pharyngeal passages until the end of the first week [22,23] and migrate subcutaneously [16] to the final infection site late in the first instar. Though direct observations were insufficient to substantiate the wheezing-sneezing syndrome in this study, the increase in activity during the first instar probably reflects nasal and/or subcutaneous irritation induced by the larvae. This conclusion is further supported by the fact that the first instar was the only period during the entire experiment when either total or running activity for experimental mice consistently exceeded that for control mice. This trend reversed between the seventh and ninth days of infection; at precisely the time when larval migration ended and the larva cut its respiratory pore and molted to the second instar.

The few observations of total and running activity taken during the second instar were all lower for infected animals. This trend continued through the third instar and persisted until at least 12 days postinfection. *Cuterebra* larvae grow most rapidly during the third instar, and energetic demands upon the host are greatest during that period. [22,23] In addition, third instar larvae are characterized by prominent, heavily sclerotized spines on their cuticle. These spines apparently irritate surrounding host tissues and induce the rapid growth of a thick-walled connective tissue capsule around the parasite. This added energetic demand, and the accompanying increase in bulk and weight all may contribute to the significant decline in activity during the third instar.

Total activity and running activity of previously infected mice began to increase soon after the larvae left the host. Activity trends of experimental and control mice showed evidence of gradual convergence when the experiment was terminated, but it was evident that parasite induced behavioral changes persisted during a postinfection recovery phase.

Low level activity trends during the experiment were reversed from total and running activity trends. Infected mice spent more time engaged in non-strenuous activities than did controls. This difference may have resulted from one or both of two causes. Running and low level activity are complementary components of total activity. If total activity were to remain fixed and running activity were to decrease, low level activity would have to increase by necessity. In this experiment, however, total activity was not constant, and changes in running and low level activity consequently need not be inversely related. On the other hand, the energetic demands of the parasitism and the loss of host body fluids through the larval respiratory pore would increase host maintenance requirements. Increases in host low level activity during the second and third larval instars and postinfection may reflect increases in host eating, drinking, and grooming behavior. This conclusion is supported by the fact that food consumption by infected mice increased by an average of about 20% during the final week of infection. [22]

Changes in the temporal distribution of nocturnal activity during *Cuterebra* infections are more difficult to interpret. The abbreviation of the early evening activity peak and the drop-off of activity prior to lights-on may indicate that infected mice tire more rapidly than control mice. The second activity peak was initiated an hour earlier by infected mice, however, and its duration (5 hrs) was identical

with the peak observed in control mice. Quantitatively, infected mice were less active than controls, so relative stamina is hard to assess in any case.

One week after larval exit, infected mice became much more active nocturnally. The early evening peak was still evident, but relatively high activity was sustained throughout the night, concealing the second peak. Previously infected mice apparently have a "rebound" activity phenomenon once they begin to recover from the parasitism.

The decline in "disturbance response" of infected mice probably results from the same factors as the declines in total and running activity. Increased bulk and weight during infection, possibly accompanied by reduced stamina of the infected host, are probably responsible.

Both groups of mice reacted to the introduction of the weasel colony by an increase in running activity. The increase was more marked in infected animals, however. Their running activity increased from 80 min./day below "normal" to preinfection levels for the two days following weasel introduction. It appears that infected mice are capable of maintaining strenuous activities for extended periods of time when the stimuli are strong enough.

Parallel trends in activity deviations of experimental and control groups probably resulted from three major causes. Long term acclimation to the apparatus and to handling during data collection may have induced similar patterns in both groups. Variations in environmental parameters such as temperature, humidity, and background noise and odors also may have affected the two groups similarly. Though a noise generator was employed to mask auditory stimuli, some between group "social facilitation" may have resulted from auditory and/or olfactory cues generated by exercise wheels, microswitches, and various mouse activities such as eating, defecating, and urinating.

The ecological consequences of behavioral changes in *Cuterebra* infected *Peromyscus* are difficult to extrapolate from laboratory studies. Quantitative changes in various activities may affect an individual's exposure and susceptibility to predators. [22,24] Reduced total activity probably reduces exposure, but the relative contributions of low level and running activities may adversely affect susceptibility to predation. If increases in low level activity reflect an increase in foraging behavior, mice may be less alert and more prone to predation. In natural situations, where food and water may be less readily available than in the laboratory, increases in low level foraging activity might be even more pronounced. Increases in low level activity are offset by decreases in running and other strenuous activities. Though these decreases probably reduce exposure to predators, they also may be important in "learning" the structure of the mouse's environment and in physical conditioning of the mouse. Reduction of these activities, in conjunction with the physical burden of the parasite, also may reduce a mouse's ability to escape predators.

The changes in temporal distribution of nocturnal activity in infected mice also may affect vulnerability to predation. The abbreviation of the early evening activity peak may reduce susceptibility to predators during the ensuing hours, but this tendency might be partially offset by the earlier initiation of the second activity period. The shift of the second activity period would probably be most significant in the hour prior to dawn. Infected mice terminate their activities an hour earlier than healthy mice, and this would reduce early morning exposure to crepuscular predators; especially to

those small predators keyed to normal *Peromyscus* activity patterns.

One additional behavioral change may have significant effects upon host survival. Diurnal response times to disturbance were of shorter duration in infected mice. This implies that infected mice may be less readily disturbed and exposed for shorter periods during daylight hours. Susceptibility to diurnal predators consequently might be reduced.

The interaction of these behavioral factors under differing ecological conditions may be partly responsible for the conflicting data on the survival of bot infected rodents reported in the literature. Behavioral changes resulting from bot fly parasitism might either reduce or increase predation upon the host population. The intensity of predation would depend upon relative susceptibilities of mice which were foraging in, as opposed to "exploring" their environment, upon the amount of time spent in each of these activities, and upon the hunting techniques and activity periods of the predators themselves.

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