

Form and Development of Predation on Crickets in Adults of *Peromyscus maniculatus bairdi* and *P. leucopus noveboracensis*

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Three experiments compared the similarities and differences in attacks on crickets by two species of laboratory-raised cricetid mice, *Peromyscus maniculatus bairdi* and *P. leucopus noveboracensis*. In Experiment 1 moderately prey-experienced 1.5-year-old mice of both species concentrated attacks on the crickets' dorsal head. *P. leucopus* also produced considerable damage to the thorax and showed a greater effect of sessions on the location and latency of attack. In Experiment 2 prey-naive .4- to .8-year-old mice of both species initially damaged crickets randomly and were slow to attack, but after two sessions both species attacked rapidly and displayed the same focus on the dorsal head shown in Experiment 1. However, *P. leucopus* did not display the thoracic focus shown by this species in Experiment 1. In Experiment 3 the *P. leucopus* from Experiment 2 were retested at 1.5 years of age without further predatory experience and showed the thoracic focus of attack found in Experiment 1. Young adults of both species markedly and similarly increased the speed and focus of predatory attacks on crickets after limited experience. The attack characteristics of older *P. maniculatus* differed very little from those of experienced young adults, whereas the attack characteristics of *P. leucopus* changed as a function of both age and subsequent test experience.

For many rodents successful predation produces an important part of their diet (see Landry, 1970, for a review). However, the form of such predation and the contribution of experience have been studied extensively in very few species. Most laboratory research has centered on the albino rat's mouse-killing response (e.g., Barr, Gibbons, & Moyer, 1975; Karli, 1956; Whalen & Fehr, 1964). Some researchers have regarded this behavior as predatory (e.g., Moyer, 1968; O'Boyle, 1974, 1975), but others have argued that mouse killing by rats is primarily a form of aggression (e.g., Van Hemel, 1975).

A less questionable example of laboratory predation is the biting attack on crickets (*Acheta domesticus*) by a variety of wild and laboratory rodents. Even naive young of many species spontaneously attack crickets, for example, grasshopper mice (*Onychomys leucogaster* and *O. torridus*; Baxter, 1979; Boice & Schmeck, 1968; Cyr, 1972; Langley, 1981, 1983), golden hamsters (*Mesocricetus auratus*; Polsky, 1975, 1977a, 1977b, 1977c, 1978a, 1978b), Mongolian gerbils (*Meriones unguiculatus*; C. Brack, 1981; G. L. Brack, 1981), and laboratory mice (*Mus musculus*; Butler, 1973; Thomas, 1969; Whelton & O'Boyle, 1977). Further, in nearly all these cases predatory behavior showed marked increases in efficiency and stereotypy of damage location with experience. The extent

and predictability of the behaviors observed in these species suggest that predatory attack can be studied profitably in the laboratory from the view of both phylogeny and the effects of experience.

The primary purpose of the present research was to document the form and development of predatory attack on crickets (*A. domesticus*) by adults of two species of *Peromyscus*, *P. maniculatus bairdi* and *P. leucopus noveboracensis*. Adults were used to avoid confounding the effects of experience with those of gross development, such as maturation of sensory-motor systems or large changes in body size. Stomach content data on both species indicate extensive ingestion of arthropods (32%–59% of volume; Whitaker, 1966; Wolff, Dueser & Berry, 1985); however, little has been reported on the characteristics of their predatory behavior (e.g., Eisenberg, 1968).

P. maniculatus, the deer mouse, is the widest ranging North American mouse, with more than 60 subspecies (Hall & Kelson, 1959). The subspecies *P. maniculatus bairdi*, found in open grassland habitats, was used in the present studies. *P. leucopus*, the white-footed mouse, occurs in a wider variety of habitats, including woodlands, brushland, fields, and bog-like areas (Drickamer, 1972; Whitaker, 1966). *P. leucopus noveboracensis*, found chiefly in drier woodlands, was used in these studies. In terms of phylogeny, the two species have been placed in related but separate assemblages within the subgenus *Peromyscus* (e.g., Hall & Kelson, 1959; Hooper, 1968; Osgood, 1909). Recent chromosomal banding analyses have supported the distinctness of these groupings while acknowledging the phylogenetic affinities between them (e.g., Robbins & Baker, 1981; Rogers, Greenbaum, Gunn, & Engstrom, 1984; Stangl & Baker, 1984).

The second purpose of the present research was to relate similarities and differences in predation behavior to the species' ecology and evolution. To the extent that predatory

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behavior is related to common phylogeny, we expected *P. maniculatus* and *P. leucopus* to show similar development and control of predation on crickets. However, to the extent that their phylogenetic divergence is related to differences in feeding ecology, we expected species differences in development and control of predation. Though the total volume of arthropods consumed was very similar, close examination of the data of Whitaker (1966) and those of Wolff et al. (1985) using a different subspecies of *P. maniculatus* (*nubiterrae*) suggests that the two species may have different predation strategies. *P. maniculatus* showed both a greater seasonal variability in intake and more specialization. For example, more than half the animal matter in the stomachs of *P. maniculatus* from grassy fields consisted of lepidopterous larvae and pupae. Stomachs of *P. leucopus* from the same habitat and season showed a greater variety of food.

The combination of greater variability in amount and more specialization of predation suggests the possibility that *P. maniculatus* specializes more rapidly and efficiently on particular prey types but as a result may not maintain as much flexibility as *P. leucopus* in dealing with a variety of prey. Such a conclusion is compatible with Drickamer's (1972) laboratory demonstration that *P. leucopus* showed fewer restrictions than *P. maniculatus* on feeding behavior when young and continued to modify its feeding behavior with experience as an adult. On the basis of these data, we expected *P. maniculatus bairdi* to rapidly develop as an efficient predator when younger but to show less subsequent change in behavior when older. *P. leucopus noveboracensis*, on the other hand, was expected to continue to show modification in predatory behavior with experience over a greater age range.

Experiment 1 documented locations of damage to crickets and attack latencies over test sessions in moderately prey-experienced older *P. leucopus* and *P. maniculatus*. Experiment 2 focused on the development of cricket predation in prey-naive young adult mice of both species. Experiment 3 retested the *P. leucopus* from Experiment 2 to determine if an important difference in the data between Experiments 1 and 2 could be attributed to maturational changes.

Experiment 1

The major purposes of Experiment 1 were to document similarities and differences in the predatory behavior of moderately experienced adult *P. maniculatus* and *P. leucopus* and to observe any effects of repeated experience with crickets as prey. The measures used were pattern of prey damage by biting and latency to attack. Both measures have been used frequently as an index of predatory efficiency (e.g., Langley, 1981; Polsky, 1977a; Whelton & O'Boyle, 1977).

Method

Subjects. The subjects were 9 laboratory-reared *P. maniculatus bairdi* (4 female and 5 male) and 9 *P. leucopus noveboracensis* (6 female and 3 male), each weighing 15–20 gm. The mice in all studies were from the captive lines of John King, Michigan State University. The mice in Experiment 1 were approximately 1.5-years old when the study began. About 1 year before, each mouse was allowed to

attack 20–30 live crickets presented singly in its home cage, 5 per day, for 4–6 days. Each mouse had been allowed to eat the last cricket on each test day. The mice were housed individually in 17 cm wide × 13 cm high × 28 cm deep plastic cages with wire covers and were maintained on ad lib access to Purina Mouse Chow and water. Ad lib feeding conditions were used to ensure that killing was not primarily a function of general nutrient deprivation.

Apparatus. The subjects were tested in their home cages, the wire cover replaced with a transparent acrylic cover for greater visibility. The floor of each cage was covered with a layer of wood chips approximately 4 cm thick. Prey was introduced through a 2 × 2 × 2 cm trap door located in the center of the cover. The prey were fully grown live house crickets (*Acheta domesticus*), housed in the same room as the mice. Latencies to attack were recorded using an analog stopwatch.

Procedure. At the start of each session, the subject's cage was moved from the holding rack to a testing area in the same room. The wire mesh top was replaced with the transparent acrylic cover, and subjects were given 10 min to habituate to the disruption. All sessions were run during the late afternoon of a 12:12-hr light/dark cycle. Long-term synchronization of eating with the dark part of the cycle was presumed to provide approximately equal degrees of deprivation for all the mice prior to testing.

On each trial one cricket was introduced into the center of the cage through the trap door, regardless of the mouse's position. When the cricket touched the wood chips, the stop watch was started. The resulting motion and sound of the cricket's striking the wood chips was typically sufficient to produce a change in the mouse's behavior. Each trial continued until the subject attacked the cricket or 5 min passed. Latency to initial contact with the cricket was recorded. To prevent confusion of damage from feeding and attack as well as any loss of predatory interest, we terminated the trial and removed the cricket when the mouse sat up on its hind legs with the prey held approximately perpendicular to the ground in its front paws (see Langley, 1981).

Each subject was tested for two sessions of five trials each. Subsequent trials in a session began 5 min after the prey from the previous trial had been removed from the cage. This period was sufficient for the mouse to groom and resume exploration. After each session one prey was introduced that the subject was allowed to eat. A minimum of 24 hr and a maximum of 48 hr passed between each session.

Attacked prey items were either preserved in a formalin solution or frozen and were later examined under a low-power binocular dissecting microscope to locate bite marks. The two methods of preservation were equivalent, though neither allowed satisfactory discrimination of multiple bites to the same location. Damaged areas were recorded on data sheets showing a line drawing of the dorsal and ventral views of a cricket, divided into head, thorax, and abdomen (top of Figure 1) and an enlargement of the dorsal head divided into eight areas, following Langley (1981; bottom of Figure 1). Marks were made on the appropriate drawings representing the size, shape, and location of the actual damage to the prey.

In scoring the drawings any mark in an area resulted in a score of 1 for that location. Thus, multiple bites in an area were recorded as a single score, and a single bite that damaged more than one area was scored in each area. If no damage was recorded in an area, a score of 0 was recorded. Both dorsal and ventral damage scores were taken on the grounds that bites to one surface do not necessarily imply bites to the other. This becomes clear when one considers the large diameter of the cricket relative to the jaw size of the mouse, the angle of attack (more from above), the different hardness and resilience of dorsal and ventral surfaces, and the mechanics of the jaw. The two sides of a clamping device with the longer side slightly more anchored will not exert equal or symmetric cutting force.

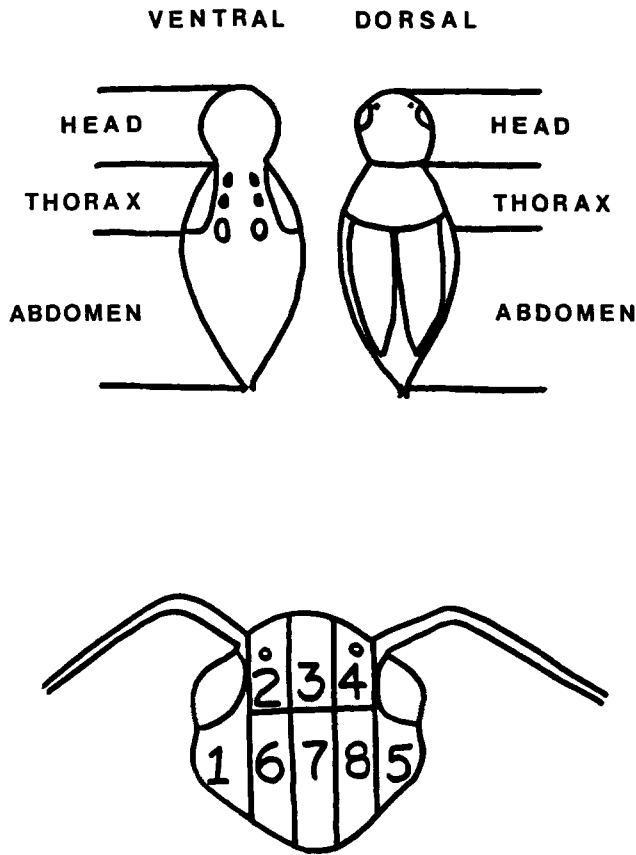


Figure 1. Line drawing of dorsal and ventral surfaces of a house cricket, divided into head, thorax, and abdomen (top); line drawing of the surface of the dorsal head of a house cricket, divided into eight areas, based on Langley (1981; bottom).

Results

General damage location. The general damage location was analyzed by a 2 (species) × 2 (session) × 2 (dorsoventral damage) × 3 (cephalocaudal damage) analysis of variance (ANOVA) with repeated measures on the last three variables. Interactions were tested for significance by computing simple main effects. All post hoc comparisons of means were made by Tukey's honestly significant difference (HSD) tests unless otherwise noted. Preliminary analysis indicated no sex differences, so sex was eliminated as a factor from the analyses presented here (see also Drickamer, 1970).

The results are plotted in Figure 2. Both the dorsoventral variable, $F(1, 16) = 181.80, p < .01$, and the cephalocaudal variable, $F(2, 32) = 129.43, p < .01$, were highly significant, as was the interaction between the two, $F(2, 32) = 32.48, p < .01$. Damage was predominantly dorsal rather than ventral and focused on the head and thorax of a cricket rather than the abdomen ($p < .01$). No simple difference was found between head damage and thoracic damage ($p > .05$). An ANOVA of the interaction between the dorsoventral and cephalocaudal factors revealed that dorsal-head bites were more likely to occur than ventral-head bites, $F(1, 48) = 166.84, p$

$< .01$, and that dorsal-thorax bites were more likely to occur than ventral-thorax bites, $F(1, 48) = 53.22, p < .01$. No difference was found between dorsal- and ventral-abdominal bites, $F(1, 48) = 0.36, p > .05$.

Considering only the dorsal bites, both the head and thorax were damaged significantly more than the abdomen ($p < .01$). No difference was found between dorsal-head and dorsal-thorax damage ($p > .05$). Along the ventral half of the cricket, however, the thorax was bitten more than the head ($p < .01$), and both the head and the thorax were bitten more often than the abdomen ($p < .01$).

A difference between the two species was evidenced by three significant interactions: Species × CephaloCaudal Damage, $F(2, 32) = 10.83, p < .01$; Species × Session × Dorso-Ventral Damage, $F(1, 16) = 10.00, p < .01$; and an interaction between all four variables, $F(2, 32) = 6.10, p < .01$ (see Figure 2). During the first session *P. maniculatus* damaged the dorsal head more often than did *P. leucopus*, $F(1, 192) = 9.62, p < .01$, and *P. leucopus* damaged the ventral thorax more often, $F(1, 192) = 8.20, p < .01$. No differences were found between the species at other locations.

P. leucopus significantly increased dorsal-head bites from the first to the second session, $F(1, 96) = 14.33, p < .01$, and dorsal-thorax bites, $F(1, 96) = 8.84, p < .01$ (see Figure 2). *P. maniculatus* increased ventral-head bites, $F(1, 96) = 7.31, p < .01$. As a result of these adjustments, differences between species during the second session were found only at the dorsal thorax, $F(1, 192) = 16.45, p < .01$, and the ventral thorax, $F(1, 192) = 4.61, p < .05$; *P. leucopus* bit both thoracic areas more than *P. maniculatus*.

Dorsal-head damage. Because the mice directed most of their attacks toward the dorsal head, a finer analysis of this area was performed by dividing the dorsal head into eight areas similar to those of Langley (1981, see the bottom of Figure 1). Data were analyzed by a 2 (species) × 2 (session) × 8 (head region) ANOVA with repeated measures on the last two variables. Significant differences were found among the head regions, $F(7, 112) = 29.87, p < .01$, and this variable interacted with species, $F(7, 112) = 2.55, p < .05$, and sessions, $F(7, 112) = 2.62, p < .05$ (see Figure 3).

Mice of both species scored the most bites in Region 7 (Tukey's HSD test, $ps < .01$). Regions 3 and 8 were the next two most highly scored areas ($ps < .01$), followed by Region 6 ($p < .05$). The mice were least likely to bite Region 1 ($ps < .05$). The only region that changed significantly between the first and second sessions was Region 7. Mice attacked Region 7 more in the second session than the first, $F(1, 128) = 10.81, p < .01$. The only region that differed in attacks between species was Region 3, $F(1, 128) = 3.99, p < .05$; *P. maniculatus* bit this area more than *P. leucopus*.

Latency data. The latencies to initial contact with the cricket were also analyzed by a 2 (species) × 2 (session) × 5 (trial) ANOVA with repeated measures on the last two variables. Again, preliminary analysis indicated no sex differences, and sex was not included in the analyses presented here. Significant main effects were found for session, $F(1, 16) = 8.60, p < .01$, and trial within session, $F(4, 64) = 8.06, p < .01$. The trial-within-session effect occurred because the first cricket

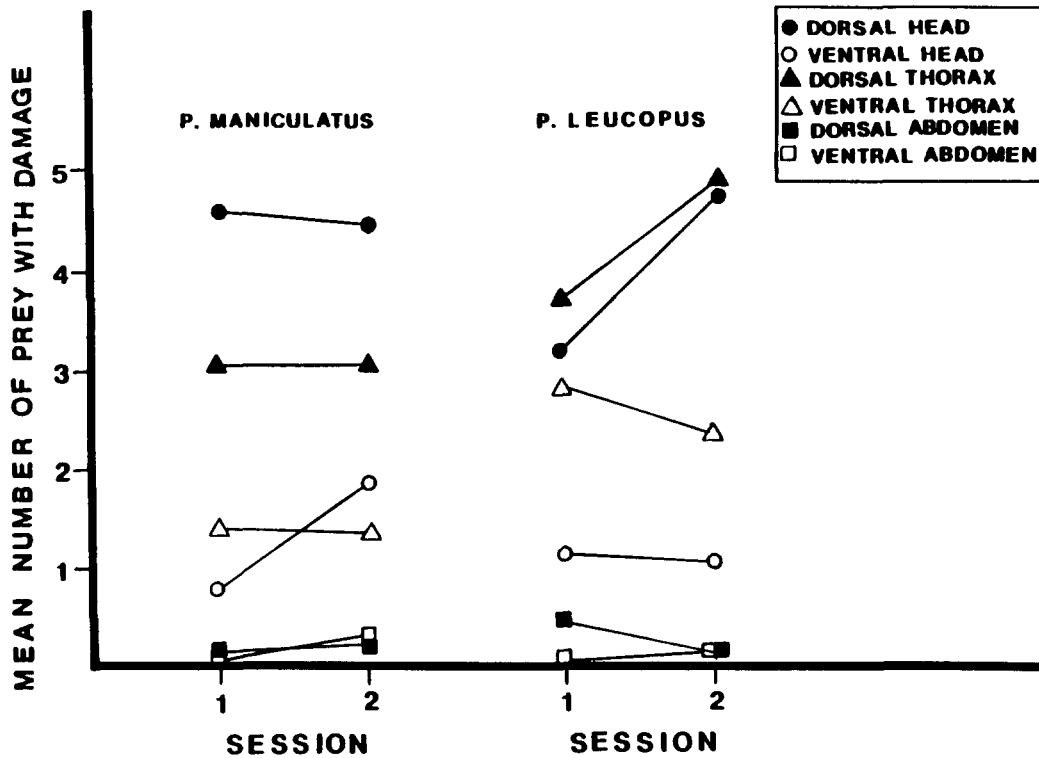


Figure 2. Mean number of crickets per session with body locations damaged by prey-experienced *Peromyscus maniculatus* and *P. leucopus* (Experiment 1).

was attacked more slowly than any others ($p < .01$). The mean latencies to contact with Crickets 1 to 5 (with standard errors in parentheses) were 31.2 (5.3), 14.7 (1.6), 15.3 (2.8), 14.1 (2.4), and 11.8 (1.6) s.

The main effect of sessions reflected an overall tendency to attack more quickly during the second session ($M = 14.7$, $SE = 1.4$) than the first ($M = 20.1$, $SE = 2.5$). A significant Species \times Session interaction reflected this difference, $F(1, 16) = 5.93$, $p < .05$. Whereas latency to contact with the prey did not change between sessions in *P. maniculatus* (Session 1, $M = 14.5$, $SE = 2.0$; Session 2, $M = 13.6$, $SE = 1.4$), *P. leucopus* tended to attack faster during the second session than during the first (Session 1, $M = 25.7$, $SE = 4.5$; Session 2, $M = 15.9$, $SE = 2.5$), $F(1, 16) = 14.41$, $p < .01$. It is worth noting that no animal ever failed to attack a cricket within the 5 min session.

Discussion

The mice of both species tended to damage the dorsal surface more than the ventral surface and to direct their attack toward the anterior portion of the cricket rather than the posterior. Two major deviations from this general topographical scheme were found. First, *P. leucopus* showed a strong thoracic preference in their attacks. Although this could be seen in greater ventral damage during the first session, a more striking difference was found in the increased dorsal-thorax damage during the second session. The tendency for the two species to attack different areas of the cricket was also found

in the analysis of the dorsal head. *P. maniculatus* damaged the center region more often than *P. leucopus*.

Second, the small degree of additional experience that the two sessions provided affected the orientation and latency of attack more for *P. leucopus* than for *P. maniculatus*. During the first session *P. maniculatus* attacked the dorsal head consistently more often than did *P. leucopus*. In the second session, however, *P. leucopus* increased attacks to the dorsal head so that they also attacked this area on nearly every trial. *P. leucopus* also greatly increased the damage to the dorsal thorax and attacked the prey more quickly in the second session. The only change between the two sessions by *P. maniculatus* was a small increase in ventral-head damage.

Experiment 2

Data from Experiment 1 suggest either that adult *P. maniculatus* have a greater natural tendency for head-oriented attacks than *P. leucopus* or that they changed their attack orientation more rapidly or permanently as a function of previous experience with crickets. Considerable previous research has shown that experience can play a large role in the initial development of predatory behavior in naive rodents. For example, experience has been shown to be an important variable in the predatory efficiency of hamsters (Polsky, 1975), northern grasshopper mice (*Onychomys leucogaster*; Boice & Schmeck, 1968), and southern grasshopper mice (*Onychomys torridus*; Langley, 1981). In a potentially related skill, Eisenberg (1968) demonstrated that *P. maniculatus* required practice to use an efficient nut-opening technique.

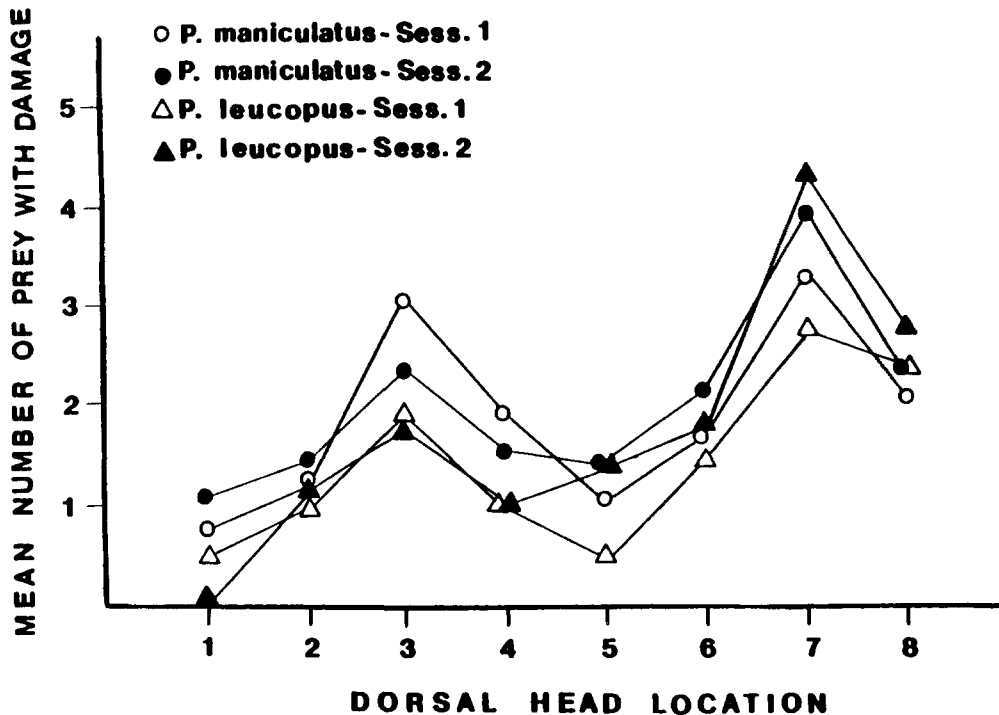


Figure 3. Mean number of crickets with dorsal head areas damaged by prey-experienced *Peromyscus maniculatus* and *P. leucopus* (Experiment 1). (The continuous lines connecting areas damaged in this and Figure 5 do not imply that location is a continuous variable. They are meant to facilitate comparison of the pattern of damage across species and sessions.)

The purpose of the present experiment was to examine the development of predatory behavior in naive adult *P. maniculatus* and *P. leucopus*. If experience was the critical determinant of species differences in Experiment 1, we expected to see these differences develop over sessions. We also expected to determine the relative contribution of initial experience to the general similarity in predatory attack of the two species.

Method

Subjects. The subjects were 6 laboratory-raised *P. maniculatus bairdi* (3 female and 3 male) and 6 laboratory-raised *P. leucopus noveboracensis* (2 female and 4 male), each weighing approximately 15–20 gm. The subjects had no previous experience with crickets and ranged in age from .4 to .8 year. The mice were maintained and housed in the same manner as the subjects in Experiment 1.

Apparatus and procedure. The method of testing the inexperienced subjects was identical to that of Experiment 1 with one exception. The mice in Experiment 2 were tested for five sessions of five trials each instead of two sessions.

Results

General damage location. Results for the inexperienced mice are shown in Figure 4. In contrast to Experiment 1, no significant species effect or interaction involving species was found. Preliminary analysis did not indicate any differences

between sexes. Thus, our analyses did not include species or sex as a variable. Again, Tukey's HSD test was used for all post hoc comparisons unless otherwise noted.

As in Experiment 1, both the dorsoventral-damage variable, $F(1, 10) = 103.36, p < .01$, and the cephalocaudal-damage variable, $F(2, 20) = 7.56, p < .01$, were highly significant, as was their interaction, $F(2, 20) = 28.62, p < .01$. Inexperienced mice tended to bite dorsally rather than ventrally and to bite the head more than the thorax or abdomen (all $ps < .01$). Also, there was more thoracic damage than abdominal damage ($p < .01$). The same linear relation between head, thorax, and abdomen was also preserved when only the dorsal bites were considered ($p < .01$). For ventral damage, however, no difference was found between head and thoracic bites ($p > .05$), and both were higher than abdominal damage ($ps < .01$).

The effect of experience on the placement of predatory bites is shown by significant interactions between sessions and the dorsoventral variable, $F(4, 40) = 16.49, p < .01$, between sessions and the cephalocaudal variable, $F(2, 20) = 28.62, p < .01$, and between sessions, dorsoventral damage, and cephalocaudal damage, $F(8, 80) = 5.74, p < .01$.

Overall, dorsal and ventral attacks during the first session did not differ, $F(1, 50) = 2.21, p > .05$. However, the ventral thorax was damaged more than the dorsal thorax, $F(1, 150) = 5.40, p < .05$, and the dorsal abdomen was damaged more than the ventral abdomen, $F(1, 150) = 6.53, p < .05$. Also, no differences were found in damage to the dorsal head, thorax, and abdomen, $F(2, 200) = 2.73, p > .05$. However,

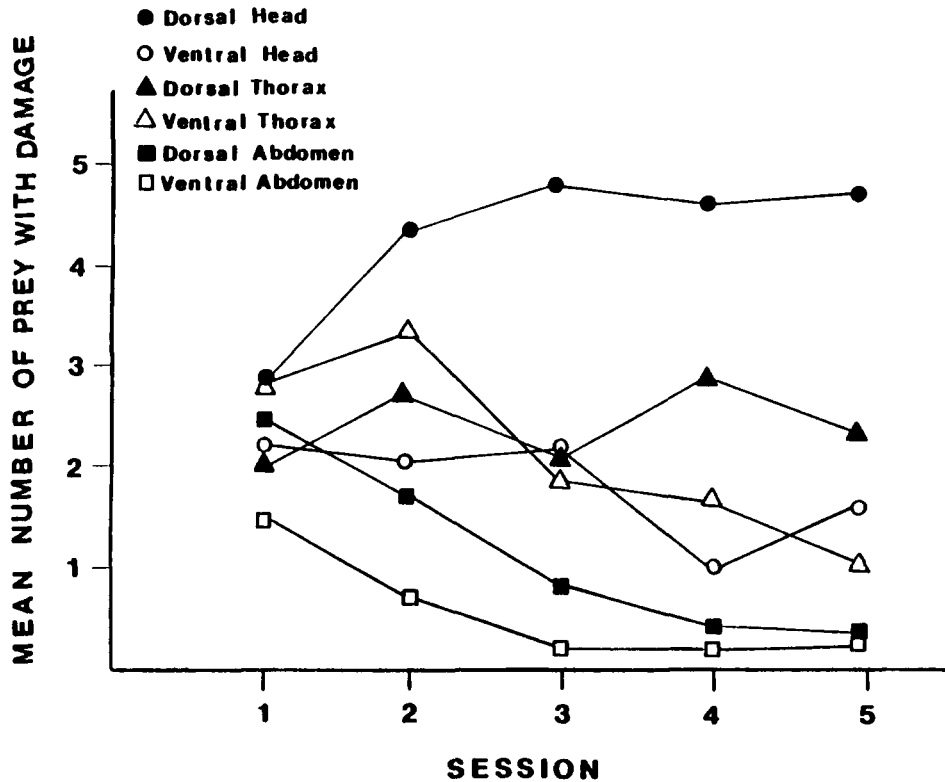


Figure 4. Mean number of crickets per session with body locations damaged by prey-inexperienced *Peromyscus maniculatus* and *P. leucopus* (Experiment 2).

the ventral thorax was damaged more than the abdomen ($p < .01$).

Dorsal-head damage increased significantly from the first session to the second ($p < .01$), and the dorsal head was the highest scored area during the second session and all subsequent sessions ($ps < .05$). This result indicates a very rapid focus on attack in this area. Bites directed toward the ventral head remained relatively constant across sessions. Attacks on the dorsal thorax also did not change over sessions, $F(4, 240) = 1.81$, $p > .05$, but with decreases in most other areas, the dorsal thorax was the second most damaged area during both the fourth and fifth sessions ($ps < .05$). Damage to the ventral thorax declined significantly from the first to the third session ($p < .01$) and remained low. Dorsal-and ventral-abdomen scores also declined significantly from the first to the third session and then remained near zero.

Dorsal-head damage. A 2 (species) \times 5 (session) \times 8 (head region) ANOVA with repeated measures on the last two variables was performed on the dorsal-head data. As in Experiment 1, the dorsal head was divided into eight areas similar to those of Langley (1981). Again, no species differences were revealed. However, a significant session effect, $F(4, 40) = 5.94$, $p < .01$, location effect, $F(7, 70) = 67.06$, $p < .01$, and interaction between session and location, $F(28, 280) = 2.03$, $p < .01$, were found.

Even during the first session, inexperienced mice that bit the dorsal head did so selectively (see Figure 5). Four areas were bitten more often than the others, 3, 6, 7, and 8 ($ps < .05$). Of these four areas Region 7 was bitten significantly more than any other ($ps < .01$). Regions 3, 6, and 8 were bitten with equal frequency ($p > .05$). Regions 7 and 8 showed significant increases in damage across sessions, $F_s(4, 320) = 14.8$ and 3.74 , $ps < .01$. During the second session both regions were damaged more often than during the first ($ps < .01$). Mice concentrated even more heavily on Region 7 during the third session than they had during the second ($p < .01$). A significant increase in bites to Region 8 was found between the second and fifth sessions ($p < .01$).

Latency data. The latencies to initial contact for the inexperienced mice were analyzed by a 2 (species) \times 5 (session) \times 5 (trials) ANOVA with repeated measures on the last two variables. Both the session variable, $F(4, 40) = 3.24$, $p < .05$, and the trials-within-sessions variable, $F(4, 40) = 6.55$, $p < .01$, showed significant decreases in latency. No differences were found between species, and no interactions were significant.

Inexperienced mice did not attack prey as quickly during their first session ($M = 70.6$, $SE = 13.7$) as they did during Session 4 ($M = 12.7$, $SE = 1.4$) and Session 5 ($M = 10.2$, $SE = 0.8$; $ps < .05$). Within sessions the mice averaged longer to

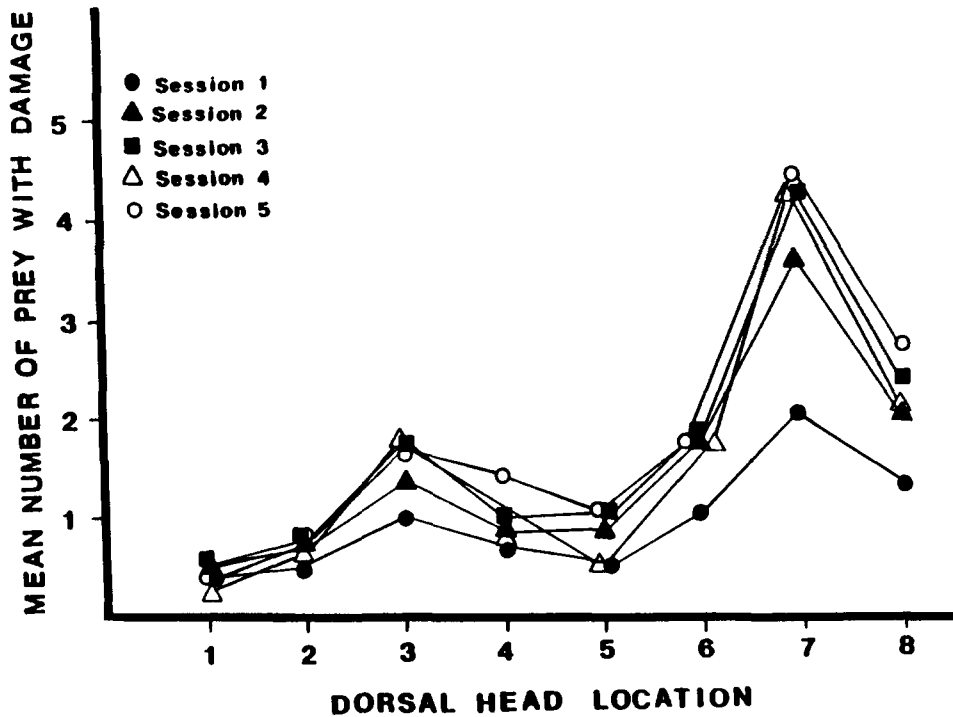


Figure 5. Mean number of crickets with dorsal head areas damaged by prey-inexperienced *Peromyscus maniculatus* and *P. leucopus* (Experiment 2).

attack the first prey item introduced ($M = 35.0$, $SE = 7.4$) than they did to attack the third ($M = 26.3$, $SE = 7.0$), fourth ($M = 23.8$, $SE = 7.2$), or fifth ($M = 20.7$, $SE = 6.8$) prey ($ps < .05$). With the exception of one animal of each species during Session 1, all animals attacked every cricket.

Discussion

The results show that prey experience was clearly an important contributor to predatory behavior. When completely naive, neither species displayed preferences for damaging the head, thorax, or abdomen of the cricket, but this changed rapidly. After one session of predatory experience, both species bit the dorsal head more than any other area although markedly decreasing attacks to abdominal areas. Furthermore, there were no significant changes in scores over the last three sessions, except that the ventral-head scores declined between the third and fourth sessions.

However, detailed analyses of the crickets' heads revealed that dorsal-head bites were concentrated on the central regions even during the first session. When coupled with the haphazard manner in which bites were distributed across segments of the cricket during the first session, this finding suggests that although mice learn many of their predatory strategies, constraints for attacking in a specific manner also exist. The extent to which these constraints are based on the interaction of the physical structure or behavior of the mouse with that of the cricket remains unclear.

Further evidence for the role of learning in the acquisition of predatory behaviors was found in the latency data. Both *Peromyscus* species contacted their prey more quickly after the first session. A priming effect was also found within sessions in that the first prey item was not attacked as quickly as subsequent prey. Informal observation indicated that the latency decreases both within and between sessions resulted from a decrease in preliminary behaviors such as sniffing and retreating, burrowing, and grooming.

Finally, contrary to the findings of Experiment 1, no species differences emerged in Experiment 2. Inexperienced *P. leucopus* did not attack the thoracic areas significantly more than *P. maniculatus* during any of the five sessions. During the last sessions both species attacked crickets in a manner similar to the attacks of experienced *P. maniculatus* from Experiment 1.

Experiment 3

In Experiment 1 we found that moderately experienced *P. leucopus* damaged the thorax of the cricket more than did *P. maniculatus*. However, the naive *P. leucopus* of Experiment 2 did not display this tendency after a comparable number of exposures to crickets; they instead resembled experienced *P. maniculatus* in their damage patterns. One obvious difference between the mice was age. The subjects used in Experiment 1 were approximately 1.5 years of age when tested, whereas the ages of subjects in Experiment 2 were between .4 and .8

years. The purpose of the present experiment was to determine if the differences in the behavior of *P. leucopus* in Experiments 1 and 2 were due simply to maturation. To this end the *P. leucopus* from Experiment 2 were tested 1 year later with no further predatory experience. This lapse of time placed them on a comparable level with the experienced animals in Experiment 1 in both age and experience with prey. Both sets of mice received brief experience with crickets as prey around .5 year of age and no further experience with any prey but meal worms until testing 1 year later. The *P. maniculatus* from Experiment 2 were not retested because their behavior was identical with that of the older *P. maniculatus* from Experiment 1.

Method

Subjects. The subjects were 5 of the original *P. leucopus noveboracensis* from Experiment 2 (2 female and 3 male), approximately 1.5 years of age. The 6th animal had died.

Apparatus and procedure. The apparatus and procedure were the same as in Experiment 1.

Results and discussion

The retest data are shown in Table 1 along with the data of the same mice 1 year earlier (Experiment 2) and the data of the group of 1.5-year-old *P. leucopus* from Experiment 1. A 2 (group) \times 2 (session) \times 2 (dorsoventral damage) \times 3 (cephalocaudal damage) ANOVA with repeated measures on the last three variables showed no significant difference between the retest data and the data from Experiment 1, $F(1, 12) = 0.53, p > .05$, and no interaction involving the group factor, $F_s(2, 24) < 2.99, p > .05$.

The data from the retest were also compared with the data from the subjects' own first and fifth sessions of testing during Experiment 2. A 2 (time of testing) \times 2 (sessions) \times 2 (dorsoventral damage) \times 3 (cephalocaudal damage) ANOVA with repeated measures showed significant interactions, Time of Testing \times Session \times CephaloCaudal Damage, $F(2, 16) = 6.03, p < .05$, and the interaction between all four variables, $F(2, 16) = 9.34, p < .01$. Computation of simple main effects

revealed that the four-way interaction was a result of the greater damage delivered to both the dorsal thorax, $F(1, 96) = 5.37, p < .05$, and the ventral thorax, $F(1, 96) = 8.88, p < .01$, by the mice during the second session of their retest.

In sum, when retested approximately 1 year after their first and only exposure to crickets, *P. leucopus* changed their attacks on crickets by increased orientation to the thoracic area. The changed distribution of attacks was consistent with the data from *P. leucopus* of comparable age from Experiment 1. Thus, it appears that whereas moderately young adult *P. leucopus* and *P. maniculatus* initially learn to attack crickets in a similar manner, *P. leucopus* later increases the frequency of attacks to the thorax. This change does not appear to depend on continued predatory experience but may be related to continued maturation.

General Discussion

Species Comparisons

P. maniculatus bairdi and *P. leucopus noveboracensis* from 5 to 18 months of age showed very similar predatory behaviors. The mice approached the cricket from the side and back, seized and pinned it with the front paws, and bit it in rapid bursts before releasing it. This pattern of predatory activity typically was repeated until the cricket remained motionless when released. Prey-naive mice randomly damaged the cricket's major body divisions (head, thorax, abdomen), whereas with a small amount of experience, mice differentially damaged the dorsal head in the area of the supraesophageal ganglion. When naive, both species decreased the latency of attack over sessions, and whether experienced or naive, they decreased the latency to attack over trials within a session.

The tendency to bite the head and especially the center area of the dorsal head is probably related to immobilizing the cricket (Langley, 1981), which presumably results from damage to the underlying supraesophageal ganglia. Such immobilization is important to small animals like *P. maniculatus* and *P. leucopus*, which otherwise have difficulty restraining the cricket while eating it. It is possible that the thoracic

Table 1

Mean numbers of crickets (out of 5) damaged at a particular location by *Peromyscus leucopus noveboracensis* as a function of sessions and experiments

Experiment and session	Location of damage					
	Dorsal			Ventral		
	Head	Thorax	Abdomen	Head	Thorax	Abdomen
	$M \pm SE$	$M \pm SE$	$M \pm SE$	$M \pm SE$	$M \pm SE$	$M \pm SE$
Experiment 1 (Experienced, $N = 9$)						
Session 1	3.1 \pm 0.5	3.7 \pm 0.4	0.4 \pm 0.2	1.1 \pm 0.4	2.8 \pm 0.3	0.0 \pm 0.0
Session 2	4.7 \pm 0.2	4.9 \pm 0.1	0.1 \pm 0.1	1.0 \pm 0.5	2.3 \pm 1.2	0.0 \pm 0.0
Experiment 2 (Naive, $N = 5$)						
Session 1	2.2 \pm 0.6	2.0 \pm 0.6	2.6 \pm 0.7	1.4 \pm 0.5	2.4 \pm 0.7	1.4 \pm 0.4
Session 5	4.8 \pm 0.2	3.0 \pm 0.3	0.2 \pm 0.2	1.0 \pm 0.4	0.8 \pm 0.4	0.2 \pm 0.2
Experiment 3 (Retested, $N = 5$)						
Session 1	3.2 \pm 0.5	2.8 \pm 0.5	1.4 \pm 0.5	1.0 \pm 0.4	2.2 \pm 0.4	0.6 \pm 0.2
Session 2	4.0 \pm 0.6	4.4 \pm 0.2	1.4 \pm 0.4	1.6 \pm 0.2	2.6 \pm 0.2	0.4 \pm 0.2

orientation of bites in older *P. leucopus* can be traced to a similar function, namely immobilization of the cricket by damage to the thoracic ganglia controlling the crickets' jumping legs.

However, in addition to obvious similarities in the predatory behavior of the two species, there were a few important differences. One difference was the emergence of a tendency for older *P. leucopus* (1.5 years) to bite the thorax as well as the anterior region of the dorsal head. A possible explanation for this change is that *P. leucopus* increased slightly in size and weight and perhaps also in jaw morphology and strength (Holbrook, 1982). A second difference between the species was that *P. leucopus* modified its behavior as a function of experience over a wider age range. As older adults with moderate experience with crickets, *P. leucopus* continued to adjust their bite placement from the first test session to the second (Experiments 1 and 3). They also significantly decreased their latency to contact the prey from the first to the second session.

The present data when combined with those of Drickamer (1972) and Whitaker (1966) support the view that *P. maniculatus bairdi* is capable of very rapid and stable adjustments in feeding behavior, especially as juveniles and young adults. These propensities are compatible with its position as a generalist within a relatively stable environment (Baker, 1968). In contrast, *P. leucopus noveboracensis* appears to make rapid but slightly less stable adjustments in feeding behavior that continue to change with experience and maturation across a wide age range. These tendencies are compatible with the greater diversity of habitats occupied by *P. leucopus* and with its dispersing ability (Drickamer, 1972). Research examining more subspecies of *P. maniculatus* and *P. leucopus*, more prey types, and experience at different ages is necessary to evaluate these hypotheses more carefully. Generalizations to other forms of learning may also be possible (e.g., Dice & Clark, 1962; King, 1960).

Role of Experience in Predation

Taken together, the results of these experiments suggest an important role for experience in cricket predation in both species. Over sessions both *P. maniculatus bairdi* and *P. leucopus noveboracensis* markedly decreased their latency of attack and increased the focus of their bites on the center region of the dorsal head. These results appear to argue for the importance of some degree of trial-and-error learning in predation (e.g., Eibl-Eibesfeldt, 1970; Langley, 1981). However, three findings markedly qualify the nature and expression of such learning. First, even in the absence of experience, when a bite to the head occurred, there was a tendency to bite the center region of the dorsal head. Apparently, the major learning effect was to focus bites on the head as opposed to the remainder of the body. A similar increased tendency to bite the head in experienced animals was shown by Cyr (1972) and Langley (1981) in studying cricket predation in the southern grasshopper mouse (*O. torridus*). Second, learning to bite the head was extremely rapid and stable. Both species markedly increased biting the head within one session of access to crickets and after five total sessions maintained this orienting

tendency without further predatory experience for a period exceeding 1 year. Third, the development of a thoracic focus of attack in older *P. leucopus* appeared to result not from experience alone but from a maturational process interacting with subsequent experience.

In sum, it appears that the predatory subsystem of feeding in *Peromyscus* consists of a bite-orientation element that is readily linked to head attacks even with minimal experience. This subsystem also allows development of thorax aiming in older *P. leucopus*. This combination of built-in and learned components of predatory behavior is surprisingly similar to that in more prototypical mammalian predators, such as cats (Eisenberg & Leyhausen, 1972; Leyhausen, 1956/1979), as well as that in other rodents (e.g., Langley, 1981; Polsky, 1977a, 1977b, 1977c, 1978a). This similarity suggests that rodents may provide a diverse and accessible mammalian group for studying the evolution and mechanisms of predation.

References

- Baker, R. H. (1968). Habitats and distribution. In J. A. King (Ed.), *Biology of Peromyscus (Rodentia)* (Special Publication No. 2, pp. 98-147). Stillwater, OK: American Society of Mammalogists.
- Barr, G., Gibbons, J., & Moyer, K. (1975). The relationship between mouse killing and intraspecific fighting in the albino rat. *Behavioral Biology*, 14, 201-208.
- Baxter, C. (1979). Cricket predation by the northern grasshopper mouse. *Behavioral and Neural Biology*, 2, 201-213.
- Boice, R., & Schmeck, R. (1968). Predatory behaviors of grasshopper mice (*Onychomys leucogaster*). *American Zoologist*, 8, 751.
- Brack, C. (1981). *Effects of maturation and experience upon a predatory sequence in the Mongolian gerbil (Meriones unguiculatus)*. Unpublished master's thesis, Purdue University, Lafayette, IN.
- Brack, G. L. (1981). *The development of cricket-catching behavior in the Mongolian gerbil (Meriones unguiculatus)*. Unpublished master's thesis, Purdue University, Lafayette, IN.
- Butler, K. (1973). Predatory behavior in laboratory mice: Sex and strain comparisons. *Journal of Comparative and Physiological Psychology*, 85, 243-249.
- Cyr, M. (1972). Predatory behavior of the grasshopper mouse (*Onychomys*) (Doctoral dissertation, University of California at Los Angeles). *Dissertation Abstracts International*, 33, 3382B.
- Dice, C. R., & Clark, P. J. (1962). Variation in measures of behavior among three races of *Peromyscus*. *Contributions from the Laboratory of Vertebrate Biology of the University of Michigan*, 76, 1-28.
- Drickamer, L. C. (1970). Seed preferences in wild caught *Peromyscus maniculatus bairdi* and *P. leucopus noveboracensis*. *Journal of Mammalogy*, 51, 191-194.
- Drickamer, L. C. (1972). Experience and selection behavior in the food habits of *Peromyscus*: Use of olfaction. *Behaviour*, 41, 269-287.
- Eibl-Eibesfeldt, I. (1970). *Ethology: The biology of behavior*. New York: Holt, Rinehart & Winston.
- Eisenberg, J. (1968). Behavior patterns. In J. A. King (Ed.), *Biology of Peromyscus (Rodentia)* (Special Publication No. 2, pp. 451-495). Stillwater, OK: American Society of Mammalogists.
- Eisenberg, J., & Leyhausen, P. (1972). The phylogenesis of predatory behavior in mammals. *Zeitschrift für Tierpsychologie*, 30, 59-93.
- Hall, E. R., & Kelson, K. R. (1959). *The mammals of North America* (Vol. 2). New York: Ronald Press.
- Holbrook, S. (1982). Ecological inferences from mandibular mor-

- phology of *Peromyscus maniculatus*. *Journal of Mammalogy*, 63, 399–408.
- Hooper, E. T. (1968). Classification. In J. A. King (Ed.), *Biology of Peromyscus (Rodentia)* (Special Publication No. 2, pp. 27–74). Stillwater, OK: American Society of Mammalogists.
- Karli, P. (1956). The Norway rat's killing response to the white mouse: An experimental analysis. *Behaviour*, 10, 81–103.
- King, J. A. (1960). Swimming and reaction to electric shock in two subspecies of deer mice (*Peromyscus maniculatus*) during development. *Animal Behaviour*, 9, 142–158.
- Landry, S. (1970). The rodentia as omnivores. *Quarterly Review of Biology*, 45, 351–372.
- Langley, W. (1981). The effect of prey defenses on the attack behavior of the southern grasshopper mouse (*Onychomys torridus*). *Zeitschrift für Tierpsychologie*, 56, 115–127.
- Langley, W. (1983). Stimulus control of feeding behavior in the grasshopper mouse. *Zeitschrift für Tierpsychologie*, 62, 291–306.
- Leyhausen, P. (1979). *Cat behavior* (B. A. Tonkins, Trans.). New York: Garland Publishing. (Original work published 1956)
- Moyer, K. (1968). Kinds of aggression and their physiological basis. *Communications in Behavioral Biology*, 2, 65–87.
- O'Boyle, M. (1974). Rats and mice together: The predatory nature of the rat's mouse-killing response. *Psychological Bulletin*, 81, 262–269.
- O'Boyle, M. (1975). The rat as a predator. *Psychological Bulletin*, 82, 460–462.
- Osgood, W. H. (1909). Revision of the mice of the American genus *Peromyscus*. *North American Fauna*, 28, 1–285.
- Polsky, R. H. (1975). The ontogeny of predatory behaviour in the golden hamster (*Mesocricetus a. auratus*) (Doctoral dissertation, University of Leicester, Great Britain). *Dissertation Abstracts International*, 37, 1011B.
- Polsky, R. H. (1977a). The ontogeny of predatory behavior in the golden hamster (*Mesocricetus a. auratus*): I. The influence of age and experience. *Behaviour*, 61, 26–57.
- Polsky, R. H. (1977b). The ontogeny of predatory behavior in the golden hamster (*Mesocricetus a. auratus*): II. The nature of experience. *Behaviour*, 61, 58–81.
- Polsky, R. H. (1977c). The ontogeny of predatory behavior in the golden hamster (*M. a. auratus*): III. Sensory preexposure. *Behaviour*, 63, 175–191.
- Polsky, R. H. (1978a). The ontogeny of predatory behavior in the golden hamster (*Mesocricetus a. auratus*): IV. Effects of prolonged exposure, ITI, size of prey and selective breeding. *Behaviour*, 65, 27–39.
- Polsky, R. H. (1978b). Influence of eating dead prey on subsequent capture of live prey in golden hamsters. *Physiology and Behavior*, 20, 677–680.
- Robbins, L. W., & Baker, R. J. (1981). An assessment of the nature of chromosomal rearrangements in 18 species of *Peromyscus* (Rodentia: Cricetidae). *Cytogenetics and Cell Genetics*, 31, 194–202.
- Rogers, D. S., Greenbaum, I. F., Gunn, S. J., & Engstrom, M. D. (1984). Cytosystematic value of chromosomal inversion data in the genus *Peromyscus* (Rodentia: Cricetidae). *Journal of Mammalogy*, 65, 457–465.
- Stangl, F. B., & Baker, R. J. (1984). Evolutionary relationships in *Peromyscus*: Congruence in chromosomal, genic, and classical data sets. *Journal of Mammalogy*, 65, 643–654.
- Thomas, K. (1969). Predatory behavior in two strains of laboratory mice. *Psychonomic Science*, 15, 13–14.
- Van Hemel, P. (1975). Rats and mice together: The aggressive nature of mouse-killing by rats. *Psychological Bulletin*, 82, 456–459.
- Whalen, R., & Fehr, H. (1964). The development of the mouse killing response in rats. *Psychonomic Science*, 1, 77–78.
- Whelton, J., Jr., & O'Boyle, M. (1977). Early experience and the development of predatory and intraspecific aggression in mice. *Animal Learning and Behavior*, 3, 291–296.
- Whitaker, J., Jr. (1966). Food of *Mus musculus*, *Peromyscus maniculatus bairdii*, and *Peromyscus leucopus* in Vigo County, Indiana. *Journal of Mammalogy*, 47, 473–486.
- Wolff, J. O., Dueser, R. D., & Berry, K. S. (1985). Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. *Journal of Mammalogy*, 66, 795–798.

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