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CONNIE ISAACS
University of New Hampshire, Durham

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University of New Hampshire PH.D. 1986

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ANTI-MOSQUITO BEHAVIOR OF ADULT AND JUVENILE WHITE-FOOTED MICE (PEROMYSCUS LEUCOPUS)

BY

CONNIE ISAACS
B.S., East Tennessee State University, 1976

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in

Zoology

May, 1986

This dissertation has been examined and approved.

Edward N. Francq

Dissertation Co-director, Edward N. Francq
Associate Professor of Zoology

John F. Burger

Dissertation Co-director, John F. Burger
Associate Professor of Entomology

Arthur C. Borror, Professor of Zoology

Wilbur L. Bullock

Wilbur L. Bullock, Professor of Zoology

John D. Edman, Professor of Entomology
University of Massachusetts at Amherst

April 16, 1986
Date

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Connie Isaacs

DEDICATION

With love to Dad, Mom, Betty, and Bill

ACKNOWLEDGMENTS

My parents, William and Betty Isaacs, have my deepest gratitude for their many expressions of love and support. Their good sense and good humor, plus astute editorial contributions, were invaluable. I thank my sister Betty and my brother Bill for their loving interest and encouragement, and for providing timely diversions.

I benefitted in many ways from the complementary input of my co-advisors. I appreciate the generous guidance, assistance, and enthusiasm of Dr. John Burger during all phases of the project. His willingness to introduce me to many aspects of the study of mosquitoes was essential. I thank Dr. Edward Francq for his kind interest and contributions, especially regarding mammals. I also thank Dr. Arthur Borror, Dr. Wilbur Bullock, and Dr. John Edman for their helpful suggestions and consideration.

I am very grateful for the congeniality and support of my fellow graduate students, especially Nadine Folino, Nick Conrad, Liz McLean, and Lauren Fellows McBride. Each has given me a cherished friendship. I also appreciate the support and assistance of John Coughlin during the research.

Dr. Jerry Nagel deserves special acknowledgment, for it was he who, as my undergraduate advisor, introduced me to the study of animal behavior and fostered my interest in graduate work. I am very thankful for his challenging, insightful advice and continued interest.

I appreciate the help of others at particular times. During my preliminary work, Dr. Paul Johnson helped provide facilities and Dr. Louis Magnarelli provided a constructive discussion. Peter Dollard aided me in collecting mosquitoes and constructing apparatus, and Bill

Collins instructed me in trapping mammals locally. Mr. Owen Durgin of the UNH Office of Biometrics offered suggestions regarding data analysis. I appreciate the sincere encouragement of Dr. Edward Tillinghast during my graduate career, and his patience as a summer employer when I needed a flexible schedule. I deeply appreciate the knowledge and cheerful assistance of Eileen Wong in preparing the dissertation and taming the word processor. The fellowship of Newmarket Community Church was a continual source of personal warmth, challenge, and inspiration.

My graduate endeavors were supported by UNH through teaching assistantships, summer fellowships, a grant from the Central University Research Fund, and a dissertation fellowship.

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ABSTRACT

ANTI-MOSQUITO BEHAVIOR OF ADULT AND JUVENILE WHITE-FOOTED MICE (PEROMYSCUS LEUCOPUS)

by

Connie Isaacs
University of New Hampshire, May, 1986

Rodents seldom are identified as hosts for mosquitoes, based on serological analysis of bloodmeals. However, due to limited survey and lack of sensitivity in most bloodmeal analyses, host species can be misrepresented or undetected. Knowledge of behavior of a potential host species can complement results of bloodmeal analysis, because active vertebrates may prevent mosquito feeding and thus rarely serve as hosts. The objectives of this study were to characterize anti-mosquito behavior in the white-footed mouse (*Peromyscus leucopus noveboracensis*) and to examine effectiveness of such behavior in mice based on age, prior exposure to mosquitoes, and immediate environment.

I used wild-stock *Aedes triseriatus* mosquitoes, reared in lab, in experiments with four groups of mice: (1) wild-caught adult males in a barren enclosure; (2) wild-caught adult males in an enclosure with seeds and nest material that could be manipulated, simulating natural activity; (3) adult males from a lab colony of *P. leucopus*; and (4) wild-stock, lab-reared juveniles with or without "practice" (prior exposure to mosquitoes). I used an electronic event recorder to monitor grooming, exploring, resting, and anti-mosquito actions. I observed each mouse without and then with mosquitoes. I then anesthetized each mouse to verify that lack of mosquito feeding success on the non-anesthetized (active) mouse was due to mouse behavior.

Results indicated that the role of prior exposure to mosquitoes was minimal. Wild adult mice maintained defense while handling and eating seeds, implying that anti-mosquito behavior probably is an integral part of their activity in nature. Certain actions, such as ear-flick, occurred almost exclusively when mosquitoes were present. Juveniles usually caught, killed, and ate more mosquitoes than did adults. Individuality of mouse behavior affected the outcome of mouse-mosquito interactions. All mice, except one, had highly effective defense against mosquitoes. Therefore, *P. leucopus* probably rarely serves as host for mosquitoes in nature and, thus, as host or reservoir for mosquito-borne diseases.

FIGURE 1. An adult mouse resting with a mosquito probing on top of his head.

FIGURE 2. An adult mouse shaking his head, preventing a mosquito from landing on the mouse. Several mosquitoes which the mouse killed are lying on the floor.

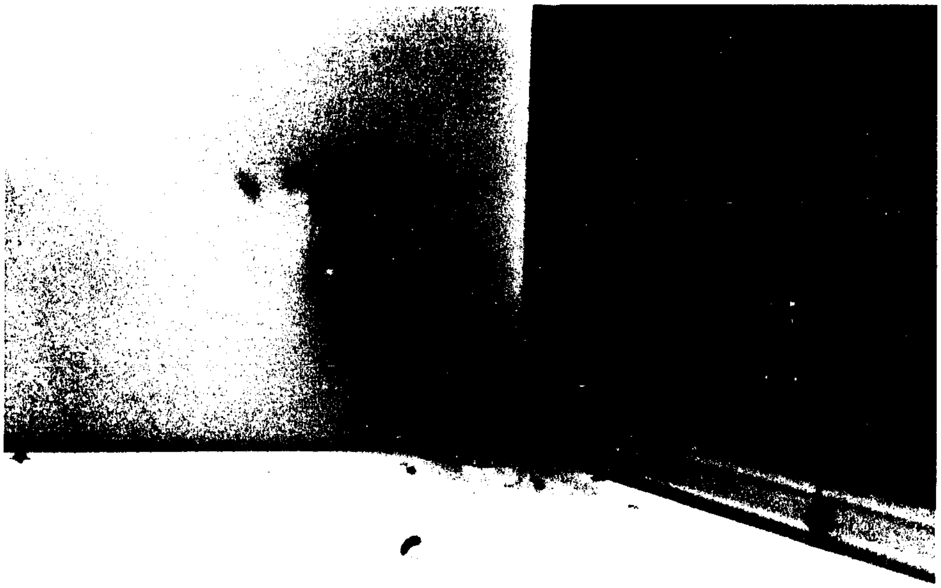

FIGURE 3. An adult mouse extending toward hovering mosquitoes.

FIGURE 4. An adult mouse catching a mosquito.

INTRODUCTION

Perspective

As vectors of disease and as pests, mosquitoes have profound effects upon human health, economy, and culture, and on the health of livestock, pets, and wildlife, in many parts of the world. Male mosquitoes feed on plant juices and nectars, but meal acquisition by females depends on species and circumstances. Female mosquitoes of autogenous species can rely on stored nutrients from the larval stage for development of eggs in the first gonotrophic cycle, but need a bloodmeal to develop subsequent clutches of eggs. However, most species are anautogenous, and must obtain a bloodmeal to complete oogenesis (Clements, 1963; Wood *et al.*, 1979), although plants may continue to be used intermittently as a food source for flight energy (Magnarelli, 1978).

Entomological and epidemiological studies have documented the biology, ecology, and behavior of major mosquito species (Diptera: Culicidae) serving as disease vectors and pests. The mosquito's feeding process can be influenced by many factors, such as carbon dioxide, heat, and odors emitted by a potential host (Gillies, 1980), phagostimulants such as ADP/ATP, parity of the mosquito (Crans *et al.*, 1976; Klowden and Lea, 1980; Mather and DeFoliart, 1984), the mosquito's past feeding history (Buescher and Bickley, 1979), and the habitat and flight path of the mosquito (Bidlingmayer, 1971; McCrae and Boreham, 1976; Nasci, 1982). Host size (Edman and Webber, 1974) and health (Day and Edman, 1983; Day *et al.*, 1983) also can affect mosquito feeding success.

However, the role of the potential host's behavioral response to the mosquito's host-seeking and feeding process has been largely ignored, particularly in mammals. Knowledge of this behavior would contribute to an understanding of the epidemiology of certain arthropod-borne diseases, including arboviruses, such as encephalitides. For example, vector potential of a mosquito may be increased if bloodmeal acquisition is interrupted by host behavior, thus causing the mosquito to seek completion of the meal on another animal.

Bloodmeal Identification

Knowledge of host behavior also is needed to complement results of bloodmeal identification studies, which usually are based on serological tests of limited value. The most commonly used method, the precipitin test, can be misrepresentative. It does not assure identification of mammal blood to the species level, since cross-reactions to serum proteins can occur between closely-related species (Tempelis, 1975; Washino and Tempelis, 1983). Although this poses a minimal problem in localities where only one species of a given mammalian family occurs, the occurrence of multiple intraspecific bloodmeals still would not be detected. This lack of sensitivity may contribute to the variation in percentages of multiple bloodmeals reported in different studies. Because inter- and intra-specific multiple bloodfeeding are important in the transmission of arthropod-borne diseases (Reeves, 1971; Watts *et al.*, 1972; Klowden and Lea, 1979), inaccurate detection can result in inaccurate estimation of the vector potential of a mosquito species and the importance of a potential host species as a reservoir for disease. Also, most workers test only for the most common, often large, mammals in a given locality, thus precluding detection of other bloodmeal sources. Other problems associated with bloodmeal identification by serological methods include inadequate samples of freshly blood-fed females in the field and potential biases associated with collecting methods, such as aspiration and sweep-netting (Bidlingmayer and Edman, 1967; Hess *et al.*, 1968; Edman, 1971).

More sensitive serological methods have been considered for use in bloodmeal identification but each has one or more serious disadvantages (Tempelis, 1975; Washino and Tempelis, 1983). The FA (fluorescent antibody) technique is impractical due to the need for elaborate equipment, and has not been used extensively. The PHI (passive hemagglutination inhibition) method has had very limited usage, because the purified reagents are difficult to prepare. ELISA (enzyme-linked immunosorbent assay) is a recently-developed technique that might be practical in automated laboratories. However, like the PHI method, it requires preliminary screening of bloodmeals by the precipitin test, and is reliable only for relatively fresh bloodmeals.

In summary, current knowledge of mosquito bloodmeal sources is inadequate and possibly inaccurate, due to limited survey and sensitivity in serological testing. Future acquisition of such knowledge, even with improved serological techniques, will be limited by the inherent difficulties in using field-collected mosquitoes, thereby possibly misrepresenting the roles of mammalian species as bloodmeal sources. Because bloodmeal identification has many limitations, an examination of host behavior may be useful for elucidating mosquito-vertebrate interactions. The following survey of studies of anti-mosquito behavior in birds and mammals summarizes current knowledge of such behavior and provides some context for evaluating the design and results of my research.

Anti-mosquito Behavior in Birds

Behavioral "self-defense" is an important factor in mosquito feeding success in several species of birds. Captive ciconiiform (wading) birds, when exposed to mosquitoes, increased their activity, including particular actions usually associated with normal grooming behavior (Edman and Kale, 1971; Webber and Edman, 1972). Increased activity resulted in decreased mosquito feeding success. There were interspecific qualitative and quantitative differences in behavior; some species of birds had more effective anti-mosquito behavior than others. Observations of captive and wild conspecific ciconiiform birds exposed to natural populations of mosquitoes demonstrated that each species had consistent anti-mosquito behavior, but there were interspecific differences (Maxwell and Kale, 1977). Limited field observations (Edman et al., 1984) confirmed evidence obtained in captivity on anti-mosquito behavior of two species of herons. Edman et al. (1972) suggested that mosquito density may influence anti-mosquito behavior. Captive birds responded to greatly increased mosquito densities with increased anti-mosquito behavior, resulting in decreased mosquito feeding success and increased percentages of partial bloodmeals, reflecting interrupted feeding.

Reeves (1971) and Edman et al. (1972) suggested that these phenomena are important because transmission of arboviruses having an avian reservoir and one primary vector may be facilitated by increased avian anti-mosquito behavior. Such behavior could result in a diversion of mosquitoes to aberrant mammalian hosts, such as humans. Edman _et al._ (1974) studied various paired combinations of birds and mammals, and found that mosquitoes had greatest feeding success if host activity was reduced or eliminated by physical restraint. Mosquitoes shifted their feeding endeavors from a defensive, unrestrained host to a restrained host, if the two hosts were relatively close to each other. When both hosts were restrained, mosquitoes had similar feeding success on both species. When neither host was restrained, feeding occurred chiefly on the host exhibiting less anti-mosquito behavior. Exposure of single, restrained hosts to mosquitoes resulted in decreased percentages of partial meals and increased percentages of complete meals, compared to the same hosts under nonrestrained conditions.

Anti-mosquito Behavior in Mammals

Small mammals, especially rodents, usually are common in most terrestrial habitats, and might offer a plentiful source of blood for mosquito feeding. However, rodents seldom are identified as common sources of bloodmeals in studies using serological methods (Downe, 1960; Washino and Tempelis, 1967; Edman, 1971; Magnarelli, 1976). There could be several explanations for this: (1) rodent bloodmeals exist but are undetected; (2) rodents are not used as hosts, due to a "host preference" by mosquitoes for other mammals, as inferred by Hess _et al._ (1968) and Means (1968); (3) rodents are not used as bloodmeal sources, due to unavailability during peak periods of mosquito biting activity. Unavailability, however, could be achieved by at least two plausible rodent behavioral mechanisms: physical concealment (as in a nest or burrow), or unconcealed physical presence with behavioral self-defense, preventing mosquitoes from obtaining a meal.

Anti-mosquito behavior in small mammals has received little attention. Edman et al. (1974) attributed a reduced rate of mosquito feeding success to defensive behavior in several species, including the cotton mouse (Peromyscus gossypinus), gray squirrel (Sciurus carolinensis), wood rat (Neotoma floridana), and cotton rat (Sigmodon hispidus). When mammals were physically restrained, mosquitoes fed to repletion more frequently, and the percentage of partial bloodmeals decreased. For unknown reasons, the young opossum (Didelphis virginiana) did not follow these trends. Direct observations of host activity in the wood rat, cotton mouse, cotton rat, gray squirrel, and marsh rabbit (Sylvilagus palustris) yielded counts of discrete actions that increased when mosquitoes were present. The data reported did not distinguish between usual grooming actions and those actions, if any, occurring only in the presence of mosquitoes. Mammals appeared relatively more active than birds, even when mosquitoes were absent, and the authors suggested that such general activity might augment direct defensive behavior. In the same study, the domestic cat (Felis catus), raccoon (Procyon lotor), armadillo (Dasypus novemcinctus), and adult opossum yielded high rates (66-88% of mosquitoes recovered) of mosquito feeding success, although there were no activity counts to determine the levels of host behavior.

Day and Edman (1984) observed greater mosquito feeding success on restrained hosts than on unrestrained ones in the house mouse Mus musculus (laboratory and wild varieties), a lab strain of golden hamster (Mesocricetus auratus), domestic chicks (Gallus gallus), and wild deer mice (*Peromyscus maniculatus*). In some cases, when mammals were unrestrained but provided with a jar for shelter, feeding success and recovery of mosquitoes had intermediate values compared to restrained or shelterless unrestrained mammals. Chicks were not tested with shelters. Some variation in data apparently was attributable to behavioral differences in the five species of colonized mosquitoes used. House mice and deer mice often slept when provided with a jar for shelter, and this inactivity probably allowed mosquitoes to feed undisturbed. Instances of vertebrates capturing and killing mosquitoes occurred, and the authors suggested that learning might play a role in such behavior in the chicks.

Host health can influence anti-mosquito behavior and, consequently, mosquito feeding success. Day and Edman (1983) found that laboratory mice (*Mus musculus*) were lethargic and did not display anti-mosquito behavior when infected with various malarias (*Plasmodium* spp.). This phenomenon, with an associated increase in mosquito feeding success, usually was most evident when malaria gametocyte infectivity to mosquitoes was greatest. Using anti-estradiol as a bloodmarker in tests with paired conspecifics (*Mus musculus*), Day *et al.* (1983) found that mosquitoes had greater feeding success on the infected member of a pair than on the member uninfected with either *P. chabaudi* or *P. berghei*. As in other work (Day and Edman, 1983), anti-mosquito behavior was reduced in infected mice. Disease-induced changes in host behavior may be an important factor in transmission of arthropod-borne infections (Day and Edman, 1983). Further study is needed to fully determine the epidemiological importance of these observations.

Walker and Edman (1986) studied anti-mosquito behavior in eastern chipmunks (*Tamias striatus*) and gray squirrels, using *Aedes triseriatus* mosquitoes, which feed on these mammals in nature. Gray squirrels and chipmunks exhibited similar anti-mosquito behavior, with head shake being the most effective action. Mosquito feeding success was greater on chipmunks than on gray squirrels, possibly because gray squirrels displayed two main defensive behaviors (head shake and forefoot scratch) more frequently than did chipmunks.

The cited studies on anti-mosquito behavior of birds and mammals provide basic behavioral information on various species. However, no one has examined in detail the anti-mosquito behavior in one species, evaluating the effectiveness of the behavior under various conditions relevant to the development and ecology of that species. I wanted to conduct a detailed, integrated study of anti-mosquito behavior in one species, and I considered several species of mammals as potential subjects. In preliminary work during 1983, I defined and characterized anti-mosquito behavior in four species of small mammals (white-footed mouse, *Peromyscus leucopus*; southern flying squirrel, *Glaucomys volans*; meadow vole, *Microtus pennsylvanicus*; short-tailed shrew, *Blarina brevicauda*). Mice and flying squirrels exhibited the most distinct, effective, and diverse anti-mosquito behavior. My subsequent research efforts focused on the anti-mosquito behavior of *P. leucopus* exposed to one species of mosquito (*Aedes triseriatus*).

Peromyscus leucopus Natural History

P. leucopus occurs in forested and brushy habitats, through most of the northeastern U.S. and southern Ontario to western Montana, eastern Arizona, and eastern Mexico (Hall and Kelson, 1959). The subspecies P. leucopus noveboracensis is found in all New England states north to the area of transition from hardwood to coniferous forests (Godin, 1977). In some locations, the morphologically similar deer mouse (Peromyscus maniculatus) is sympatric with P. leucopus, but only P. leucopus occurs in southeastern New Hampshire (Choate, 1973). White-footed mice are 157-191 mm long and weigh 16-29 g. Adults of both sexes have a dark dorsal streak on the reddish-brown upper parts, with a white ventral area; juveniles are evenly dark-gray (Godin, 1977).

White-footed mice are nocturnal, becoming active soon after sunset with a peak in activity about one hour later (Behney, 1936; Kavanau, 1967). They are somewhat arboreal (Madison, 1977); McShea (1981) suggested that juveniles may be more arboreal than adults. Juveniles and adults have good visual acuity and function well at various light levels (Vestal, 1973; King and Vestal, 1974). Auditory sensitivity is well-developed (Ralls, 1967). During the day, mice use refuges in cavities of dead trees, under logs and debris (Wolff and Hurlbutt, 1982), and possibly in stone fences (Barry and Francq, 1980). Nests are globular, made of dried plant materials (Godin, 1977). The diet includes seeds, mast, larval and adult insects (including Diptera), and fruits (Hamilton, 1941; Whitaker, 1966). Litters are born between late March and late November (Godin, 1977). Juveniles are weaned between 25-30 days after birth (Nicholson, 1941) and leave the nest when they are about four to six weeks old (Layne, 1968; Goundie and Vessey, 1986).

Aedes triseriatus Natural History

The mosquito Aedes triseriatus (Say) occurs in deciduous forests throughout the United States east of the Rocky Mountains and in Nova Scotia, Ontario, Quebec, and New Brunswick (Jenkins and Carpenter, 1946; Darsie and Ward, 1981). It breeds in tree-holes, which are cavities formed by the junction of two or more main trunks usually near the base of a tree, frequently beech, maple, or oak (Jenkins and Carpenter, 1946; Beier and Trpis, 1981; Haramis, 1984). It also breeds in discarded automobile tires and, occasionally, artificial containers such as cemetery urns (Jenkins and Carpenter, 1946). It overwinters in the egg stage and, in the south, occasionally as larvae (Jenkins and Carpenter, 1946; Sims, 1982); these eggs provide the initial brood that hatches in late spring. More eggs hatch throughout the summer until photoperiodic and thermal cues induce egg diapause in the autumn (Kappus and Venard, 1967; Shroyer and Craig, 1980, 1983).

In southeastern New Hampshire, the only other aedine mosquito species breeding in such containers is the uncommon but morphologically similar Aedes hendersoni (Cockerell). Fourth instar larvae of the two species may be distinguished chiefly by characteristics of the anal gills and body coloration (Grimstad et al., 1974; Wood et al., 1979). Larvae feed on fungi in debris (Haramis, 1984) or on other small organisms such as rotifers and protozoans (Jenkins and Carpenter, 1946) before entering a brief stage as aquatic, non-feeding pupae.

Because water temperatures often are higher in tires than in tree-holes, adult emergence may occur earlier in tires, particularly if they are not shaded. Means et al. (1977) suggested that females from the tire habitat may differ behaviorally from females produced from tree-hole larvae, but evidence for this is not convincing.

Greatest biting activity near ground level occurs in the late afternoon (Loor and DeFoliart, 1970). Some feeding in nature occurs during dusk at ground level and in the canopy (Scholl *et al.*, 1979; Novak *et al.*, 1981), and females are eager biters in captivity during twilight. Like most aedine mosquitoes, *Ae. triseriatus* is believed to be a generalized feeder on mammalian species. Based on few identified bloodmeals, it is known to feed in nature on dogs, raccoons, muroid and sciurid rodents (Magnarelli, 1976), and ruminants (Edman, 1971). Analysis of 98 *Ae. triseriatus* bloodmeals (Nasci, 1982) indicated that the mosquitoes fed mainly on chipmunks and deer, although some feeding occurred on tree squirrels, raccoons, rabbits, canines, cats, and birds; tests were not done for muroid bloodmeals. Outdoor exposures of hosts to natural mosquito populations indicate that *Ae. triseriatus* will feed on gray squirrels, chipmunks, humans, deer, raccoons, opossums, and rabbits (Wright and DeFoliart, 1970); Magnarelli (1979) observed outdoor feeding on anesthetized *Peromyscus leucopus* and raccoons. The feeding habits of *Ae. triseriatus*, and behavioral responses of its potential hosts, are epidemiologically important. This species is the chief vector of LaCrosse virus of the California group of encephalitides (Watts *et al.*, 1972), which can cause illness in humans and has been present in the northcentral U.S. *Ae. triseriatus* is a potential vector of dog heartworm (*Dirofilaria immitis*), although the magnitude of its role in transmission of this parasite is uncertain (Ludlam *et al.*, 1970; Fortin and Slocombe, 1981). Under experimental conditions, *Ae. triseriatus* transmits eastern equine encephalitis (EEE) (Chamberlain and Sudia, 1961; Whitfield *et al.*, 1971), and is susceptible to some species of avian malaria (Huff, 1965).

In addition to epidemiological interest in *Ae. triseriatus*, practical reasons prompted its use in my study. I wanted to use a single species directly from the wild, because interspecific variation in feeding habits and aggressiveness exist (Wood *et al.*, 1979), and mosquitoes maintained in lab colonies for several generations may show intraspecific variation. I needed a species with multiple generations, so I could conduct experiments during most of the summer using adult mosquitoes of uniform age and feeding history. Most mosquitoes in southeastern New Hampshire have one major generation per year. Although the salt marsh mosquitoes *Ae. sollicitans* and *Ae. cantator* have several broods, they exhibited high larval mortality, minimal adult longevity, and inadequate feeding behavior when exposed to small mammals under lab conditions in my preliminary study. *Ae. triseriatus* proved satisfactory in all respects: larvae were plentiful and easily obtained during most of the summer; adults could be reared by simple, albeit time-consuming procedures; and feeding behavior was adequate and consistent in captivity.

Overview of Objectives and Methods

The objectives of my study were to quantify anti-mosquito behavior in *P. leucopus*, and to determine its effectiveness in decreasing mosquito feeding success under various conditions. I attempted to answer several questions about this behavior: (1) Were there differences in anti-mosquito behavior between wild-caught and lab-reared adult mice? (2) Did juveniles exhibit anti-mosquito behavior and, if so, was exposure to mosquitoes a factor in its development? (3) Could adult mice maintain successful defensive behavior while engaged in ordinary natural activities, such as handling food and nesting material?

I conducted four series of experiments, using four groups of mice. The first and second series used wild-caught mice. In the first series, mice were in plain enclosures; however, in the second series, mice had opportunity to manipulate food and nesting material during the observation period. In the third series, I examined anti-mosquito behavior in lab-reared adult mice, for comparison with wild-caught mice. In all adult series, as a control, I first observed each mouse in an enclosure without mosquitoes, to determine normal levels of non-aggravated behavior. On a subsequent evening, I observed each mouse in the enclosure with mosquitoes. On the final evening, I anesthetized each mouse and placed it in the enclosure with mosquitoes. This final control verified the fact that a lack of feeding success in the second test was due to the mouse's anti-mosquito behavior, and not to a lack of attraction by mosquitoes to the potential host.

The format of the juvenile series differed slightly from that of the adult series. Each juvenile was observed initially without mosquitoes. In the second test, some juveniles had a "practice session" with mosquitoes, whereas their siblings did not experience mosquitoes then. All juveniles experienced mosquitoes in the third test, and were anesthetized for exposure to mosquitoes in the final test.

MATERIALS AND METHODS

Facilities

Because mosquitoes and mice are sensitive to environmental factors such as temperature, humidity, and light, all animals were maintained, and observations conducted, in the animal behavior laboratory of Spaulding Life Science Building. Separate rooms were used for keeping mice, rearing mosquitoes, and conducting observations. Each room was approximately 2 x 3 m, with overhead fluorescent lighting and one air vent. Each room contained a portable humidifier (West Bend Co.), and air flow from the vent was minimized. Room temperature was kept at 21-24°C with 70-75% RH, gauged daily by a sling psychrometer. Small lamps with 40-watt incandescent bulbs and automatic timers provided two 2-hour crepuscular (0.35 foot-candle) periods daily, approximating dawn and twilight conditions. The timing of these periods was adjusted every 10-14 days to closely simulate the natural environment.

Acquisition and Maintenance of Mice

I used males in all tests involving adult *P. leucopus*, to avoid potential complications due to behavioral differences (and, possibly, scent differences that might affect mosquito feeding) associated with the rodent estrous cycle. During June and July, 1984, I trapped wild, adult male mice in a deciduous woodlot on Kingman Farm, 5.6 km from UNH, using Sherman live traps (8 x 23 x 9 cm) placed approximately 1.5 m above ground on tree trunks. I baited traps with sunflower seeds and occasionally apple, and supplied them with two cotton nestlets (Ancare Corp., Manhasset, N.Y.). I set traps at 5:00-8:00 p.m. and checked them within 15 hours. I kept mice in captivity for 5-7 days before using them in observations. After completion of testing, each mouse was ear-punched for identification, and later released at the site of capture. I obtained lab-reared adult male mice 8-10 months old from the *P. leucopus* colony in the animal behavior lab in June, 1984. The lab colony was established in 1981 with locally wild-caught mice. All mice were kept individually in 31 x 38 x 17 cm polypropylene cages with wire-grid lids, and provided with wood shavings and nestlets. Lab chow (Agway Rat-Mouse-Hamster 2000) and water were supplied *ad libitum*, and small amounts of sunflower seed or apple were given every other day.

In May, 1985, I trapped and maintained pregnant *P. leucopus* females using the same procedures as for the wild-caught males. I noted births of litters but, other than ear-punching mice at three weeks of age, I handled juveniles only for routine cage changing. From six litters, I used eight pairs (six male, two female) of siblings for testing. Each juvenile was 26-30 days old at the time of its first test. All juveniles remained housed with their mothers until after completion of testing, and then were released.

Acquisition and Maintenance of Mosquitoes

In June, 1983, I placed twenty-six discarded automobile tires in deciduous woods on East Foss Farm, 1.6 km from UNH. I primed them with distilled water, tree-hole water, and organic leaf litter, and maintained the water level during the summer by the addition of distilled water whenever rain was insufficient. Although *Culex* spp. bred abundantly in the tires during 1983, the tires contained *Ae. triseriatus* almost exclusively during 1984 and 1985. In May, 1985, for security reasons, I moved 19 of the tires to the deciduous woodlot where mice were trapped on Kingman Farm. During 1984 and 1985, I obtained third- and fourth-instar larvae of Ae. triseriatus from the woodlot tires, from similar tires through the courtesy of Dr. John Burger, and from tree-holes on East Foss Farm and Kingman Farm. I collected nearly equal numbers of larvae from tires and tree-holes throughout both summers, but did not maintain them separately in lab.

I placed larvae in distilled water in 29 x 36 x 15 cm white polyethylene trays and fed them brewer's yeast daily, with occasional supplements of crushed lab chow. Periodic visual examination allowed detection and removal of the uncommon Ae. hendersoni larvae. I collected pupae from trays daily and placed them in distilled water in 28 x 17 x 5 cm polypropylene trays within 30 x 30 x 31 cm screen cages with cloth sleeves. Most of the male pupae, distinguished by small body size, were removed. Newly-emerged adults were collected daily by aspiration. I placed females in lots of approximately 60 in 22 x 22 x 21 cm screen cages with cloth sleeves, and released the males.

Adult females were fed daily on a nestlet soaked in a 10% sucrose solution. I used females between 7-10 days of age for testing. Approximately 26-28 hours prior to a test, I aspirated 55 females into a 30 x 30 x 31 cm screen enclosure modified with a wooden floor, wooden back, and glass front, in addition to the cloth sleeve which was positioned at the top. The sucrose pad was replaced by a distilled water-soaked pad 22-24 hours prior to a test; the water pad was removed 8-9 hours before the test. One to two hours before the test, I removed any dead mosquitoes, plus some alive ones if necessary, so that there were 50 mosquitoes in the enclosure. After the test, I placed the enclosure in a chilled (13°C) room for 30-45 minutes, thus facilitating collection of mosquitoes by aspiration. I recorded the number of dead or severely mutilated mosquitoes, and froze all others for 36-48 hours. I examined frozen mosquitoes under a dissecting microscope to determine percentages of unfed (no blood apparent in abdomen), partly fed (insufficient blood to expand the abdomen), and completely fed (abdomen expanded with blood) mosquitoes, based on the number recovered after the test.

Components of the Series of Tests

Table 1 summarizes components of the test series; detailed descriptions of testing protocol follow.

Wild Plain (WP) Series

I observed wild-caught, adult male mice in plain enclosures, i.e., without manipulatable material.

WPA (control). After a 5-minute period for familiarization with the enclosure, I monitored the behavior of each mouse for 45 minutes, without mosquitoes. I recorded discrete actions individually, but recorded only duration for the relatively non-discrete actions of walking and resting.

WPB (treatment). I placed each mouse in the enclosure with mosquitoes. I monitored behavior as in WPA, after the initial 5-minute familiarization period.

WPC (control). I placed each anesthetized mouse in the enclosure with mosquitoes for 50 minutes.

Lab Plain (LP) Series

I observed lab-reared, adult male mice in plain enclosures, using the same protocol as in the wild plain series. The tests in this series were LPA (control), LPB (treatment), and LPC (control).

TABLE 1

Components of Series of Tests

	Adult Series			Juvenile Series	
Type of Test	Wild Plain	Lab Plain	Wild Manipulating	No Practice	With Practice
Active mouse, no mosquitoes	WPA	LPA	WMA	JNA	JPA
Active mouse, no mosquitoes	---	---	---	JNB	---
Active mouse, with mosquitoes	WPB	LPB	WMB	---	JPB
Active mouse, with mosquitoes	---	---	---	JNC	JPC
Anesthetized mouse, with mosquitoes	WPC	LPC	WMC	JND	JPD

Wild Manipulating (WM) Series

I observed wild-caught, adult male mice in enclosures containing nest material and food that could be manipulated by the mice.

WMA (control). I placed each mouse in the enclosure containing two nestlets torn in quarters, 50cc of wood shavings, 50 sunflower seeds, and four small pieces of apple scattered on the floor. I recorded behavior as in WPA, with the addition of one action, "manipulation", recorded as duration.

WMB (treatment). I placed each mouse in the enclosure with mosquitoes and with food and nesting materials on the floor. I monitored behavior as in WPB, plus the "manipulation" action.

WMC (control). I placed each anesthetized mouse in the enclosure with mosquitoes for 50 minutes, without food and nesting materials.

Juvenile Series

This consisted of two subseries of tests. One group of juveniles had a "practice" session with mosquitoes, whereas their siblings, in the corresponding subseries of tests, had less experience with mosquitoes.

Juveniles with practice (JP) subseries.

JPA (control). I placed each juvenile in a plain enclosure without mosquitoes, and monitored behavior as in WPA.

JPB (treatment). I placed each juvenile in the enclosure with mosquitoes; this was the juvenile's "practice" session, and I monitored behavior as in WPB.

JPC (treatment). I placed each juvenile in the enclosure with mosquitoes again, and monitored behavior as in WPB.

JPD (control). I placed each anesthetized juvenile in the enclosure with mosquitoes for 50 minutes.

Juveniles with No Practice (JN) Subseries.

JNA (control). I placed each juvenile in the plain enclosure with mosquitoes, and recorded behavior as in WPA.

JNB (control). I placed each juvenile in the enclosure without mosquitoes again, and monitored behavior as in WPA.

JNC (treatment). I placed each juvenile in the enclosure with mosquitoes, and monitored behavior as in WPB.

JND (control). I placed each anesthetized juvenile in the enclosure with mosquitoes for 50 minutes.

Blocking

I did all behavioral testing during the twilight period, with only one or two tests per day, occurring during either the early or late half of the period. I tested each mouse on alternate evenings, consistently in either the early or late period. Within each adult mouse series, I blocked tests so that equal numbers of mice were tested during the early and late segments. In the juvenile series, this was not completely compatible with the scheduling requirements based on the ages of the mice. Among the juveniles with practice, I tested three early and five late; in the JN subseries, I tested five early and three late. Within the eight pairs of juvenile siblings, I arranged tests so that members of each pair were tested on the same evenings, to ensure that behavioral variation within a pair was not due to possible age-related factors.

Anesthesia

I used anesthetics (Ketaset and Rompun in combination) to eliminate each mouse's behavior during its final control test. Studies with laboratory animals have shown that Ketaset acts mainly as a dissociative, analgesic anesthetic, affecting the central nervous system with some depression of respiration and possible cardiovascular stimulation (Harkness and Wagner, 1977; Wright, 1982). When used alone in mice during preliminary work (pers. obs.), Ketaset did not keep P. leucopus anesthetized long enough, and did not eliminate tonic movements of the limbs. The addition of Rompun, which acts as a sedative, analgesic, and muscle relaxant (Mulder and Mulder, 1979), eliminated tonic movements in all mice, and provided adequate duration of anesthesia in the adult mice. Duration of anesthesia in juveniles varied from 25-50 minutes; however, it was not feasible to extend it by increasing the dosage, since respiratory problems and some mortality occurred during preliminary work in establishing the juvenile dosage. Because most mosquito feeding occurred in the first 20 minutes on anesthetized mice, test results probably were not significantly affected by the juveniles' activity and removal from the enclosure prior to the end of the 50-minute period.

The anesthesia mixture contained 0.95 ml Ketaset (ketamine hydrochloride, 100 mg/ml, Bristol Laboratories), 3.55 ml Rompun (xylazine, 20 mg/ml, Miles Laboratories), and 1.9 ml sterile Ringer's solution. For the adult mice, I used a dosage of approximately 74 mg Ketaset plus 55 mg Rompun per kg body weight. Juvenile mice received a dosage of approximately 26 mg Ketaset plus 20 mg Rompun per kg body weight. I injected the solution with a disposable 1cc tuberculin syringe with a 25G 5/8" needle. I briefly exposed each mouse to ether and, while it was in the resultant subdued condition, swabbed the lateral portion of the right thigh with 75% ethanol, and then inserted the needle intramuscularly. I injected the drugs as the mouse began to recover from the ether. Although the drugs usually took effect completely within one minute, I observed the mouse for 3-4 minutes for any sign of respiratory irregularity. Because the eyes remained open, I applied softened petroleum jelly to preserve their moist condition. Each mouse was placed in the enclosure lying on its left side, with chest and head slightly elevated by two nestlets, to help maintain normal drainage of saliva.

Monitoring the Behavior

During testing, each mouse was in a 30 x 30 x 31 cm screen enclosure with a glass front, wooden floor and back, and cloth sleeve ceiling. As the observer, I was separated from the enclosure by a wooden room partition containing a 7 x 3 cm glass window, to minimize the effect of my presence on the mouse and mosquitoes. I used an Esterline-Angus 20-pen electronic event recorder to monitor behavior. The recorder was wired to a keyboard made of 14 doorbell buttons mounted on a 29 x 16 cm board, so that, when I observed an action, I could press the appropriate button and cause the corresponding pen on the recorder to mark the chart paper, moving 7.6 cm/minute. An additional doorbell button was arranged on a 23 x 14 cm board placed on the floor and foot-activated, for recording resting behavior. The recorder was enclosed within a semi-soundproof box, to subdue the slight ticking noise of the mechanism.

Behavioral and Mosquito Feeding Success Categories

Mosquito feeding success on non-anesthetized and anesthetized mice was evaluated and recorded after tests (Table 2). Based on preliminary, qualitative observations of adult mice in 1983 and juveniles in 1984, I monitored fifteen actions (Table 3; Figures 1-4). These actions are arranged in the same behavioral categories used in data analysis. I recorded walking, resting, and manipulating actions by duration only, and recorded all other actions as discrete events.

Grooming Behavior

Although I observed grooming actions when mosquitoes were present, and often their occurrence clearly prevented mosquitoes from settling or feeding on an area of the body, they also occurred as part of ordinary bodily maintenance when mosquitoes were absent. These actions, therefore, are not included in anti-mosquito behavior in my data analysis. Because a grooming action often included clusters of movements of very short duration that could not be separated by the observer and by the recorder at the set chart pace, I modified the definitions of the grooming actions. For example, face grooming often occurred as a series of rapid hand-licking movements followed by a contrasting movement such as pulling the hands forward over the face. By observing the small breaks which occurred when switching between components of the major action (face grooming), I could record behavior as 4 face-grooms rather than attempt to distinguish and record 28 hand-nibbles and 8 face-rubs within 9 seconds.

Groom face/ear(s). The mouse interspersed brief episodes of chewing and/or licking the hand(s) or a hindfoot between single or multiple actions such as rubbing the sides of the face, pulling the

TABLE 2

Categories of mosquito feeding success on adult and juvenile mice.

Mosquitoes on Non-anesthetized Mice	Mosquitoes on Anesthetized Mice
% Recovered[a]	% Recovered[a]
% Killed[b]	---
% Eaten[c]	---
% Dead[d]	% Dead[d]
% Unfed[e]	% Unfed[e]
% Completely fed[e]	% Completely fed[e]
% Partly fed[e]	% Partly fed[e]
---	% Disturbed[f]

a (Number of dead and alive mosquitoes recovered after test) x 2.
b (Number of mosquitoes eaten + number of dead ones recovered) x 2.
c (Number of mosquitoes not recovered after test) x 2.
d (Number of dead mosquitoes recovered) x 2.
e Based on number of mosquitoes recovered after test.
f (Number observer disturbed at end of test of anesthetized mouse) x 2.

TABLE 3

Behaviors monitored in adult and juvenile mice.

Behavioral Category	Individual Actions in Category
Grooming	Groom face/ear(s) Groom hand(s)/arm(s) Groom body Groom hindfoot Groom hindquarters/genital area/tail
Exploratory*	Extend Jump Walk (s.)
Anti-mosquito	Ear-flick Headshake/twitch Lunge/whirl
Catch-kill	Catch-kill mosquito
Rest	Rest (s.)
Manipulate	Manipulate seeds/nest material (s.)
Chew/tug**	Chew/tug on enclosure

(s.) = seconds

* Explore = Extend + Jump + (Walk(s.)/6)

** Not included in data analysis

hands forward over one or both ears, or scratching the base of an ear or the side of the face with a hindfoot.

Groom hand(s)/arm(s). Usually the mouse licked or chewed these areas, although occasionally the mouse used one hand to scratch the other arm.

Groom body. The mouse chewed, licked, and/or scratched the chest, belly, side, or back areas.

Groom hindfoot. The mouse groomed the part of the hindleg below the knee by licking or chewing it, often using one or both hands to maneuver the leg as it was extended forward.

Groom hindquarters/genital area/tail. The mouse groomed these by chewing and/or licking the area(s), as well as scratching or picking through the fur with the hands. The mouse usually held the tail in the hands while grooming it, often beginning at the base and proceeding to the tip.

Exploratory Behavior

These actions served primarily to help familiarize the mouse with its surroundings. They occurred in the absence as well as the presence of mosquitoes. To integrate values for discrete actions (extend, jump) and a duration-based action (walk), I defined one "unit" of walking as being equal to six seconds of walking, and made the following calculation: Explore = Extend + Jump + (Walk(s.)/6).

Extend. The mouse stretched forward (occasionally with one front leg raised off the floor) or upward (resting one or both hands on the side of the enclosure).

Jump. The mouse jumped from the floor onto the side of the enclosure, or vice versa; occasionally a mouse jumped from the floor directly to the cloth ceiling, or from the ceiling to the floor or side of the enclosure.

Walk. This occurred on the floor, screen sides, and ceiling of the enclosure; it also included brief bursts of running or semi-saltatorial locomotion on the floor.

Anti-mosquito Behavior

Among the adult mice, anti-mosquito actions occurred almost exclusively in the presence of mosquitoes, usually in response to tactile stimulation by the mosquitoes. Although these actions occurred infrequently among juvenile mice in the absence of mosquitoes, I categorized them as anti-mosquito behavior in the collection and analysis of the data, due to their great increase in frequency in the presence of mosquitoes.

Ear-flick. The mouse rapidly flicked one or both ears forward.

Headshake/twitch. The mouse shook the head from side to side, or twitched it in a vertical and/or slightly backward direction.

Lunge/whirl. The mouse lunged forward or slightly sideways, occasionally striking out with one hand; or, it whirled around rapidly, reversing its walking or resting direction. These actions apparently were in response to visual, tactile, or perhaps auditory stimulation by the insects.

Catch/Kill Mosquito

The mouse caught the mosquito in its hands, brought the mosquito to its mouth, and appeared to kill it by nibbling. The mouse then either ate the mosquito, frequently dropping legs as crumbs, or placed the uneaten mosquito on the floor and subsequently paid little or no attention to it. Catching and killing mosquitoes certainly is defensive behavior, but for statistical purposes it was not included in the anti-mosquito category, because I wanted to compare levels of anti-mosquito behavior between tests in which mosquitoes were absent and tests in which they were present. By definition, catching/killing could not occur in tests when mosquitoes were absent.

Rest

Usually the mouse huddled quietly, while remaining awake; occasionally a mouse would go to sleep, often with the head tucked down, resting on or between the arms.

Manipulate

The mouse used the hand(s) and/or mouth to examine, carry, eat, shred, or arrange either food items or nesting material.

Chew/tug

The mouse used the hands and/or mouth to grasp and pull on the screen or cloth of the enclosure, sometimes chewing. I did not include this action in the data analysis, because it was not clearly for grooming, exploring, or defense against insects, and it did not occur in all mice.

Statistical Analysis

As in many behavioral studies, assumptions of normal distribution and homogeneous variation of data, underlying parametric statistics, were not considered reasonably valid. I used non-parametric statistics (Siegel, 1956; Pratt and Gibbons, 1981) to compare parameters in testing hypotheses. These tests could be applied to the small sample sizes ($n = 8$) in each of the adult series and juvenile subseries. One-sided tests were used, with alpha = 0.05.

I used the Wilcoxon Matched-Pairs Signed-Ranks test to compare related samples, such as the behavior of one mouse under different conditions (i.e., without and with mosquitoes); ties had negligible effect and were not corrected. I used the Mann-Whitney U test for independent samples, such as comparing one parameter for lab-reared vs. wild plain mice, JP vs. JN juveniles, and adult vs. juvenile mice. Corrections for ties were made according to Siegel (1956) in eleven comparisons involving large proportions of ties when the uncorrected p value was close to 0.05.

RESULTS

Behavior of Adult Mice

All three groups of adult mice increased anti-mosquito behavior and decreased resting behavior when mosquitoes were present (Table 4). All mice showed anti-mosquito behavior in the first nine minutes of the test; ear-flick was the predominant anti-mosquito action. All mice, except one WP mouse, caught and usually killed mosquitoes, but not every mouse ate mosquitoes. Only two LP mice, and no WP or WM mice, exhibited any anti-mosquito actions (ear-flick, headshake/twitch, lunge/whirl) when mosquitoes were absent. WP and WM mice groomed more when mosquitoes were present than when they were absent. One LP mouse had a huge decrease in grooming; this value caused a lack of statistical significance for the increase in grooming in LP mice. Face grooming was the predominant grooming action in nearly every mouse, when mosquitoes were absent or present. Exploratory behavior increased among WP mice when mosquitoes were present. WM mice manipulated sunflower seeds and nesting material less when mosquitoes were present, but did not have a significant change in number of uneaten seeds compared to when mosquitoes were absent.

There were few significant differences in behavior between the groups of mice. WM mice rested less than WP mice when mosquitoes were absent, and less than LP mice when mosquitoes were present.

Behavior of Juvenile Mice

Juvenile behavior was so variable that significant differences between the two groups of juveniles, and within the groups under

TABLE 4

Behavior of adult mice* without and with mosquitoes**

Behavior Category	Without Mosquitoes			With Mosquitoes		
	WPA	WMA	LPA	WPB	WMB	LPB
	a	b	c	d	e	f
Groom	255.1(86.2)d	218.4(99.8)e	272.5(155.0)	487.6(148.8)a	399.8(164.3)b	349.9(155.9)
Explore	88.8(93.5)d	140.1(95.5)	129.2(107.6)	134.7(95.3)a	144.3(93.8)	109.7(62.6)
Anti-mosquito	0.0(0.0)d	0.0(0.0)e	0.9(2.1)f	101.0(74.7)a	142.1(50.6)b	119.6(57.6)c
Catch/kill	---	---	---	18.9(20.7)	25.8(21.5)	10.4(10.1)
Rest**	25.3(12.8)bd	11.5(9.8)ae	18.8(12.2)f	10.5(9.0)a	5.1(7.8)bf	12.3(8.0)ce
Manipulate**	---	10.5(5.4)e	---	---	8.3(5.3)b	---
Seeds uneaten	---	34.5(14.3)	---	---	36.0(8.6)	---

*WP = Wild Plain, WM = Wild Manipulating, LP = Lab-reared Plain adults

**Table values are means; standard deviations are in parentheses. Within each behavior category, means followed by letter(s) are significantly different ($p<0.05$) from means in the columns headed by those letters. Comparisons were made for all combinations within the two groups (without and with mosquitoes) and for corresponding adult types (WP, WM, LP) between the two groups. Values for rest and manipulate are in minutes.

different conditions, were rare (Table 5). Every mouse, except one in each group, displayed some anti-mosquito actions when mosquitoes were absent. Every juvenile increased anti-mosquito behavior in the first nine minutes of the test when it first experienced mosquitoes; however, in the JP group, every mouse, except one, decreased anti-mosquito behavior when mosquitoes were present for the second time. Every mouse caught and killed mosquitoes, and, except for two JN mice, every juvenile ate mosquitoes. Ear-flick was the predominant anti-mosquito action. Face grooming was the most common grooming action in all mice, with or without mosquitoes. JN mice rested less when mosquitoes were present than in their first and second tests (when mosquitoes were absent).

Behavior of Adults vs. Juveniles

JP juveniles had more grooming, exploring, and anti-mosquito behavior in the absence of mosquitoes than WP, WM, and LP mice, and rested less than WP and LP mice (Table 6). JN juveniles, in their first and second tests without mosquitoes, had more anti-mosquito behavior than WP, WM, and LP mice and explored more than WP and LP mice. JN mice groomed and explored more in their second test without mosquitoes than WM mice had in their first (only) test without mosquitoes, and groomed more than WP mice.

All comparisons of adults vs. juveniles showed that juveniles had more exploratory behavior when mosquitoes were present (Table 7). WP adults groomed more than JP mice groomed in their first test with mosquitoes. There were no significant differences in anti-mosquito behavior between juveniles and adults. The catch-kill action occurred more in the JP juveniles' first test than in any of the adult groups, and more in their second test than in WP or LP adults. Juveniles tended

TABLE 5

Behavior of juvenile mice* without and with mosquitoes**

	Without Mosquitoes			With Mosquitoes		
Behavior	JPA	JNA	JNB	JPB	JPC	JNC
Category	a	b	c	d	e	f
Groom	363.3(71.1)	316.0(149.3)	321.6(116.2)	337.9(86.9)	369.8(133.9)	442.8(268.8)
Explore	300.0(75.4)	252.2(117.7)	246.7(102.9)	373.0(156.9)	341.4(192.4)	296.4(137.7)
Anti-mosquito	9.5(4.9)de	6.1(4.9)f	8.4(6.6)f	154.1(43.6)ae	114.0(37.9)ad	133.9(46.7)bc
Catch/kill	---	---	---	48.0(9.4)	42.8(13.4)	32.8(25.5)
Rest (min.)	6.6(4.1)	12.1(11.4)f	10.6(9.9)f	3.9(5.1)	5.1(4.4)	2.3(3.1)bc

*JP = Juveniles with Practice, JN = Juveniles with No Practice

**Table values, indications of significance, and comparisons as in Table 4.

TABLE 6

Comparison of behavior of adult vs. juvenile mice, without mosquitoes*

	Adults			Juveniles		
Behavior Category	WPA	WMA	LPA	JPA	JNA	JNB
	a	b	c	d	e	f
Groom	255.1df	218.4df	272.5d	363.3abc	316.0	321.6ab
Explore	88.8def	140.1d	129.2def	300.0abc	252.2ac	246.7abc
Anti-mosquito	0.0def	0.0def	0.9def	9.5abc	6.1abc	8.4abc
Rest (min.)	25.3def	11.5	18.8d	6.6ac	12.1a	10.6a

*Table values and indications of significance as in Table 4. Comparisons were made for all combinations between the two groups (adults and juveniles); table does not reflect comparisons within the two groups.

TABLE 7

Comparison of behavior of adult vs. juvenile mice, with mosquitoes*

	Adults			Juveniles		
Behavior Category	WPB	WMB	LPB	JPB	JPC	JNC
	a	b	c	d	e	f
Groom	487.6d	399.8	349.9	337.9a	369.8	442.8
Explore	134.7def	144.3def	109.7def	373.0abc	341.1abc	296.4abc
Anti-mosquito	101.0	142.1	119.6	154.1	114.0	133.9
Catch/kill	18.9de	28.5d	10.4de	48.0abc	42.8ac	32.8
Rest (min.)	10.5f	5.1	12.3def	3.9c	5.1c	2.3ac

*Table values and indications of significance as in Table 4. Comparisons as in Table 6.

to rest less than adults, but not all differences were statistically significant.

Mosquito Feeding Success on Adult Mice

In all groups of adult mice, the percentage of unfed mosquitoes decreased and the percentage of completely fed mosquitoes increased when mice were anesthetized (Table 8). Non-anesthetized LP mice had a higher percentage of unfed mosquitoes and a lower percentage of dead mosquitoes than WM mice; anesthetized LP mice had a higher percentage of completely fed and a lower percentage of unfed mosquitoes than WM mice. Most mosquitoes fed on anesthetized adult mice within the first twenty minutes of the test.

Mosquito Feeding Success on Juvenile Mice

Trends between JN and JP juveniles were simiiar (Table 9). Percentages of recovered and completely fed mosquitoes increased when mice were anesthetized, compared to when they were not. The percentage of partly fed mosquitoes in anesthetized JP mice did not increase compared to their first test with mosquitoes, but did increase compared to their second exposure to mosquitoes. The percentage of partly fed mosquitoes increased in anesthetized JN juveniles. Most mosquitoes fed on anesthetized juveniles within the first twenty minutes of the test.

There were no significant differences between the groups of juveniles under the same conditions. One JN mouse killed and ate all 50 mosquitoes. I believe no mosquitoes fed on that mouse prior to being killed, but, because this was not certain, I eliminated the data for that mouse in the unfed, completely fed, and partly fed categories. The JP sibling of that mouse killed and ate 47 mosquitoes; only one other JP mouse ate more (49) mosquitoes.

TABLE 8

Mosquito feeding success on non-anesthetized and anesthetized adult mice*

	Non-anesthetized			Anesthetized		
	WPB	WMB	LPB	WPC	WMC	LPC
Mosquitoes	a	b	c	d	e	f
% Recovered	80.3(32.7)	97.8(3.1)	93.8(6.8)	99.3(1.5)	99.8(0.7)	99.5(0.9)
% Killed**	25.3(31.4)	22.3(20.4)	10.3(7.0)	---	---	---
% Eaten	19.8(32.7)	2.3(3.1)	6.8(6.8)	---	---	---
% Dead***	7.6(8.7)	20.4(20.4)c	3.6(2.5)b	0.5(0.9)	0.3(0.7)	0.0(0.0)
% Unfed***	81.6(22.2)d	78.4(19.9)ce	94.4(6.0)bf	16.1(9.5)a	18.8(5.0)bf	12.0(6.0)ce
% Completely fed***	7.5(19.6)d	0.5(0.7)e	0.9(1.8)f	82.6(8.2)a	79.5(5.6)bf	87.3(6.1)ce
% Partly fed***	3.3(4.1)	0.8(0.9)	0.9(1.8)	0.8(1.5)	1.5(1.4)	0.8(1.5)
% Disturbed	---	---	---	2.5(3.0)	1.8(1.3)	2.8(2.1)

---

*Table values, standard deviations, and indications of significance as in Table 4. Comparisons were made for all combinations within the two groups (non-anesthetized and anesthetized) and for corresponding adult types (WP, WM, LP) between the two groups.

**% Killed = (number of mosquitoes eaten + number of dead mosquitoes recovered) x 2.

***Based on number of mosquitoes recovered.

TABLE 9

Mosquito feeding success on non-anesthetized and anesthetized juvenile mice*

Mosquitoes	Non-anesthetized			Anesthetized	
	JPB	JPC	JNC	JPD	JND
	a	b	c	d	e
% Recovered	45.5(16.3)d	38.0(27.8)d	51.8(39.9)e	99.8(0.7)ab	99.5(0.9)c
% Killed**	58.0(10.7)	63.8(25.3)	60.3(36.9)	---	---
% Eaten	54.5(16.3)	62.8(26.7)	48.3(39.9)	---	---
% Dead***	4.6(11.9)	1.5(3.2)	1.1(2.3)	0.3(0.7)	0.0(0.0)
% Unfed***	94.9(11.8)d	98.1(3.6)d	98.9(2.3)e^{+}	16.3(11.5)ab	16.8(6.7)c
% Completely fed***	0.0(0.0)d	0.4(1.1)d	0.0(0.0)e^{+}	81.8(11.8)ab	81.5(6.8)c
% Partly fed***	0.5(1.4)	0.0(0.0)d	0.0(0.0)e^{+}	1.8(1.7)b	1.8(1.3)c
% Disturbed	---	---	---	2.5(1.8)	3.3(2.4)

*Table values, standard deviations, and indications of significance as in Table 4. Comparisons as in Table 8.

**%Killed = (number of mosquitoes eaten + number of dead mosquitoes recovered) x 2.

***Based on number of mosquitoes recovered.

$^{+}$n = 7.

Mosquito Feeding Success on Adults vs. Juveniles

JP juveniles, in their first and second tests with mosquitoes, had lower percentages of mosquitoes recovered and higher percentages of killed mosquitoes than all adult groups (Table 10). They had higher percentages of eaten mosquitoes than WM and LP adults and of unfed mosquitoes than WP and WM mice, and lower percentages of dead ones than WM mice and of partly fed ones than WP mice. JP juveniles in their first test with mosquitoes had a higher percentage of dead insects than LP mice. In their second test with mosquitoes, JP mice had a lower percentage of dead mosquitoes than WP and LP adults, and ate a higher percentage of mosquitoes than did WP mice.

Non-anesthetized JN juveniles had a higher percentage of unfed mosquitoes than all adult groups (Table 10). They had higher percentages of eaten mosquitoes than LP and WM mice and of killed mosquitoes than LP mice. They had lower percentages of mosquitoes recovered than LP mice, of dead mosquitoes than WM and LP mice, and of completely fed and partly fed mosquitoes than WP mice.

Anesthetized JN juveniles had a higher percentage of partly fed mosquitoes than WM adults (Table 11). There were no other significant differences between the anesthetized adult and juvenile groups.

TABLE 10

Comparison of mosquito feeding success on non-anesthetized adult vs. juvenile mice*

	Adults			Juveniles		
	WPB	WMB	LPB	JPB	JPC	JNC
Mosquitoes	a	b	c	d	e	f
% Recovered	80.3de	97.8de	93.8def	45.5abc	38.0abc	51.8c
% Killed**	25.3de	22.3de	10.3def	58.0abc	63.8abc	60.3c
% Eaten	19.8e	2.3def	6.8def	54.5bc	62.8abc	48.3bc
% Dead***	7.6e	20.4def	3.6def	4.6bc	1.5abc	1.1bc
% Unfed***	81.6def	78.4def	94.4f	94.9ab	98.1ab	98.9^{+}abc
% Completely fed***	7.5df	0.5	0.9	0.0a	0.4	0.0^{+}a
% Partly fed***	3.3def	0.8	0.9	0.5a	0.0a	0.0^{+}a

*Table values and indications of significance as in Table 4. Comparisons were made for all combinations between the two groups (adults and juveniles); table does not reflect comparisons within the two groups.

**% Killed = (number of mosquitoes eaten + number of dead mosquitoes recovered) x 2.

***Based on number of mosquitoes recovered.

$^{+}$n = 7.

TABLE 11

Comparison of mosquito feeding success on anesthetized adult vs. juvenile mice*

	Adults			Juveniles	
	WPC	WMC	LPC	JPD	JND
Mosquitoes	a	b	c	d	e
% Recovered	99.3	99.5	99.8	99.8	99.5
% Dead**	0.5	0.0	0.3	0.3	0.0
% Unfed**	16.1	12.0	18.8	16.3	16.8
% Completely fed**	82.6	87.3	79.5	81.8	81.5
% Partly fed**	0.8	0.8e	1.5	1.8	1.8b
% Disturbed	2.5	2.8	1.8	2.5	3.3

*Table values and indications of significance as in Table 4. Comparisons as in Table 10.

**Based on number of mosquitoes recovered.

DISCUSSION

Effectiveness of Defensive Behavior

The major objective of my research was to provide behavioral information useful to estimate the role of *Peromyscus leucopus* as a potential host for mosquitoes. The defensive behavior of *P. leucopus* was so effective that I believe this species rarely is a host for mosquitoes having a level of aggressiveness comparable to *Aedes triseriatus*. All mice, except one adult, exhibited such effective behavior that mosquitoes rarely fed successfully. The successful defense of WM mice suggests that similar defense exhibited by WP and LP mice was not simply a result of being in an enclosure with nothing to do but fight mosquitoes. Because the ability of WM mice to handle and eat seeds was not diminished while mice successfully defended themselves against mosquitoes, mice probably can conduct their usual foraging and, presumably, other activities in nature while maintaining defense. Defensive behavior need not occur at the expense of other behaviors; it can be an integral part of mouse activity.

These results are difficult to correlate with literature, because there are no published studies of *P. leucopus* anti-mosquito behavior, and bloodmeal identification studies rarely include tests for mice. Edman (1971,1979) tested for bloodmeals from mice, but *P. leucopus* does not occur in Florida where he did the studies. Although blood of the family Cricetidae (including *Peromyscus* spp.) may be distinguished serologically from blood of the family Muridae (Old World rats and mice, including house/lab mice) (Edman *et al.*, 1974), some reports do not indicate the mouse species used in preparing antisera for bloodmeal analysis. Burkot and DeFoliart (1982) reported five mouse-positive bloodmeals (out of 1245 bloodmeals tested) in Wisconsin, using "deer mice" antisera. Because P. leucopus and P. maniculatus both occur in that region, such bloodmeal analysis precludes making inferences about the anti-mosquito behavior of either species. Generally, due to lack of specificity in bloodmeal analysis, a mouse-positive test can indicate any one of several species in an area or, possibly, a mixed bloodmeal taken from different species of mice. The results of my behavioral research on P. leucopus provide evidence unobtainable from reports of sparse, often ambiguous bloodmeal analysis.

No one has tried to determine whether a mammalian potential host can maintain defense while performing ecologically relevant activities (except perhaps Day and Edman, 1984, as discussed later). Comparisons of free and captive wading birds (Maxwell and Kale, 1977; Edman et al., 1984) showed that each species had consistent anti-mosquito behavior. Free and captive birds foraged in the presence of mosquitoes, but the data reported did not indicate whether foraging activity was affected by defensive behavior, and of course mosquito feeding success on free birds could not be measured. Currently, extrapolation of behavioral results from lab to nature must be done cautiously, based on suggestive but not extensive studies of various species.

Actions Employed in Defensive Behavior

P. leucopus employed various actions to prevent mosquitoes from feeding. Grooming and exploratory behavior did not increase in every group of mice when mosquitoes were present, but those actions discouraged mosquitoes from landing and feeding on mice. *P. leucopus* is a relatively active species of small mammal, and it is plausible that an ordinarily high level of activity complements actions directed particularly against mosquitoes. Webber and Edman (1972) and Waage and Nondo (1982) similarly suggested that ordinary behavior, especially grooming, contributed to successful defense in ciconiiform birds and laboratory rabbits, respectively.

Grooming actions often obviously affected the outcome of a mosquito's attempt to obtain a bloodmeal from *P. leucopus*. When a mouse groomed, a mosquito could only hover near the moving body part; no landing occurred on that area. One grooming action sometimes protected the area being groomed plus other body areas. For example, when licking a hindleg, a mouse usually moved the head up and down vigorously while using both hands to maneuver the leg. This effectively protected the head, arms, and most of the belly, plus the hindleg. When a mosquito landed on a resting mouse, the mouse usually began to groom that area within a few seconds, and the mosquito flew away. The rarity of partial bloodmeals (based on total number of mosquitoes recovered) associated with all groups of mice may attest to the rapidity of behavioral responses to mosquitoes. However, because percentages of partial bloodmeals usually were not significantly different on anesthetized mice, it is possible that, under the testing conditions, *Aedes triseriatus* was not inclined to obtain partial bloodmeals. Because the tests of active as well as anesthetized mice often resulted in no partial bloodmeals, there usually was no difference in percentage of partial bloodmeals (based on number of all bloodmeals) between active and anesthetized mice. (The calculation of percentage of partial bloodmeals based on number of all bloodmeals represents another analytical approach, but is not included in my data.)

Ear-flick was the most common of the three actions occurring almost exclusively when mosquitoes were present. Mosquitoes usually focused their landing attempts on the large, highly vascularized, thinly-furred ears, and ear-flick was a quick, vigorous response, often occurring several times in rapid succession when one mosquito hovered near an ear or when several mosquitoes were near the upper part of the head. Because it required no head or limb movement, ear-flick was easily done while mice were handling seeds, walking, grooming, or resting. It may be a reflex response to tactile stimulation of the vulnerable ear area, but further study is needed to ascertain this. Waage and Nondo (1982) described an ear-flick action occurring in laboratory rabbits; Walker and Edman (1986) observed a similar action ("ear twitch") in gray squirrels and chipmunks.

The other anti-mosquito actions, headshake/twitch and lunge/whirl, probably are voluntary. Head movement apparently occurred in response to touch. Lunging directly at a mosquito, without attempting to catch it, occurred when a mosquito hovered in front of a mouse and probably was a response to visual stimulation. Mice whirled around rapidly when mosquitoes either landed on the dorsal area (tactile stimulation) or hovered near the nape of the neck (possibly auditory stimulation). These vigorous actions repelled mosquitoes but were relatively infrequent, perhaps because they require more energy to perform and generally disrupt any other activity.

P. leucopus is not unusual among vertebrates in employing various actions to protect the head area, where fur or feathers are minimal and skin is tender and highly vascularized. Chipmunks and gray squirrels (Walker and Edman, 1986), laboratory rabbits (Waage and Nondo, 1982), cotton mice, cotton rats, and marsh rabbits (Edman *et al.*, 1974), and ciconiiform birds (Edman and Kale, 1971; Webber and Edman, 1972) follow this trend. The wading birds also use various actions and spend a larger proportion of time protecting their long, exposed legs than do small mammals, whose legs are fairly well furred. General effectiveness of anti-mosquito behavior in various species was cited in the introduction, but I want to re-emphasize the phenomenon, noting that my results for *P. leucopus* augment evidence for it.

I attempted to expand my analysis of data, but was unable to determine, by Spearman's rank correlation coefficient test (Siegel, 1956), which individual actions contributed most to successful defense. Because mosquitoes simply could not feed on non-anesthetized mice, I found no significant correlations between particular actions and lack of mosquito feeding success. Walker and Edman (1986) found some evidence for such correlations in gray squirrels and chipmunks, because in their study mosquito feeding success on active mammals varied more than in my study, i.e., it was not such an all-or-none phenomenon as in *P. leucopus*.

Effects of Absence of Defensive Behavior

A decrease in mouse activity often occurred during the final 10-20 minutes of tests, with or without mosquitoes. When mosquitoes were absent, this decrease probably happened because mice were finished with exploratory and grooming behavior. If boredom exists among small mammals, it may have occurred then, particularly among mice without seeds to eat. Mice often settled down and rested for several minutes at a time. Such behavior was not surprising in the relatively barren environment of the enclosure. When mosquitoes were present, however, I expected that stimulation provided by the mosquitoes would prevent mice from settling down. However, nearly all mosquitoes also were inactive during these intervals of mouse resting behavior; such mosquito inactivity probably cannot be attributed just to the time of testing, because the trend occurred during early and late tests.

I believe the phenomenon of biting persistence (Walker and Edman, 1985b) plays a major role in this pattern of resting. Aedes triseriatus, like most mosquito species, will continue attempting to feed on a potential host only for a limited time; if an animal is defensive, making a bloodmeal difficult or impossible to obtain, it is to the mosquito's advantage to "give up" and go away from that animal. This decreases the risk of injury or death of the mosquito due to defensive behavior of one animal, and lets the mosquito seek a meal elsewhere. In my observations, mice and mosquitoes contributed behaviorally to a mutual resting period. As more mosquitoes gave up on a mouse and rested (usually on the screen walls), the mouse received less aggravation and could settle down. Furthermore, when the mouse was resting, it provided less stimulation (including visual cues and vibration due to movement) to activate the mosquitoes. This trend was broken, however, if any mosquitoes ceased resting and approached the mouse, eliciting defensive behavior.

One WP adult mouse remained almost completely inactive for the first 18 minutes of its exposure to mosquitoes. During that time, mosquitoes fed freely; 28 fed completely and six fed partially. I cannot explain why the mouse was so passive, because he appeared healthy and alert and, during the remainder of the observation, capably defended himself using actions similar to other mice in type and relative frequency. This isolated example reinforces the concept that the behavior of a defensive host prevents mosquitoes from feeding. In effect, this mouse acted as his own control during the first part of the test by eliminating his behavior.

Aside from such irregular instances of mouse resting behavior when mosquitoes were present, the effectiveness of defensive behavior in _P. leucopus_ is supported by the fact that, when behavior was eliminated by anesthesia, mosquitoes fed successfully on all mice. This control substantiates the concept that lack of feeding success on non-anesthetized mice was due primarily to their behavior, not a lack of attraction to mice by mosquitoes. Other studies of defensive behavior in mammals and birds, cited in the introduction, had similar results, although physical restraint in a nylon stocking or hardware-cloth cylinder generally was used instead of anesthesia. Physical restraint for this control has three drawbacks: (1) restraint is uneven, allowing animals to squirm or move some parts of the body; (2) the physical barrier, although of a mesh type, may deny or limit mosquito access to some areas of an animal; and (3) due to stress of confinement (and perhaps discomfort), an animal's efforts against restraint may increase levels of known mosquito attractants, such as CO_2 and warmth. Anesthesia has none of these disadvantages.

Mosquito Feeding Sites

Fur type and relative abundance may play a minor role in lack of feeding success on non-anesthetized _P. leucopus_. Mosquitoes rarely landed on the dorsal body area of non-anesthetized mice. When mice were anesthetized, mosquitoes landed and walked on this area more often, but I did not observe mosquitoes feeding there. They concentrated feeding attempts on the head, particularly ears, but also fed freely on other areas (limbs, feet, belly, hindquarters, tail) of every anesthetized mouse. The fur on the back area of P. leucopus is long, thick, and tends to lie down with hairs overlapping from front to back. Belly fur is fairly thick but short, and does not tend to lie down. Fur is short and sparse in other areas, and nearly absent on the feet. These observations on fur and mosquito feeding sites were incidental to my study and were not quantified. Walker and Edman (1985a) studied the role of fur in feeding-site selection by Ae. triseriatus on chipmunks and gray squirrels, and suggested similar conclusions.

The Role of Experience

My research was designed to compare groups of mice having various levels of experience with mosquitoes. The effect of experience could be observed, although details of the experience itself, such as particular learning mechanisms, could not be determined. Generally, the role of experience in defensive behavior seems minimal in P. leucopus, because there were few major differences between groups of mice. All adults, except one, and all juveniles displayed effective defensive behavior from the start of a test period (including the five-minute familiarization time, although behavior was not recorded during that interval). The individual actions were fairly consistent in appearance and rate of occurrence among all mice, except possibly ear-flick. Juvenile mice occasionally exhibited a relatively slow ear-flick, like pinning an ear forward briefly. This slight variation did not diminish the effectiveness of the movement. Ear-flick may be a reflex in response to tactile stimulation, relatively unaffected by experience after a mouse attains an adequate level of neurological development and motor ability. The other actions in grooming, exploring, and anti-mosquito behavior might depend on experience for perfection of coordination, but their employment as defensive actions against mosquitoes does not seem linked to the experience of encountering mosquitoes.

Grooming and exploring actions are integral parts of ordinary, non-mosquito-related, activity. The three actions designated as "anti-mosquito" seemed dependent in adult mice on the presence of mosquitoes, but also occurred at very low rates in juveniles when mosquitoes were absent. Because the actions do not have any clear purpose in the absence of mosquitoes, perhaps some type of behavioral "fine-tuning" occurs as mice mature, and the actions become limited to situations where they are useful responses to certain stimuli.

The catch/kill action is more difficult to interpret. Because it was linked directly and exclusively to the presence of mosquitoes, I expected that it would be influenced by experience. However, there was no significant difference in catch/kill between juveniles with and without practice. This suggests that either the action is not affected by experience, or, if it is, different or more precise criteria are needed to elucidate the relationship. Interpretation is even more challenging because JP mice, in both tests with mosquitoes, generally had more catch/kill than all groups of adult mice, but the JN mice did not. Thus, there may be a tendency for the catch/kill action to decrease as mice mature. This trend generally agrees with the tendency for juveniles to kill and eat more mosquitoes than the adults.

I can only speculate on possible factors that could influence these trends. Juveniles may possess more behavioral plasticity than adults, being predisposed to experience new features of habitat, diet, and conspecific encounters. Juveniles in my experiments were of the age when mice commonly disperse from the natal nest. Behavioral plasticity may peak near that age, diminishing as mice mature and learn what works best to promote survival. The actions of catching, killing, and eating mosquitoes may be practice for predation. _P. leucopus_ does eat larval and adult insects, but the relative contribution of insects to diet is variable (Hamilton, 1941; Whitaker, 1966), and any differences in the habit between age groups are not known. If juveniles are more arboreal than adults (McShea, 1981), adult insects such as mosquitoes may contribute relatively more to the juvenile diet, and thus juveniles may be more predisposed than adult mice to catch and eat insects. Finally, the juvenile attacks on mosquitoes may be a type of play behavior, associated with a tendency to be more active than adults and having a nebulous purpose. Although trapping studies can reveal patterns of dispersal, very little is known about the actions of juvenile wild small mammals; thus, it is hard to relate certain actions to the behavioral repertoire.

Extrapolation of Results to Nature

Given that, in the laboratory, adult and juvenile _P. leucopus_ exhibited effective defensive behavior against _Ae. triseriatus_, and wild adults maintained this defense with undiminished foraging behavior, one may cautiously extrapolate results to the wild. This leads to further questions about the universality of such behavior in _P. leucopus_. For instance, is defensive behavior adequate against mosquito species (or possibly other species of biting flies) more aggressive than *Ae. triseriatus*? This question is pertinent when restricted to species *P. leucopus* is likely to encounter, based on known biting habits, activity times, and habitats of the adult flies.

Are there natural situations when anti-mosquito behavior against moderately aggressive species is inadequate or absent? I believe other behavioral features of *P. leucopus* minimize the chance of anti-mosquito behavior being ineffective. When mice sleep, they are enclosed in a globular nest within some type of refuge, such as a pile of debris or the base of a tree, and are not exposed to mosquitoes. Day and Edman (1984) reported instances of mosquitoes feeding on *P. maniculatus* when the mice were provided with jars for refuge, and attributed this feeding success to the fact that the mice slept in the jars. However, mice did not have opportunity to construct more natural, fully-enclosing nests within the jars.

Mosquitoes might feed on *P. leucopus* if a mouse was so ill that it was lethargic, with reduced defensive behavior. A similar situation occurred in experiments with lab mice (*Mus musculus*) infected with malaria (Day *et al.*, 1983). Although experimental evidence is lacking, I doubt that a seriously ill *P. leucopus* would be exposed to mosquitoes for an extended period. An ill mouse probably would stay in its nest, minimizing risk of predation; if it left the nest, its lethargic condition would greatly increase the chance of its being preyed upon, and it probably would soon be killed and eaten. There is a slim chance that a mouse could die in an exposed site, not be eaten immediately by a predator, and serve briefly as a host for mosquitoes, until its body cooled substantially and mosquitoes were not attracted or could not feed on the altered blood supply. When one juvenile mouse (not included in my data) died of an overdose of anesthetics, mosquitoes fed successfully on the body during the entire test period, although most of them fed during the first 15 minutes. A similar situation occurred with a dead shrew during my preliminary study.

Mather and DeFoliart (1984) suggested that relatively high rates of successful mosquito feeding on paired chipmunks might have been influenced by the rodents' awareness and preoccupation with the position of each other, accompanied by reduced anti-mosquito behavior. *P. leucopus* adults are moderately sociable; intraspecific interactions might influence the effectiveness of anti-mosquito behavior, but the extent (if any) of this factor is hard to estimate.

Epidemiological Significance

Many factors, possibly varying geographically in relative importance, affect the epidemiology of a given disease. Contributions from research in many disciplines, such as entomology, immunology, and behavioral ecology, are needed to provide insight into complex interrelationships between species involved as vectors, pathogens, primary hosts, and reservoir hosts. Transmission of disease by a vector, and acquisition of disease by a host, can be directly affected by behavior of the potential host species. An examination of anti-mosquito behavior in one potential host species may provide information relevant to multiple species of mosquitoes and multiple diseases. The results of my study suggest that, due to its effective defensive behavior, *P. leucopus* is a minor host for mosquitoes and thus is unimportant as either a primary host or reservoir for mosquito-borne diseases (including many of the more than 200 arboviruses).

Relatively little is known about which mosquito-borne diseases, if any, can be carried by _P. leucopus_. If, as in _P. maniculatus_ with respect to several viruses (Nasci, 1982; Fairbrother and Yuill, 1984), _P. leucopus_ is not likely to sustain some viral infections, one may relate the fact to anti-mosquito behavior and speculate on co-adaptedness of _P. leucopus_, mosquitoes, and viruses. It should be advantageous to a virus to have a high likelihood of transmission to a favorable host. Similarly, it should be to a mosquito's advantage to concentrate feeding attempts on potential hosts likely to provide a bloodmeal without causing excess energy expenditure or risk of injury to the mosquito. Thus, anti-mosquito behavior may encourage efficiency in mosquitoes and their associated viruses. However, if _P. leucopus_ is able to sustain any viruses, one must consider the potential results of the catch/kill behavior in mice which eat mosquitoes. Even though mosquitoes would not transmit a virus to a mouse via bloodfeeding (due to effective anti-mosquito behavior), the virus might enter a mouse via ingestion of the killed mosquito. More study is needed to determine whether this situation is important epidemiologically.

What advantage(s) does _P. leucopus_ gain from not serving as a host? If there are mosquito-borne diseases symptomatically affecting _P. leucopus_, avoidance of infection is a possible benefit for _P. leucopus_. This is not necessarily disadvantageous to the virus, if it can be perpetuated in other vertebrate species. Any advantage to _P. leucopus_ in avoiding asymptomatic infections is more obscure. Another possible benefit to _P. leucopus_ is prevention of blood loss.

The extent of potential blood loss probably is related to factors of mosquito density and the availability of other, less defensive hosts in a given area. Mice did not seem adversely affected by the loss of blood to 40 mosquitoes in one hour in my study; however, it is possible that prevention of blood loss is worthwhile in an animal as small as *P. leucopus*. Several hundred bites per night, averaging, for example, 7.6 µl/bite (Klowden and Lea, 1979), might cause physiological stress and adverse behavioral effects in a mouse, resulting from blood loss plus the effects of toxins in mosquito saliva.

It is important to place the results of many studies (including mine) on anti-mosquito behavior in perspective. One may execute extensive laboratory and field experiments, postulate trends in mosquito-vertebrate interrelationships, and speculate on type and magnitude of cause and effect. However, it is crucial to realize that individual vertebrates can react to situations in unique ways. This is particularly true for mammals that have highly-developed sensory and learning capabilities. Thus, no matter how extensive and detailed the research on a species may be, it is not possible to predict how every member of the species will behave in a given situation involving mosquitoes.

Such individuality of behavior has several epidemiological implications. Knowledge of defensive behavior of a species allows one to estimate the species' role as host or reservoir for disease as minimal, but one cannot exclude the species from any involvement in the epidemiology of a given disease. Furthermore, any bloodmeal survey, even if it includes comprehensive and sensitive analysis, can indicate mosquito feeding patterns only for the locality and time of its execution. A series of such bloodmeal surveys, using data gathered throughout the mosquito season during several years in one area, would provide a fairly reliable profile of mosquito feeding patterns, but exceptions in the patterns can and probably will occur, due to individuality of vertebrate behavior. Since any profile will be vulnerable to exceptions, the most accurate understanding of mosquito feeding patterns will be provided by integrating knowledge gained from comprehensive bloodmeal surveys and from studies of behavior of potential hosts.

Summary

(1) Lab-reared and wild-caught adult and lab-reared, wild-stock juvenile *Peromyscus leucopus* exhibit effective defensive behavior toward *Aedes triseriatus*. Increased levels of grooming and exploring actions, plus particular anti-mosquito actions (ear-flick, headshake/twitch, and lunge/whirl), may occur.

(2) Maintenance of successful defense against mosquitoes does not diminish foraging ability in wild-caught *P. leucopus* adults.

(3) Experience plays a minimal role in development of this defensive behavior in *P. leucopus*. Catching/killing and eating mosquitoes may decrease with maturity.

(4) *Aedes triseriatus* is willing and able to feed on *P. leucopus* when mouse defensive behavior is absent.

(5) *P. leucopus* probably plays a minimal role as host for moderately aggressive mosquitoes and, thus, as primary host or reservoir for many mosquito-borne diseases.

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APPENDIX

TABLE 12

Statistically significant ($p<0.05$) comparisons of behavior of adult and juvenile mice.

Comparison	Behavior	p value
	Adults	
WMB > WMA	Groom	0.004
WPB > WPA	"	0.004
WPB > WPA	Explore	0.008
WMB > WMA	Anti-mosquito	0.004
WPB > WPA	"	0.004
LPB > LPA	"	0.004
WMA > WMB	Rest	0.020
WPA > WPB	"	0.004
LPA > LPB	"	0.012
WPA > WMA	"	0.032
LPB > WMB	"	0.014
WMA > WMB	Manipulate	0.027
	Juveniles	
JPB > JPA	Anti-mosquito	0.004
JPC > JPA	"	0.004
JPC > JPB	"	0.027
JNC > JNB	"	0.004
JNB > JNC	Rest	0.008
JNA > JNC	"	0.004

TABLE 13

Statistically significant ($p<0.05$) comparisons of behavior of adult vs. juvenile mice.

Comparison	Behavior	p value
JPA > WPA	Groom	0.010
WPB > JPB	"	0.019
JPA > WMA	"	0.003
JNB > WPA	"	0.032
JNB > WMA	"	0.010
JPA > LPA	"	0.032
JPA > WPA	Explore	0.000
JNA > WPA	"	0.003
JPB > WPB	"	0.002
JNC > WPB	"	0.014
JPA > WMA	"	0.005
JPB > WMB	"	0.002
JNC > WMB	"	0.010
JNB > WPA	Anti-mosquito	0.002
JPC > WPB	"	0.005
JNB > LPA	"	0.032
JPC > LPB	"	0.001
JNB > WMA	"	0.041
JPC > WMB	"	0.010
JPA > LPA	"	0.001
JNA > LPA	"	0.041
JPB > LPB	"	0.000
JNC > LPB	"	0.003
JPA > WPA	"	0.005
JPA > WMA	"	0.001
JNA > WPA	"	0.005
JNA > WMA	"	0.000
JNB > WPA	"	0.001
JNB > LPA	"	0.003
JNB > WMA	"	0.001
JPA > LPA	"	0.007
JNA > LPA	"	0.019
JPB > WPB	Catch-Kill	0.005
JPB > WMB	"	0.041
JPC > WPB	"	0.014
JPC > LPB	"	0.000
JPB > LPB	"	0.000
WPA > JPA	Rest	0.001
WPA > JNA	"	0.025
WPB > JNC	"	0.014
WPA > JNB	"	0.014
LPB > JPC	"	0.025
LPA > JPA	"	0.014
LPB > JPB	"	0.014
LPB > JNC	"	0.001

TABLE 14

Statistically significant ($p<0.05$) comparisons of mosquito feeding success on adult and juvenile mice.

Comparison	Mosquitoes	p value
	Adults	
WMB > LPB	% Dead	0.001
WMB > WMC	% Unfed	0.004
WPB > WPC	"	0.004
LPB > LPC	"	0.004
LPB > WMB	"	0.005
LPC > WMC	"	0.003
WMC > WMB	% Completely fed	0.004
WPC > WPB	"	0.004
LPC > LPB	"	0.004
WMC > LPC	"	0.007
	Juveniles	
JPD > JPC	% Recovered	0.004
JND > JNC	"	0.016
JPD > JPB	"	0.004
JPC > JPD	% Unfed	0.004
JNC > JND	"	0.008
JPB > JPD	"	0.004
JPD > JPC	% Completely fed	0.004
JND > JNC	"	0.008
JPD > JPB	"	0.004
JPD > JPC	% Partly fed	0.031
JND > JNC	"	0.031

TABLE 15

Statistically significant ($p<0.05$) comparisons of mosquito feeding success on adult vs. juvenile mice.

Comparison	Mosquitoes	p value
WPB > JPB	% Recovered	0.032
WPB > JPC	"	0.014
WMB > JPC	"	0.000
WMB > JPB	"	0.000
LPB > JNC	"	0.041
LPB > JPB	"	0.000
LPB > JPC	"	0.000
JPC > WPB	% Killed	0.014
JPC > WMB	"	0.002
JPB > WPB	"	0.032
JPB > WMB	"	0.003
JPB > LPB	"	0.000
JNC > LPB	"	0.019
JPC > WPB	"	0.014
JPC > WMB	"	0.002
JPC > LPB	"	0.000
JNC > LPB	"	0.032
JPB > LPB	"	0.000
JPC > LPB	"	0.000
JPC > WPB	% Eaten	0.014
JPC > WMB	"	0.000
JPB > WMB	"	0.000
JNC > WMB	"	0.019
JNC > LPB	"	0.040
JPB > LPB	"	0.000
JPC > LPB	"	0.000
WPB > JPC	% Dead	0.041
WMB > JPC	"	0.000
WMB > JPB	"	0.003
WMB > JNC	"	0.001
LPB > JNC	"	0.014
LPB > JPB	"	0.025
LPB > JPC	"	0.025
JPB > WPB	% Unfed	0.010
JNC > WPB	"	0.020
WPB > JPC	"	0.014
JPC > WMB	"	0.001
JPB > WMB	"	0.003
JNC > WMB	"	0.001
JNC > LPB	"	0.014
WPB > JPB	% Completely fed	0.032
WPB > JNC	"	0.019
WPB > JPB	% Partly fed	0.041
WPB > JNC	"	0.020
JND > WMC	"	0.047
WPB > JPC	"	0.019