FACTORS INFLUENCING NIGHTLY ACTIVITY OF DEER MICE (*Peromyscus maniculatus*) IN TALLGRASS PRAIRIE

by

RYAN L. REHMEIER

B.S., Trinity University, 1997
M.S., Kansas State University, 2000

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2005

ABSTRACT

Little is known about nightly activity patterns of nocturnal small mammals under natural conditions, and how these activity patterns might be affected by photoperiod, season, and sex, age, and reproductive status of individuals. The main objectives of this research were: 1) to find an appropriate method for marking individual deer mice (*Peromyscus maniculatus*) so that their activity could be monitored remotely; 2) to design a portable activity-monitoring system to investigate temporal patterns of shelter use by deer mice under natural conditions; 3) to determine the influence of environmental conditions such as photoperiod and season on nightly activity of deer mice; and 4) to compare effects of demographic or physiological factors such as sex, age, and reproductive status on nightly activity of deer mice at artificial burrows in tallgrass prairie. In general, commencement of activity was correlated positively with timing of sunset, and time of retirement to the burrow was correlated positively with sunrise. Among adults, males first emerged from the burrow earlier and made more trips of shorter duration in a night than did females, although total duration of trips was similar. Return visits and subsequent stays typically were shorter for males than females, but total time spent in the burrow and retirement time relative to sunrise were similar for both sexes. Young deer mice emerged significantly later, made more trips of shorter duration, spent less total time outside, and retired to their burrow earlier than adults. Reproductive females emerged later, made fewer trips of generally longer duration, and spent shorter total amounts of time away from the burrow each night than non-reproductive females. Return visits of reproductive females were of longer duration than non-reproductives, but total time spent inside and time of retirement for the night did not differ relative to reproductive status. From parturition through lactation, activity of females showed a number of directional trends. Results suggest that under natural conditions, activity patterns of

deer mice are highly variable but responsive to both the changing physical environment and internal conditions related to sex-specific maximization of fitness.

FACTORS INFLUENCING NIGHTLY ACTIVITY OF DEER MICE (*Peromyscus maniculatus*) IN TALLGRASS PRAIRIE

by

RYAN L. REHMEIER

B.S., Trinity University, 1997
M.S., Kansas State University, 2000

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2005

Approved by:

Co-Major Professor

Glennis A. Kaufman

Co-Major Professor

Donald W. Kaufman

ABSTRACT

Little is known about nightly activity patterns of nocturnal small mammals under natural conditions, and how these activity patterns might be affected by photoperiod, season, and sex, age, and reproductive status of individuals. The main objectives of this research were: 1) to find an appropriate method for marking individual deer mice (*Peromyscus maniculatus*) so that their activity could be monitored remotely; 2) to design a portable activity-monitoring system to investigate temporal patterns of shelter use by deer mice under natural conditions; 3) to determine the influence of environmental conditions such as photoperiod and season on nightly activity of deer mice; and 4) to compare effects of demographic or physiological factors such as sex, age, and reproductive status on nightly activity of deer mice at artificial burrows in tallgrass prairie. In general, commencement of activity was correlated positively with timing of sunset, and time of retirement to the burrow was correlated positively with sunrise. Among adults, males first emerged from the burrow earlier and made more trips of shorter duration in a night than did females, although total duration of trips was similar. Return visits and subsequent stays typically were shorter for males than females, but total time spent in the burrow and retirement time relative to sunrise were similar for both sexes. Young deer mice emerged significantly later, made more trips of shorter duration, spent less total time outside, and retired to their burrow earlier than adults. Reproductive females emerged later, made fewer trips of generally longer duration, and spent shorter total amounts of time away from the burrow each night than non-reproductive females. Return visits of reproductive females were of longer duration than non-reproductives, but total time spent inside and time of retirement for the night did not differ relative to reproductive status. From parturition through lactation, activity of females showed a number of directional trends. Results suggest that under natural conditions, activity patterns of

deer mice are highly variable but responsive to both the changing physical environment and internal conditions related to sex-specific maximization of fitness.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

I thank my co-major professors, Glennis A. Kaufman and Donald W. Kaufman for their advice, support, and countless (I do mean countless) suggestions for improving manuscripts from my dissertation and other projects. I also greatly appreciate the efforts of my supervisory committee, including James J. Higgins, Brett K. Sandercock, Janice C. Swanson, and C. Michael Smith (Outside Chairperson), in helping to guide me through the completion of my dissertation.

I also wish to recognize the efforts of several family members or friends, who accompanied me to my site on Konza Prairie or made the trek with me to my other study site in northcentral Kansas (the data from which did not make it into this dissertation). These unlucky souls included Tara and Caden Rehmeier, Bob Bailey, Jim Rivers, and Justin Boyles. For some reason, each of these people visited either site only once. Thanks to Aaron Reed for assistance with trapping from 1999-2001 on the West site in Chapter 1. Aaron also suggested the specific location for my study site on watersheds 1B and 2A at Konza Prairie, which turned out to be a superb study site.

Over the years of my graduate training, I have learned a great deal from discussions about science (among other topics) from Aaron Reed, Ray Matlack, Jim Rivers, Jake Goheen, Beth Ross, and Brock McMillan. They all have been great colleagues and have provided fine advice to me on a number of professional matters in the last 5 years. Each of these people have played a part in making me the teacher-scholar I am today (thus, they are to be blamed).

Last, but not least, I thank my whole family for their undying support throughout this tortuous (and sometimes torturous) journey. My wife, Tara, and son, Caden, bring me more joy each day than I deserve. Professionally, I am thankful to Tara for serving as my sounding board for ideas and a tough editor for my job application materials over the past few months. Thanks

also to Tara for taking me to the emergency room at 4 a.m. after I hurt my back carrying deep cycle batteries for my "portable" activity-monitoring system. Many thanks to my parents, Lynn and Rinda Rehmeier, and my sister, Ann Rehmeier, for their support and love. Thanks also to other important members of my family, including Bob and Sharon Bailey, and Jessica and Jake Dodson, who have always acted interested in the trials and tribulations of little mice on the prairie.

The National Science Foundation through the Konza Prairie Long-Term Ecological Research Project provided partial financial support for this research. I am thankful for several years of support from Graduate Teaching Assistantships from the Division of Biology at Kansas State University and for Graduate Research Assistantship funding provided by the Kansas GAP Education Project. Research awards from the Central Plains Society of Mammalogists and the Kansas Academy of Science aided collection of data for Chapters 3 and 4. Use of animals in this dissertation project followed recommendations of the Animal Care and Use Committee of the American Society of Mammalogists and was approved by the Kansas State University Institutional Animal Care and Use Committee (protocols #1597, #2184, and #2184.1). Scientific collection permits were acquired from the Kansas Department of Wildlife and Parks (#SC-036-99, #SC-030-2000, #SC-057-2001, #SC-127-2002, #SC-035-2003, #SC-043-2004, and #SC-051-2005) for this research.

DEDICATION

I dedicate this dissertation to two people who have had a profound influence on the way I live my life. My wife, Tara, has made countless sacrifices to support me and help me accomplish my goals, academic or otherwise, and just generally makes me happy every day. My sister, Ann, shows me what hard work really is and reminds me to be thankful for all the little things in life.

Chapter 1: Marking small mammals for field studies: recent trends and new observations.

Abstract

Mark-recapture studies of small mammals require that individuals be uniquely marked and that individuals retain the mark permanently. Selection of a marking technique can be difficult, due to physical constraints imposed by the morphology or behavior of the animal, as well as restrictions imposed by permit-granting agencies or institutional animal care and use committees. I surveyed all articles published in Journal of Mammalogy from 1980 to 2004 (volumes 61-85) describing field studies of rodents, lagomorphs, or insectivores. My objective was to determine historical trends and body-size specific trends in use of different marking techniques in these taxonomic groups. Ear tags or punches were the most commonly used technique ($n = 217$ articles), followed by toe-clips ($n = 148$), hair dye or unique hair clips ($n = 61$), and PIT tags ($n = 17$). Relative prevalence among techniques remained relatively stable over time. Body mass of the small mammal influenced the marking technique chosen. I also conducted a field study to compare numbers of human errors associated with each marking technique, loss of marks, pain response to marking, and effects of topical antiseptic on infection and recapture rates among several marking techniques in deer mice (*Peromyscus maniculatus*) and white-footed mice (*P. leucopus*). A higher proportion of ear tags than PIT tags were lost in deer mice. Ear-tagging elicited a greater pain response than toe-clipping in deer mice, but no difference was found in white-footed mice. Application of iodine did not affect the proportion of infections observed or the probabilityof recapture for either species. Evidence from this study suggests that several species-specific factors (i.e., body size and morphology, study duration, and ethical concerns) must be considered when selecting a marking technique.

Introduction

When individuals cannot be recognized by use of distinguishing physical features, such as natural variation in scarring and pelage coloration patterns (Blackmer et al. 2000; Whitehead 2001), individuals must be permanently marked for studies of population ecology and behavior. Species of small mammals are often numerically abundant and similar in pelage coloration, which generally requires that individuals be marked permanently and uniquely. Three methods commonly used by wildlife researchers and approved by the American Society of Mammalogists (ASM) include: placing tags in ears, injecting passive integrated transponder (PIT) tags under skin, and clipping of toes when other methods of identification are not feasible (Animal Care and Use Committee of the American Society of Mammalogists 1998). Studies that employ mark-recapture analyses assume that marks are not lost, are recorded correctly, and do not affect catchability of individuals (Otis et al. 1978; Pollock et al. 1990). Additionally, permanent markings of individuals are not always permanent, as tags can be lost. Tag loss is equivalent to mortality in mark-recapture models but can be assessed with multiple marking techniques. Even when tags are retained, human error in reading numbers on tags can affect the usefulness of data.

Not all marking techniques approved by the ASM are accepted by governmental agencies that issue permits, or by university institutional animal care and use committees (IACUCs) that approve protocols. Generally, boards granting permits within governmental agencies consist of professionals in biology, whereas IACUCs approving study protocols generally consist of professionals from biological and non-biological fields. Permit-issuing agencies tend to restrict the techniques that can be used, especially when species of conservation concern are to be studied. In contrast, IACUC have to approve marking protocols for vertebrates for both laboratory and field-based studies. The decisions that researchers must make in writing the research protocol for designing a laboratory-based study are quite different from the decisions made in designing a field-based study. For example, field researchers must select a marking protocol that allows a large number of free-ranging individuals to be marked uniquely, whereas in most laboratory studies individuals are confined to a limited space or cage. Further, field researchers must select a marking technique that shortens handling time to reduce physiological stress on animals that might be under foraging constraints in their natural environment, whereas laboratory organisms often are fed *ad libitum*. Finally, field researchers must select a marking protocol that allows animals to remain alert and vigilant relative to predators soon after marking, whereas laboratory organisms can be anesthetized relative to marking with no fear of a predator attacking them as they recover.

Members of IACUCs rarely have sufficient information available regarding historical trends in use of different marking techniques for small mammals (e.g., rodents, insectivores, and lagomorphs) studied under field or natural conditions. If this information were available, it could highlight methods that have been used most often by researchers studying different groups of small mammals. Patterns of use over time and across body sizes might allow for more informed decisions (by both researchers and IACUC members) concerning which techniques should be considered for each taxonomic group.

Marking techniques *per se* rarely garner much attention in most published articles, as the method used might be mentioned briefly, if at all. This is unfortunate, as marking methods may differ in efficacy and some might have advantages and disadvantages associated with their use. These differences could include mark-specific loss rates (Williams et al. 1997), probability of introducing human errors, and variability in occurrence of infection caused by each marking technique. Further, physical reactions to the marking process have been noted anecdotally

(Lindner and Fuelling 2002), but no attempt has been made to quantify perceived-pain responses to marking techniques commonly used in field studies.

My goal was to examine historical and body-size patterns in use of different marking techniques and to extend my knowledge by testing several marking techniques simultaneously in the same individual. My first objective was to examine historical and body size patterns via a survey of published articles in the Journal of Mammalogy over the last 25 years that allowed me to quantify temporal trends in use of marking techniques on small mammals. My second objective was to quantify several parameters important in natural environments through two field studies on deer mice (*Peromyscus maniculatus*) and white-footed mice (*P. leucopus*) conducted in native tallgrass prairie from 1999 through 2004. More specifically, I first quantified reading/recording errors associated with several common marking methods (PIT tags, ear tags, and toe-clips). Second, I compared the proportion of marks lost among alternative marking methods. The relatively large external pinnae of most small mammals are simple to tag, but the thin tissue of pinnae may be poor at resisting loss of tags through social interactions or normal movements through complex microhabitats. From the literature and my own observations in previous studies, I predicted that a higher proportion of ear tags would be lost than in other marking methods. Third, I evaluated the physical reaction associated with each marking technique within and among individual *Peromyscus*. Because toe-clipping involves removal of a digit, it might be expected to elicit greater response from an individual than would another technique. Finally, I examined the effect of application of a topical antiseptic on likelihood of infection and recapture rates relative to toe-clipping. I predicted that antiseptic treatment would lower likelihood of infection and perhaps increase rates of recapture. My study differed from previous studies as I report on information regarding the effects that a marking technique can have on the individual marked as well as how this might affect the results of a field study.

Materials and Methods

Literature Survey

Collection of data.—I searched every article and note published in the Journal of Mammalogy from 1980 to 2004 (volumes 61-85) for field studies involving rodents, insectivores, and lagomorphs. I used 477 articles, which had been initiated between the years of 1959 and 2001. I noted the species reported in each published record; only studies in which small mammals were recaptured or re-sighted were used. Some large, outdoor-enclosure studies were included because potentially large numbers of animals were marked and they interacted with their environment similar to that of free-living species. I also recorded the method of marking for each small mammal species. When more than 1 marking technique was used, each technique was scored for that species for that article.

Categorization of data.—Each marking technique was grouped into one of 5 general categories; these were ear tags, toe-clips, hair dye/trim, PIT tags, and other. Ear tags included all marks that were placed in or on the ear, such as monel-type fingerling ear tags, color- or symbol-coded tags, plastic tags, and reflective tags as well as wire rings and notching or punching of unique codes into the pinnae. Toe-clips included the removal of one or more phalanges from each foot to produce unique codes (e.g., numerical codes). Hair dye/trim included all marks that were placed in or on the pelage and included permanent dye applied to the fur to produce identifying patterns, and clipping of fur, such as guard hair, on different positions of the body. I recognize that cutting or dying hair was not a truly permanent mark, but this technique was relatively permanent given the short lifespan of most small mammals in the wild and the goals of the majority of studies using hair-marking techniques. PIT tags included included implanted PIT tags and magnetically coded beads (Lacey et al. 1997, 1998). An "other" category contained miscellaneous techniques for which 1) there were too few studies or too few individuals marked, or 2) marking was not sufficiently long-lasting or unique among individuals. This category included tattoo, freeze branding, fluorescent powder, picric acid, metal band on limb, color-coded collars, irradiated wires, non-positional hair clipping, or clipping of the same single toe for all captures. In addition, radiotelemetry (attachment of receiver typically by implantation or collar) was included in the "other" category because it typically was used to mark only a subset of individuals within a population being studied. I deleted the marking method for a given species when an article implied use of a marking technique that was morphologically improbable (i.e., use of ear tags to mark shrews of the genus *Sorex*, which lack external pinnae). These generally occurred in community studies where an author made a blanket statement about a single technique used to mark individuals of all species.

Statistical analysis.—I used the log-likelihood ratio (*G*) test to test whether prevalence of marking techniques have changed through time among 6 time categories. Each article was assigned to one of the time categories by using the first year of a study. If no dates of study were provided (11 articles - 2.3%), I estimated dates by using the year the manuscript was submitted. I used six 5-year time categories starting in 1970 and ending in 1999; the earliest (before 1970) and most recent time intervals (2000 and after) were excluded because each interval contained too few studies for analysis. One marking category (PIT tags) also was excluded, as it was not available to researchers in all time intervals.

I also examined whether marking techniques chosen were independent of body size of the study animal. I assigned a standardized body mass (averaged for males and females) for each species based on information in a published database (Smith et al. 2003). Estimates of mass were available for ~ 95% of the species tagged; any species not found in the database was excluded from this analysis. Further, I only entered the body mass for a species for a marking technique once to keep from weighting the analysis relative to common species studied. That is, although 25 and 21 studies have used toe-clips and ear tags, respectively, to mark deer mice (*Peromyscus maniculatus)*, the value of 21.3 g was used only once to calculate median mass for each technique. I used a Kruskal-Wallis test (*H*) to compare body mass of species among marking techniques. If an *H* statistic was significant, I did multiple pairwise comparisons to determine which techniques differed, by using Wilcoxon rank-sum tests (*W*). After Bonferroni adjustment, a *P* value < 0.0083 was required to declare significant differences between pairs of marking techniques. I use a *G*-test to examine if the distribution of body-mass categories (based on a $\log_{\text{base2}}$ scale) was distributed randomly among marking techniques.

Field Study

Description of study sites.—The field study was conducted on Konza Prairie Biological Station (39°05’N, 96°35’W), a 3,487 ha native tallgrass prairie research site in the northern Flint Hills of eastern Kansas, near Manhattan. Konza Prairie is subdivided into > 50 experimental fire-grazer treatment units, which vary in size from 16-133 ha. Data were collected on 4 adjacent, ungrazed treatment units in the southwest portion of Konza Prairie, R1A and R20A (termed the "West" site hereafter) and 2A and 1B (termed the "East" site).

Collection of field data.—Mice were live-trapped on the West site between 7 December 1999 and 1 December 2001, and on the East site from 1 July 2003 to 17 December 2004. The West site had 4 traplines that were 20 stations long and 2 traplines that were 10 stations long, whereas the East site had 6 traplines from 7 to 15 stations in length. For all traplines, inter-station distance was 15 m. Two large Sherman live traps (7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) were placed at each station. Traps were baited with peanut butter and rolled oats (Kaufman et al. 1988). Polyester fiberfill was provided as nesting material in winter, spring, and autumn. I trapped for 4 consecutive nights (West site) or 2 consecutive nights (East site) during each season. In addition to live trapping on the East site, deer mice were surveyed in 20 artificial burrows during 1 July 2003–17 December 2004. I followed guidelines for capturing and handling small mammals as published by the American Society of Mammalogists (Animal Care and Use Committee of the American Society of Mammalogists 1998) and as approved by the Kansas State University IACUC.

Marking methods.—Each deer mouse and white-footed mouse (*Peromyscus leucopus*) captured were marked by two different marking techniques on the two study sites. Ear tags and toe-clips were used simultaneously on the West site from December 1999 through December 2001. From June 2000 to December 2001, I marked deer mice with PIT tags, toe clips, and ear tags. On the East site, deer mice (the only *Peromyscus* captured) were double-marked with ear tags and PIT tags; toe clips were not used at this site.

A single ear tag was applied to either the right or left ear of those individuals (≥ 7 g) that were to receive this mark. The ear tag that I used to mark *Peromyscus* was a size-1, monel, self-piercing fingerling tags (style #1005-1, National Band and Tag Co., Newport, Kentucky, USA), which had a standard 4-digit stamp. I applied ear tags by using applicator pliers (style 1005s1, National Band and Tag, Co.) that had been modified by grinding excess metal from the tips of the pliers. This modification improved my ability to apply the tag at the base of the pinna.

A single PIT tag was inserted in those individuals (≥ 5 g) that were to receive this mark. The PIT tag that I used to mark deer mice was an implantable, glass-encapsulated tag (12 mm x 2.1 mm; Model TX1400L, Biomark, Inc, Boise, Idaho, USA). Before tags were taken to the field, they were soaked in 70-95% isopropyl alcohol for ≥ 24 hours. Each tag was then coated with a thin layer of triple antibiotic ointment and loaded into a sterilized 1.9-cm long, 12-gauge stainless steel needle (Model N75, Jorgensen Laboratories, Loveland, Colorado, USA). The needle was screwed onto a disposable plastic 5-cc implanter syringe (Model MK5, Biomark, Inc.). The syringe was modified with 2-3 longitudinal slits cut along the sides of the rubber gasket at the tip of the plunger. This modification helped me to avoid injection of air into the animal along with the PIT tag. Once a needle was loaded with a PIT tag, the needle was placed, tip-down, into a sterilized, plastic vial that could carry about 12 pre-loaded needles. Pre-loading tags into needles in the laboratory provided a faster and more sterile environment than attempting to load tags at each trap station in the field. PIT tags were injected subcutaneously in the dorsal surface of the interscapular region. After injection, the location of the inserted PIT tag was ascertained by palpation and pushed backward and laterally, away from the insertion hole. When a PIT tag was retained and working, a brief (1 sec) scan with the PIT-tag reader was sufficient to detect the tag. However, if the PIT tag was not detected with this brief scan of a known recaptured mouse, a longer scan (5-10 sec) was performed while moving the reader around the mouse. If the tag still was not detected by the reader in a long scan, the mouse was examined visually and palpated to determine if the tag was present but not working. If neither the reader scan nor the manual search detected the presence of the PIT tag, the tag was assumed to have been lost.

A single digit was clipped at the basal interphalangeal joint (Kumar 1979) from three of the four feet in those individuals that were marked by toe-clipping. I also examined whether the application of a topical antiseptic (iodine) affected the number of toes that became infected. From June 2000 to December 2001 on the West site, animals were paired sequentially and assigned at random to either a treatment or a control group to assess infection. A cotton swab

(Q-tip) soaked in iodine tincture was dabbed on wounds immediately following marking for the treatment group. The control mice received no additional attention and were released immediately after toes were clipped. I assessed toe-clipped mice for an infection of the toe, defined by swollen, red tissue near the joint, on subsequent captures (the next day and first capture in next trapping session). I also examined if application of iodine after toe clipping influenced the likelihood of recapture, as I assumed that if mice perceived the act of toe-clipping as a painful experience exacerbated by application of iodine, then they would avoid entering a trap the next day and potentially the next trapping session. In this case, I compared the iodine treated animals with those individuals that had not received iodine after toe-clipping. Mice marked on the last day of a trapping session and in the last trapping session (December 2001) were excluded relative to the appropriate analysis.

Pain assessment.—I observed and assessed the pain response of each mouse relative to the 2 marking techniques applied from November 2000 to December 2001 for the West site and from July 2003 to December 2004 for the East site. The response of each mouse was rank-scored as a 1, 2, or 3, in order of increasing reaction. A "1" indicated no outward physical or vocal response. A response was scored as a "2" if the animal flinched at the moment the mark was applied. A response was scored as a "3" if a mouse flinched or moved and vocalized. The order in which the 2 marking techniques were applied was chosen at random for each individual. The 2 field workers (RLR and A. W. Reed) received similar training in scoring these events to minimize inter-observer bias; these two individuals also applied all marks. During training, both workers separately scored the same marking events and then compared scores; workers agreed on scores in all cases.

Once a worker had securely grasped a mouse by the nape of its neck, it rarely ever continued to move or struggle. The mice also did not vocalize under normal handling. To this end, if a mouse was struggling or vocalizing, I did not attempt to mark it until it calmed. Thus, the observed response to marking should have been to the mark application and not part of a continuous escape response.

Statistical analysis.—I used nonparametric statistics in analysis of all field measures because some data were categorical and few continuous measures were distributed normally. I used the StatXact-3 statistical package (Cytel Software Corp., Cambridge, Massachusetts, USA) to test for significant differences and patterns among the measured variables. Two-tailed *P*-values were calculated where no *a priori* directional prediction of response could be made. *P*-values < 0.05 were considered significantly different.

Human errors were calculated for handling, marking, and recording data for each marking technique. Data for each individual was entered from field data sheets into an electronic database that tracked the original marks given to each individual as well as any subsequent mark losses of tags and any additional marks that were applied (e.g., replacing a lost ear tag). Subsequently, entries from daily field data sheets for each individual were compared with the electronic database to determine if any errors had been made in the field. These errors were categorized as (1) error in reading the tag or writing the information on the field data sheet (hereafter called misread/write error); (2) error in giving two individual the same mark (hereafter called duplication error), and (3) error in applying the mark (hereafter called an application error). Ear tags and PIT tags were only subject to misread/write errors, but not duplication or application errors. In contrast, toe clips were subject to misread/write, duplication, and application errors because researchers had to both track the numerical codes that were available as well as clip the appropriate digit on each foot. Number of errors was counted and the proportion of errors was calculated as the number of errors made divided by the total number of individuals marked or subsequently handled by researchers for each marking technique and error type for each species.

I compared mark retention by the *G* test for ear tags and PIT tags, but not for toe clips as the latter was retained 100% of the time. Only individuals that were recaptured were used for these comparisons, as the fate of marks was unknown for individuals captured only once. I divided the number of recaptured individuals that lost the mark at some time in their residency on the site by the number of recaptured individuals that received the given mark for each tagging methods.

I used Jonckheere-Terpstra (*J*) tests for doubly ordered contingency tables to compare the distribution of pain responses for paired marking techniques. This test improved upon a χ^2 test of association by accounting for the ordinal nature of pain categories for both marking techniques within a paired data set. I also compared pain response to paired marking techniques by using a Wilcoxon signed rank (SR_+) test. Further, I tested by using Spearman rank correlation (r_S) analysis whether response to each mark type was related within individuals. That is, an individual either responded weakly or strongly to both marking methods that were applied.

Finally, I used *G* tests to compare the effect of the presence/absence of iodine on the likelihood of toe infections and on recapture rates. *G* tests also were used to examine if individuals avoided traps after being marked by toe-clipping as compared to ear-tagging and PIT tagging.

Results

Literature Survey

A total of 310 species of small mammals was reported in the 477 articles that met my criteria for inclusion in the literature survey (Appendix 1). In the 477 articles, 281 species of rodents, 21 species of insectivores, and 8 species of lagomorphs were represented. Sixteen species (all rodents) appeared in ≥ 10 different articles, but white-footed mice (n = 56 articles) and deer mice (n = 53) numerically dominated and were about equally represented over the survey period. Three other species were fairly common; these included the cotton rat (*Sigmodon hispidus*; n = 35 articles), prairie vole (*Microtus ochrogaster*; n = 34), and meadow vole (*M. pennsylvanicus*; n = 28). Conversely, 156 species appeared in only 1 article during the same time period. Most studies were conducted in North America, but studies carried out in Europe, South America, Asia, Africa, and Australia also were represented in Journal of Mammalogy.

The highest numbers of reported marking methods for individual species were recorded for studies initiated during a 10-year period (1975-1984; Fig. 1). During this 10-year period, a total of 97 and 109 were reported for 1975-1979 and 1980-1984, respectively. The 15-year period of 1985 through 1999 also had greater than 50 studies initiated in each 5-year interval.

Markings in or on the ear were the most commonly used technique (n = 217; 45% of articles); this might be expected because this category was very broad and included multiple types of ear tags as well as ear notches and punches. The second most commonly used marking method was toe-clipping (n = 148; 31% of articles). Infrequently used marking methods included marks to the pelage (hair dye/clip: n = 61), other (25), and PIT tags (17). A total of 66 articles tracked individuals via radiotelemetry. Further, I found that animals either were not marked or the marking technique was not stated in the methods in 77 articles (16%).

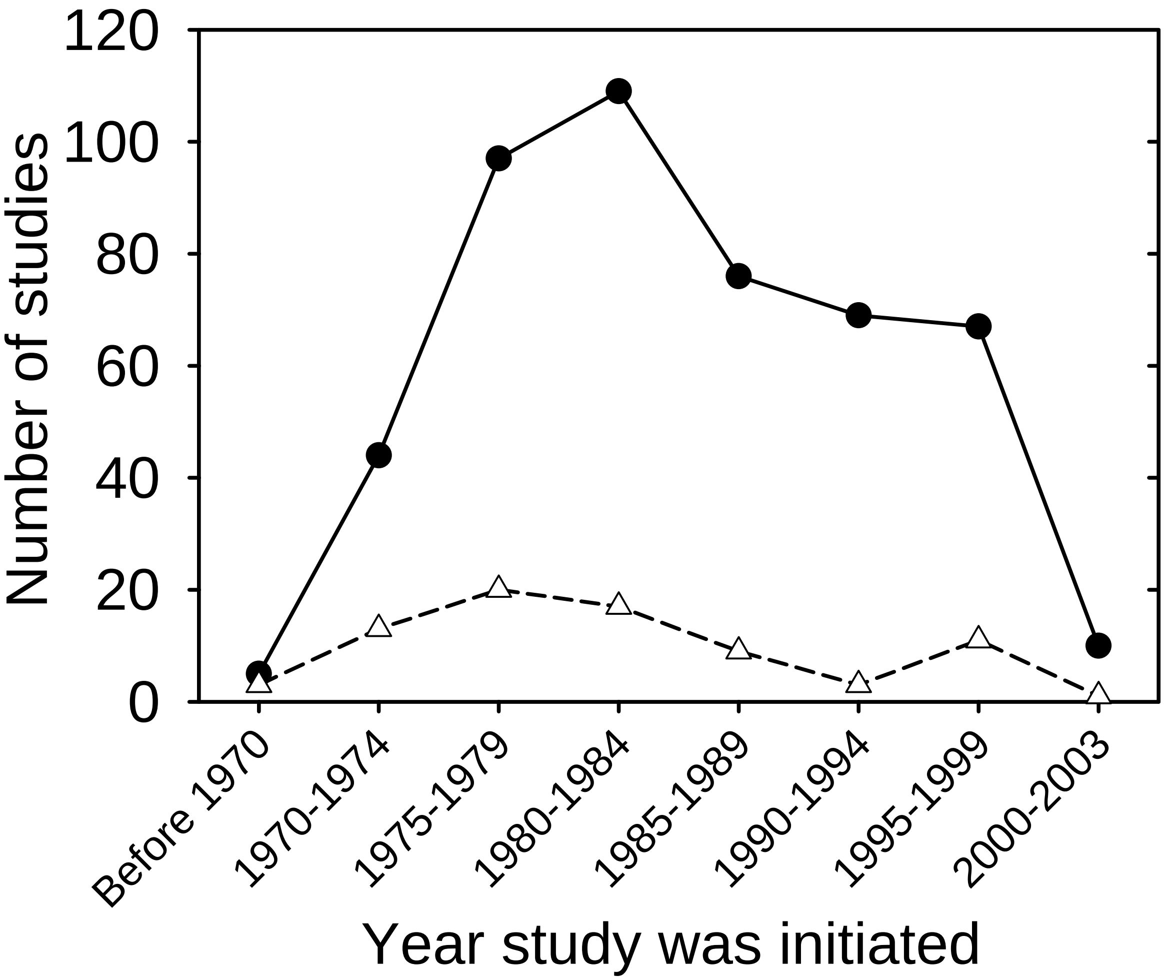

Figure 1. Number of field studies published in the Journal of Mammalogy from 1980-2004 in which the technique used to mark individual small- or medium-sized mammals was discernible (solid circles) or not discernible/individuals were not marked (open triangles), by 5-year intervals within which each study began.

Markings to the ear were the most commonly used marking technique from 1975 through 2001 (Fig. 2). Toe-clipping was used similarly to ear markings from 1970 through 1984, but then declined in use from 1985 through 2001. Marks to the pelage (e.g., dyeing or clipping of fur) were the third most popular technique in all but the 1990-1994 interval, when PIT tags had it highest frequency of use. The proportional distribution of ear, foot, and pelage marks remained similar across the 6 time intervals compared ($G = 16.2$, *d.f.* = 10, $P = 0.094$).

Number of species identified by markings to the ear, foot, pelage, or internally varied significantly among species-specific body-mass categories ($G = 60.0$, *d.f.* = 30, $P < 0.001$; Fig. 3). Clipping of digits on feet was most prevalent for species that weighed < 256 g, and then declined at larger body masses, although in one case, a species (Central American agouti, *Dasyprocta punctata*) that weighed more than 2048 g, still was marked by toe-clipping. In contrast, markings to the ear were not used commonly on species that had a body mass < 16 g. The highest use of markings to the ear occurred in the body size class of 16-31.9 g; this method became the predominant marking technique for species weighing ≥ 256 g. Marks to the pelage occurred from 4 g to > 2048 g, but were not commonly used (< 10 studies) within any body size category. Internal tags also were not used commonly, but use of this new technology was observed in species whose body mass ranged between 16 g and 1023.9 g.

The typical body mass of species marked by the three techniques differed significantly (Fig. 4; $H = 28.4$, *d.f.* = 3, $P < 0.001$). Species marked with toe clips were significantly smaller in body size (median = 38.0 g,) than those that were ear tagged (median = 63.3 g; $W = 3.68$, $n_{\text{toe clip}} = 185$, $n_{\text{ear tag}} = 148$, $P < 0.001$) or marked with hair dye or hair clipping (median = 206.0 g; $W = -4.71$, $n_{\text{toe clip}} = 185$, $n_{\text{hair}} = 57$, $P < 0.001$). All other pairwise comparisons were not significantly different.

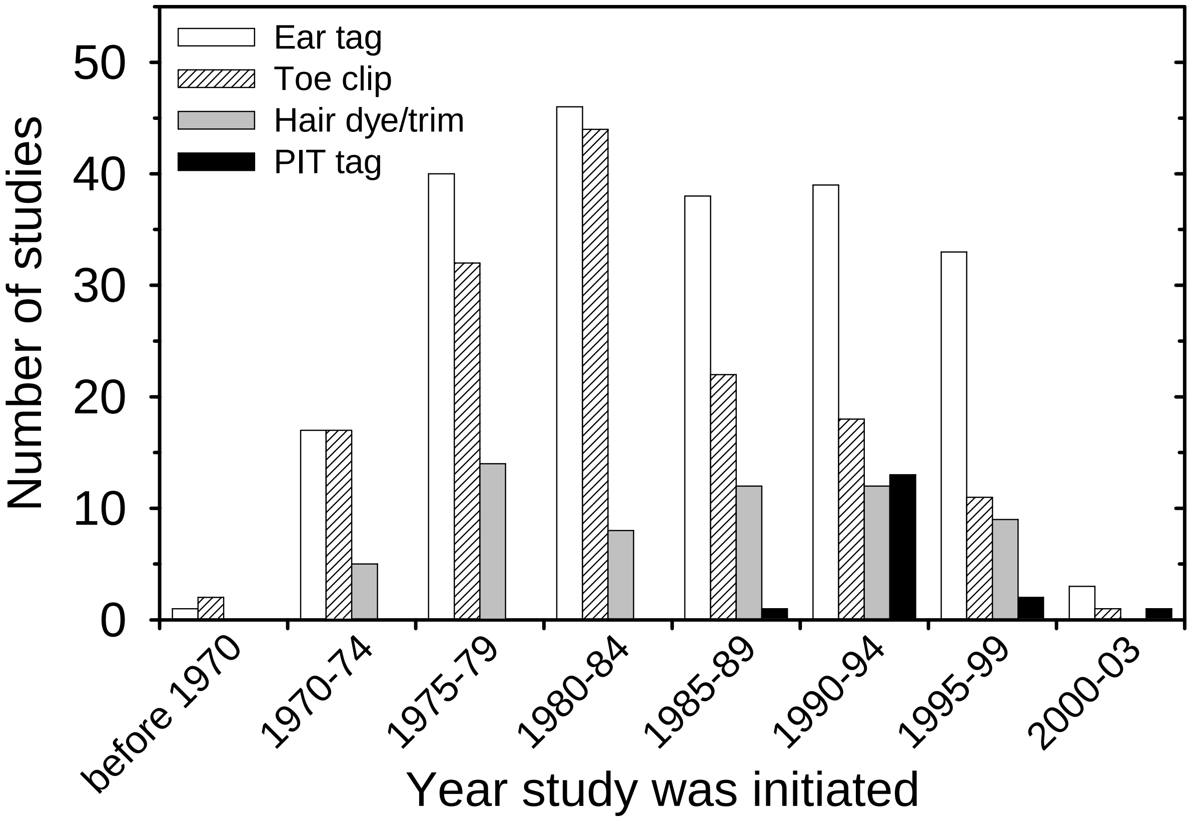

Figure 2. Temporal variation in number of field studies published in the Journal of Mammalogy from 1980-2004 that used each of 4 common, permanent marking techniques for rodents, insectivores, and lagomorphs, grouped by the year in which each study was initiated.

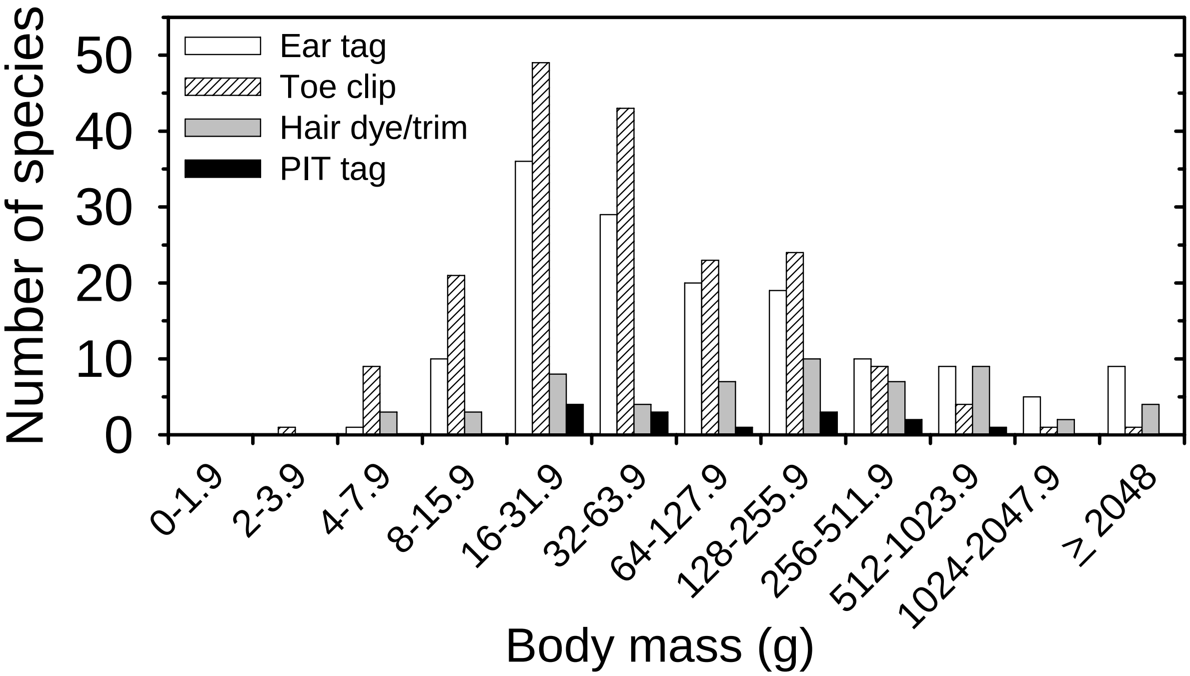

Figure 3. Number of species of rodents, insectivores, and lagomorphs on which each of 4 common, permanent marking techniques were used in articles published in the Journal of Mammalogy from 1980-2004. A $\log_2$ scale was used to define mass classes, to distribute species as equally as possible among classes.

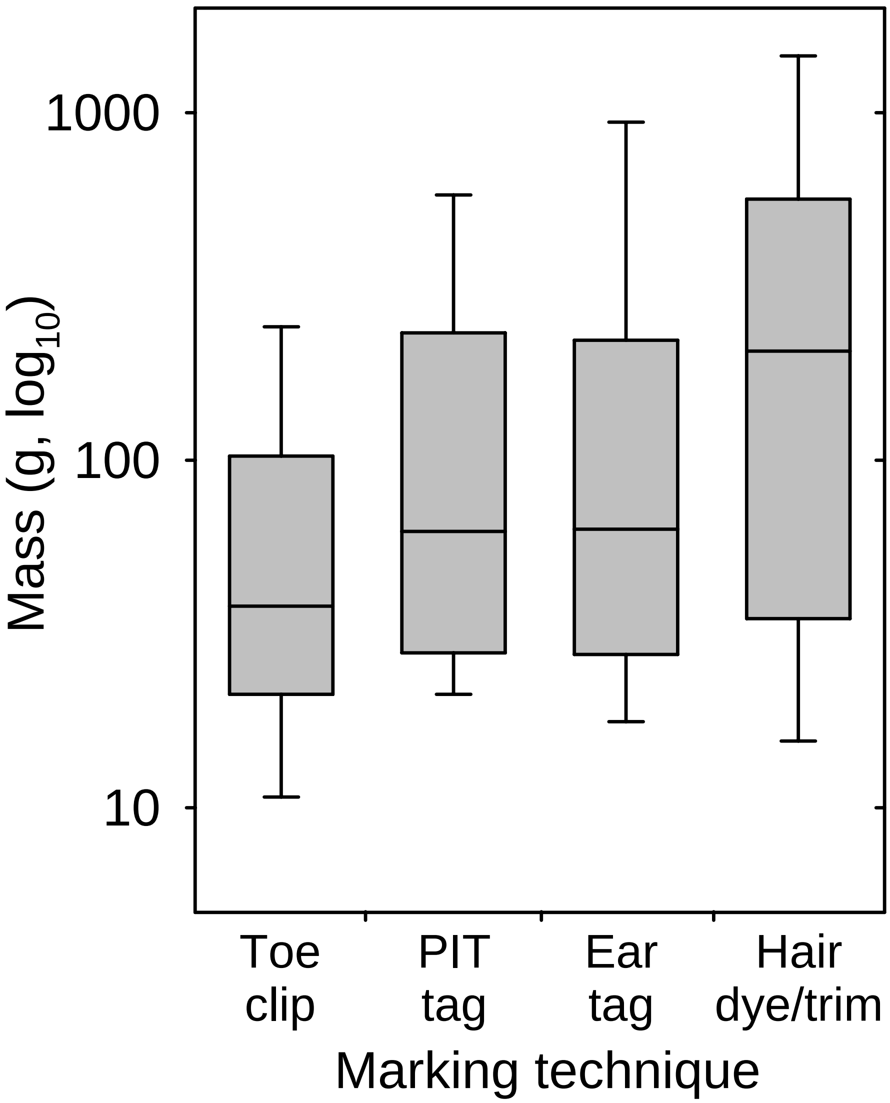

Figure 4. Mass of all small- or medium-sized mammal species marked using 4 general marking techniques, from a literature review of the Journal of Mammalogy from 1980-2004. Boxes define 25th and 75th percentiles, error bars designate the 10th and 90th percentiles, and the line within each box denotes the median. Number of species making up each group follow: $n_{\text{toe clip}}$ = 185 species, $n_{\text{PIT tag}}$ = 14, $n_{\text{ear tag}}$ = 148, $n_{\text{hair dye/trim}}$ = 57.

Field Study

The percent of human errors were relatively low; percentages ranged from 0 to 4.5% (Table 1). The highest percentages were found in misread/write errors for PIT tags in deer mice (4.5%) and for toe clips in white-footed mice (3.1%), both on the West site. The 5 errors for PIT tags in deer mice included 2 recording errors and 3 occasions where observers forgot to scan a mouse known to be carrying a PIT tag (i.e., same pit tag scanned in later trapping sessions). The misread/write errors were low (0.8%) for both ear tags and toe clips in deer mice for both sites. Duplication errors occurred on only 3 occasions (2 for white-footed mice and 1 for deer mice) and were relatively low (0.9-1.1%) given that > 300 individuals were marked with toe clips. Only one error occurred in application of the toe clip and this occurred in a deer mouse. The overall number of human errors made on the West site was higher for one observer (35 of 57 total errors; 61%) than the other observer during 24 months of the study.

Proportion of lost ear tags did not differ between study sites (West: 25 lost, 60 retained; East: 32 lost, 83 retained; $G = 0.06$, *d.f.* = 1, $P = 0.806$). Similarly, proportion of lost PIT tags did not differ between study sites (West: 2 lost, 40 retained; East: 3 lost, 111 retained; $G = 0.415$, *d.f.* = 1, $P = 0.519$). Therefore, I pooled data from both study sites for deer mice for within tag comparisons. A larger proportion of recaptured deer mice lost ear tags (28.5%) than lost PIT tags (3.2%; $G = 46.9$, *d.f.* = 1, $P < 0.001$). Only one of 309 toe clips (0.3%) was altered during the study period; 1 deer mouse had a toe amputated naturally, but its original toe-clip number still was discernable from that of other individuals, so no errors were made in determining its identity.

Table 1. Number of errors made during handling, marking, or recording data related to use of toe-clipping, ear tags, or PIT tags from deer mice (*Peromyscus maniculatus*, *Pm* in table) and white-footed mice (*P. leucopus*, *Pl*) on Konza Prairie in 1999-2001(West site) and 2003-2004 (East site). Parenthetical values are occurrence, calculated from the total number of times animals were handled. Only deer mice were captured on the East site.

	Study Site	
Error type	West	East
Misread/write:		
Ear tag	*Pm*: 3 (356 captures; 0.8%) *Pl*: 11 (922 captures: 1.2%)	*Pm*: 6 (716 captures; 0.8%)
PIT tag	*Pm*: 5 (111 captures: 4.5%)	
Toe-clip	*Pm*: 3 (374 captures: 0.8%) *Pl*: 31 (985 captures: 3.1%)	
Duplication	*Pm*: 1 (87 individuals: 1.1%) *Pl*: 2 (222 individuals: 0.9%)	
Application	*Pm*: 1 (87 individuals: 1.1 %) *Pl*: 0 (222 individuals: 0.0%)	

Pain response was more pronounced for ear tags than toe clips in deer mice ($SR_+ = 35$, $P_{1\text{-tailed}} = 0.048$; Table 2); in contrast, white-footed mice did not differ in their responses to these two marking methods ($SR_+ = 255$, $P_{1\text{-tailed}} = 0.206$). Deer mice also responded more strongly to injection of PIT tags than to application of ear tags ($SR_+ = 121$, $P_{1\text{-tailed}} = 0.041$; Table 2). Pain responses for the two species were not distributed in the same manner among the 3 response categories (deer mice with an ear tag and toe-clip: $J = 302.5$, $n = 43$, $P < 0.001$; white-footed mice with ear tag and toe-clip: $J = 1144$, $n = 80$, $P < 0.001$; deer mice with ear tag and PIT tag: $J = 1240$, $n = 91$, $P < 0.001$). More specifically, the response of individuals to each marking method was correlated when compared at the time of marking (deer mice with ear tag and toe-clip: $r_S = 0.61$, $d.f. = 41$, $P < 0.001$; white-footed mice with ear tag and toe-clip: $r_S = 0.37$, $d.f. = 78$, $P < 0.001$; deer mice with ear tag and PIT tag: $r_S = 0.44$, $d.f. = 89$, $P < 0.001$).

Number of infections associated with toe-clipping was low; only 2 joints exhibited swollen red tissue, out of 1121 digits clipped (0.2%). I observed only 1 deer mouse and 1 white-footed mouse with infections on their feet in the days following the clipping of a digit. The application of iodine did not affect the number of infections observed in deer mice ($G = 1.01$, $d.f. = 1$, $P = 0.315$). Twenty deer mice that received iodine treatment had 0 infections, whereas 31 deer mice that did not receive iodine on the wound had 1 infection. Likewise, the application of iodine did not affect the number of infections observed in white-footed mice ($G = 2.00$, $d.f. = 1$, $P = 0.158$). Thirty-nine white-footed mice treated with iodine had 1 infection, whereas 66 that received no iodine had 0 infections. Further, no association was found between application of iodine and number of the same individuals recaptured in the same trapping period (deer mice: $G = 0.47$, $d.f. = 1$, $P = 0.493$; white-footed mice: $G = 2.12$, $d.f. = 1$, $P = 0.146$) or

Table 2. Perceived pain response by deer mice and white-footed mice relative to marking by toe-clipping and ear tags on the West site and between ear tags and PIT tags on the East site (deer mice only) on Konza Prairie. Paired response categories index increasing reaction to application of each tag type by an individual mouse, because each animal received both marks.

		Toe-clipping								PIT tag			
		Deer mice				White-footed mice				Deer mice			
	Response	1	2	3	Total	1	2	3	Total	1	2	3	Total
Ear tag	1	29	1	0	30	35	12	1	48	54	7	6	67
	2	6	5	1	12	13	9	6	28	8	8	3	19
	3	0	1	0	1	0	2	2	4	0	3	2	5
	Total	35	7	1	43	48	23	9	80	62	18	11	91

recaptured in subsequent trapping periods (deer mice: $G = 0.04$, $d.f. = 1$, $P = 0.845$; white-footed mice: $G = 2.26$, $d.f. = 1$, $P = 0.133$).

Discussion

The relative proportion of published studies that used markings to ears, feet, and pelage remained similar across the six 5-year intervals between 1970 and 1999. Although new technologies, such as PIT tags became available as early as the late 1980s, these tags did not appear to affect the number of studies, which still used the lower-tech marking techniques for small mammals. Perhaps, this is because of the high cost inherent in marking all individuals with PIT tags in a field population detected by a large grid or other configurations used to sample small mammals. Also, it is highly likely that many studies initiated in the late 1990s are still ongoing or have not been published; I predict that the use of PIT tags will increase over the next 20 years as costs decrease and more methods for remote sensing of individuals are developed.

As expected, the prevalence of use for each marking technique differed across body masses. Toe-clipping was used more than expected by chance in the smaller mass classes (< 64 g), and was used less than expected on larger animals (≥ 256 g). This result likely was owing to the relatively large number of dark-colored, nocturnal species lacking external pinnae in the smaller mass classes, such as shrews. For small insectivores, ear tagging is not possible, and marking the pelage uniquely for a large number of individuals also is not possible. Ear tags were used at near expected frequency in small to medium-sized species (from ≥ 16 g to < 1024 g) and were over represented in species >1024 g. In small to medium-sized species, numbered monel fingerling tags typically were used, whereas in larger species, ear tags often were colored plastic or metal that allowed identification of marked individuals from a distance. Pelage marks were underrepresented in smaller body mass classes (from ≥ 8 g to < 64 g) and over-represented in species ≥ 128 g. Hair dyes were used in many studies of diurnal, ground-dwelling sciurids because it allowed identification from a distance, an especially important advantage in studies of behavior in this group.

Despite efforts to avoid marking or tag reading errors, it seems likely that errors will occur in any large field study, regardless of level of training and experience (Le Boulenge-Nguyen and Le Boulenge 1986; Morley 2002; Williams et al. 1997). So, researchers should design their studies to identify where errors might occur and then take steps to minimize their occurrence. The human errors committed in my study were low, most around 1%. Most errors were made in reading or recording a unique sequence of numbers from an ear tag or toe clip. In a previous study (Kaufman and Kaufman 1994), these types of errors did not occur because a master list was carried in the field that contained toe clip and ear tag numbers associated with each deer mouse on the study site. It would have been an interesting comparison, if I had quantified the number of times an error was avoided because of having the information for a double marking system in the field. I suspect that most of the errors in my current study occurred when a large numbers of individuals were processed in a short period of time. Because I wanted to quantify this type of human error, I did not take advantage of the double-marking approach that I had in place. That is, each worker could have carried a list of all individuals captured previously, with their corresponding sex, ear tag number, toe-clip number, and PIT tag number, so that the identity of an individual could have been confirmed before the individual was released. Other solutions to decrease reading errors on ear tags might be to use non-standard tags (i.e., laser-etched or paint-filled numbers), apply all tags so that they face forward, or mark the same ear for all individuals (I generally marked the right ear, but the left ear was used if a tag had ripped out of the right ear). For PIT tags, actual reading or transcription errors occurred only twice (1.8% of captures), and both occurred on the West site. Transcription errors were avoided on the East site by carrying a list of all previously injected PIT tags and ear tags that was consulted at the time of capture of individuals. Further, most PIT-tag readers can store read tag codes, which can be downloaded via a computer interface and checked against field notes later.

As expected, individuals lost a significantly larger percentage of ear tags than PIT tags. My percentage of ear-tag loss (28.5%) was higher than that reported from most other studies of rodents (2.2% and 5.1% for prairie voles, *Microtus ochrogaster*, and meadow voles, *M. pennsylvanicus*, Krebs et al. 1969; 9.5% for house mice, *Mus musculus*, Bias et al. 1992; 9.1% for giant kangaroo rats, *Dipodomys ingens*, 11.1% for Heermann's kangaroo rat, *D. heermanni*, and 15.0% for the Fresno kangaroo rat, *D. nitratoides*; Williams et al. 1997; and 16% for prairie voles, Wood and Slade 1990). However, the larger of these estimates come from studies that properly included only recaptured mice; some previous studies likely underestimated tag loss by not excluding single capture mice, some of which undoubtedly would have been observed to lose tags had they been recaptured. In my study, PIT tags were lost at 3.2%, which was similar to loss rates observed for giant and Heermann's kangaroo rats (2.9% and 2.6%, respectively, Williams et al. 1997), and Townsend's ground squirrel, *Spermophilus townsendii* (3.4%, Schooley et al. 1993), but lower than rates observed for Fresno kangaroo rats (8.7%, Williams et al. 1997).

Because I double marked mice, the occasional loss of a PIT tag did not impede my continued success of identifying individuals on my study sites. It appears that currently no mark other than toe clips have 100% retention through the lifetime of an individual. Retention success is high for PIT tags, but dependent on proper placement of the tag, which varies with species (Germano and Williams 1993; Jackson and Bünger 1993). Researchers should experiment to find the best injection location for their study animal (Gibbons and Andrews 2004). PIT tags that I lost tended to occur within 24 hours of the insertion of the tag. This suggests that the tag simply backed out of the opening in the skin left by the injecting needle, as others have observed (Freeland and Fry 1995). Loss of PIT tags may be reduced by physically moving the tag away from implantation site (Williams et al. 1997).

Although IACUCs often provide forms for scoring pain and suffering and for calculating overall ethical values of laboratory experiments (Porter 1992), rarely do researchers quantify the direct, physical response of individuals to marking. While it is assumed that some marking techniques cause greater discomfort than others, until now, pain-response scores have not been reported that would allow for comparison between techniques within or among individuals or species. In my study, the most common response to the 2 marking techniques each mouse received was a "1," or no response. Specifically, 67.4% of deer mice and 43.8% of white-footed mice showed no reaction to either ear tagging and toe-clipping and 59.3% of deer mice showed no reaction to both ear tagging and PIT tagging (Table 2). Overall, deer mice marked with both an ear tag and toe-clip showed greater physical reaction to the ear-tagging procedure when compared to toe-clipping in the same individual. Therefore, my data suggest that any objections to marking deer mice by toe-clipping should not be based on the argument that it is more painful than the ear-tagging procedure. Perhaps ear tagging enjoys favor by most IACUCs over toe-clipping, because applying an ear tag is perceived to be similar to ear piercing, an activity done without anesthesia in humans. Clearly, I do not suggest that use of ear tags should be abandoned, but rather I urge caution against using anthropomorphic biases in determining policy for use of marking techniques.

I found that deer mice responded more strongly to injection of PIT tags than ear tags. The use of PIT tags might be viewed favorably by IACUCs because this technique is mechanically similar to a human receiving an injection relative to medicinal needs. From my literature survey, PIT tags had been not used on species with masses < 16 g (Fig. 3). However, adult deer mice on my study sites averaged 17.3 ± 0.2 g, and most of these mice weighed <16 g when PIT-tagged. Further, I have successfully marked nestling deer mice with PIT tags (Chapter 3 and 4). However, I still suggest that researchers consider body size of the small mammal when deciding whether PIT tags are a viable option.

A caveat to my analysis of pain response is that it is possible that the response I recorded for deer mice and white-footed mice to marking had little to do with actual levels of pain or discomfort. For example, individual responses of humans to pain vary considerably and might be different when different levels of pain occur under the same experimental conditions (Bateson 1991). Nevertheless, wise use of animals in research requires use of a marking technique that minimizes the magnitude and duration of pain, while providing the most information possible (Animal Care and Use Committee of the American Society of Mammalogists 1998; Association for the Study of Animal Behavior 2002). If the pain associated with PIT-tagging is momentary and minimal, its use may be warranted, especially given the potential unique behavioral insights possible with the use of these tags, compared to toe-clipping and ear tags. Specifically, PIT tags allow for remote monitoring of presence by individual small mammals at fixed locations associated with movement (Harper and Batzli 1996), foraging (Burns 2005), or activity at artificial burrows (Chapters 2, 3, and 4).

The development of infections related to toe-clipping was very low in my study. Only 2 mice out of 156 marked (1.3%) and recaptured developed minor infections. Further, only one mouse was in the control group (no iodine), whereas the other mouse that developed an infection was in the experimental group and received iodine on the affected area. Further, application of iodine did not influence whether mice were recaptured in the same or subsequent trapping sessions and thus likely did not influence survival rate above that experienced when no iodine was applied. I suggest that the application of iodine is not needed and introduces a foreign odor on individuals that are treated with it that might influence their behavioral interactions with their conspecifics in this extremely olfactory species (Vander Wall et al. 2003). Further, previous observations from other field studies (G. A. Kaufman pers. comm.) indicated that application of topical antiseptic (iodine) appeared to increase loss of blood from the wound following toe-clipping. However, the 2 field workers (RLR and A. W. Reed) in this study did not observe a difference in blood loss of individuals relative to iodine treatment.

The selection of a proper marking technique requires that the researcher, IACUC, and permit-issuing agencies involved consider the objectives of the study and life-history characteristics of the study animal (Animal Care and Use Committee of the American Society of Mammalogists 1998). Occasional tag loss might not affect the results greatly if the goal of the study is simple enumeration (Arnason and Mills 1981). However, if the goal is to study behavior of individuals or ecology of populations of a species, I advocate the use of double-marking procedures for these and longer-term studies (Kaufman and Kaufman 1994). Evidence from this study and others (Morley 2002; Williams et al. 1997) indicates that tags regularly are lost or become inoperative, and double marking can save a study from loss of identities and the loss of history related to individuals. In addition, these multiple markings provide another method to quantify errors in the data and allow corrections to be made more easily.

Literature Cited

Animal Care and Use Committee of the American Society of Mammalogists. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416-1431.

Arnason, A. N., and K. H. Mills 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences 38:1077-1095.

Association for the Study of Animal Behavior. 2002. Guidelines for the treatment of animals in behavioral research and teaching. Animal Behavior 63:195-199.

Bateson, P. 1991. Assessment of pain in animals. Animal Behavior 42:827-839.

Bias, M. A., N. L. Breuner, and M. L. Morrison. 1992. House mice as indicators of potential marking effects on salt marsh harvest mice. Transactions of the Western Section of the Wildlife Society 28:34-37.

Blackmer, A. L., S. K. Anderson, and M. T. Weinrich. 2000. Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). Marine Mammal Science 16:338-354.

Burns, C. E. 2005. Behavioral ecology of disturbed landscapes: the response of territorial animals to relocation. Behavioral Ecology 16:898-905.

Freeland, W. J., and K. Fry. 1995. Suitability of passive integrated transponder tags for marking live animals for trade. Wildlife Research 22:767-773.

Germano, D. J., and D. F. Williams. 1993. Field evaluation of using passive integrated transponder (PIT) tags to permanently mark lizards. Herpetological Review 24:54-56.

Gibbons, J. W., and K. M. Andrews. 2004. PIT tagging: simple technology at its best. BioScience 54:447-454.

Harper, S. J., and G. O. Batzli. 1996. Monitoring use of runways by voles with passive integrated transponders. Journal of Mammalogy 77:364-369.

Jackson, D. N., and W. H. Bünger. 1993. Evaluation of passive integrated transponders as a marking technique for turkey poults. Journal of the Iowa Academy of Science 100:60-61.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

Kaufman, G. A., and D. W. Kaufman. 1994. Changes in body mass related to capture in the prairie deer mouse (*Peromyscus maniculatus*). Journal of Mammalogy 75:681-691.

Krebs, C.J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50:587-607.

Kumar, R. K. 1979. Toe-clipping procedure for individual identification of rodents. Lab Animal Science 29:679-680.

Lacey, E. A., S. H. Braude, and J. R. Wieczorek. 1997. Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). Journal of Mammalogy 78:556-562.

Lacey, E. A., S. H. Braude, and J. R. Wieczorek. 1998. Solitary burrow use by adult Patagonian tuco-tucos (*Ctenomys haigi*). Journal of Mammalogy 79:986-991.

Le Boulenge-Nguyen, P. Y., and E. Le Boulenge. 1986. A new ear-tag for small mammals. Journal of Zoology 209:302-304.

Lindner, E., and O. Fuelling. 2002. Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. Journal of Zoology 256:159-164.

Morley, C. G. 2002. Evaluating the performance of PIT tags and ear tags in a capture-recapture experiment. New Zealand Journal of Zoology 29:143-148.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1-135.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1-97.

Porter, D. G. 1992. Ethical scales for animal experiments. Nature 356:101-102.

Schooley, R. L., B. Van Horne, and K. P. Burnham. 1993. Passive integrated transponders for marking free-ranging Townsend's ground squirrels. Journal of Mammalogy 74:480-484.

Smith, F. A., et al. 2003. Body mass of Late Quaternary mammals. Ecological Archives E084-094; Ecology 84:3403.

Vander Wall, S. B., et al. 2003. Interspecific variation in the olfactory abilities of granivorous rodents. Journal of Mammalogy 84:487-496.

Whitehead, H. 2001. Direct estimation of within-group heterogeneity in photo-identification of sperm whales. Marine Mammal Science 17:718-728.

Williams, D. F., W. Tordoff, III, and D. J. Germano. 1997. Evaluation of methods for permanently marking kangaroo rats (*Dipodomys*: Heteromyidae). Pp. 259-271 in Life Among the Muses: Papers in Honor of James S. Findley (T. L. Yates, W. L. Gannon, and D. E. Wilson, editors). Museum of Southwestern Biology, University of New Mexico, Albuquerque.

Wood, M. D., and N. A. Slade. 1990. Comparison of ear-tagging and toe-clipping in prairie voles, *Microtus ochrogaster*. Journal of Mammalogy 71:252-255.

Appendix 1. Marking techniques from all field studies of small- or medium-sized mammals (rodents, lagomorphs, and insectivores) published in the Journal of Mammalogy from 1980 through 2004. Average mass values came from the published database of Smith et al. (2003); an asterisk (*) in the "Mass" column indicates that average mass could not be found in the literature. An asterisk in the "Years of study" column indicates that time period over which the study was conducted was not indicated in the manuscript; the year given is the year of manuscript submission. Marking techniques that include the word "plus" indicate that, in addition to the primary marking technique, some portion of the study population was given radiotelemetry transmitters.

Scientific name	Common name	Mass (g)	Marking technique	Years of study	Citation
Abrocoma bennetti	Bennett's chinchilla rat	250.5	ear tag(s) only	1983-1984	Iriarte et al. 1989
			ear tag(s) only	1987-1989	Jimenez et al. 1992
			not indicated	1976	Jaksić et al. 1981
Acomys cahirinus	common spiny mouse	38.7	toe-clip only	1993-1995	Shargal et al. 2000
Acomys russatus	golden spiny mouse	49.7	toe-clip only	1993-1995	Shargal et al. 2000
Acomys subspinosus	Cape spiny mouse	21.0	either:ear/toe-clip	1978-1979	Rickart 1981
Aethomys chrysophilus	red rock rat	72.4	toe-clip only	1994-1995, 1998	Johnson et al. 2002
Aethomys namaquensis	Namaqua rock rat	48.8	either:ear/toe-clip	1978-1979	Rickart 1981
			toe-clip only	1994-1995, 1998	Johnson et al. 2002
Akodon azarae	Pampean grassland mouse	25.0	toe-clip only	1989	Cittadino et al. 1994
Akodon cursor	South American field mouse	39.9	ear notch/punch	1993-1995	Bergallo and Magnusson 1999
			ear notch/punch	1983-1984	Mares and Ernest 1995

Akodon longipilis	long-haired grass mouse	37.6	ear tag(s) only	1983-1984	Iriarte et al. 1989
			ear tag(s) only	1987-1989	Jimenez et al. 1992
			either:ear/toe-clip	1980-1985	Kelt et al. 1994
			either:ear/toe-clip	1982-1985	Meserve et al. 1999
			other	1981-1982	Murúa et al. 1987
			toe-clip only	1979-1981	Meserve et al. 1982
Akodon molinae	Molina's grass mouse	33.0	not indicated	1986-1987	Ojeda 1989
Akodon olivaceus	olive-backed field mouse	27.0	ear tag(s) only	1983-1984	Iriarte et al. 1989
			ear tag(s) only	1987-1989	Jimenez et al. 1992
			either:ear/toe-clip	1980-1985	Kelt et al. 1994
			either:ear/toe-clip	1982-1985	Meserve et al. 1999
			not indicated	1976	Jaksić et al. 1981
			other	1981-1982	Murúa et al. 1987
Akodon sanborni	Sanborn's grass mouse	24.7	either:ear/toe-clip	1980-1985	Kelt et al. 1994
			either:ear/toe-clip	1982-1985	Meserve et al. 1999
			toe-clip only	1979-1981	Meserve et al. 1982
Akodon urichi	northern grass mouse	34.0	toe-clip only	1976-1977	O'Connell 1989
Ammospermophilus harrisi	Harris's antelope squirrel	122.0	combo:ear/toe-clip	1984-1986	Simons 1991
Ammospermophilus leucurus	white-tailed antelope squirrel	103.7	either:hair/toe-clip	1991	O'Farrell et al. 1994
Apodemus flavicollis	yellow-necked mouse	26.7	PIT only	1994-1996	Gockel and Ruf 2001
			toe-clip only	1995-1997	Torre et al. 2004
Apodemus sylvaticus	wood mouse	30.5	ear tag(s) only	1990	Tew et al. 1994
			toe-clip only	1995-1997	Torre et al. 2004

Apomys littoralis	Mindanao lowland forest mouse	31.0	not indicated	1982-1984	Heideman et al. 1987
Arvicanthis niloticus	African grass rat	138.8	ear notch/punch	1978-1981	Packer 1983
			ear notch/punch	1998	Blanchong and Smale 2000
Baiomys taylori	northern pygmy mouse	8.0	not indicated	1977-1983	Grant et al. 1985
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1982-1983	Gust and Schmidly 1986
Berylmys bowersi	Bower's white-toothed rat	300.0	toe-clip only	1997-1998	Adler et al. 1999
Blarina brevicauda	northern short-tailed shrew	28.0	combo:ear/toe-clip	1978-1980	Yahner 1982
			ear tag(s) only	1993-1994	Yunger and Randa 1999
			ear tag(s) only	1996-1997	McShea et al. 2003
			either:ear/toe-clip	1978-1980	Yahner 1983
			hair dye/bleach/clip only	1999-2000	Glennon et al. 2002
			not indicated	1978	Zegers and Ha 1981
			toe-clip only	1972-1985	Getz 1989
			toe-clip only	1978	Kitchings and Levy 1981
			toe-clip only	1979	Seagle 1985
			toe-clip only	1982	Buckner and Shure 1985
			toe-clip only	1983-1984	Merritt 1986
			toe-clip only	1985-1989	Andersen and Folk 1993
Blarina carolinensis	southern short-tailed shrew	13.5	ear tag(s) only	1996-1997	McCay 2000
			not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1990-1994	Loeb 1999
Blarina hylophaga	Elliot's short-tailed shrew	14.5	other	1981-1999	Matlack et al. 2002
			toe-clip only	1981-1984	Clark et al. 1987

Bolomys lasiurus	South American grass mouse	39.9	toe-clip only	1983-1984	Mares and Ernest 1995
Callosciurus caniceps	Malaysian tree squirrel	257.0	other	1990-1991	Tamura 1993
Callosciurus erythaeus	red-bellied tree squirrel	280.0	combo:ear/hair	1976-1982	Setoguchi 1990
			combo:ear/hair	1976-1982	Setoguchi 1991
			other	1982-1985	Tamura et al. 1988
Callosciurus finlaysonii	Finlayson's squirrel	*	not indicated	1998-1999	Bertolino et al. 2004
Callosciurus notatus	Malaysian tree squirrel	190.0	other	1990-1991	Tamura 1993
Calomys callosus	large vesper mouse	45.0	not indicated	1985	Lacher and Alho 1989
Calomys laucha	small vesper mouse	14.0	toe-clip only	1989	Cittadino et al. 1994
Calomys musculinus	drylands vesper mouse	20.1	not indicated	1986-1987	Ojeda 1989
			toe-clip only	1989	Cittadino et al. 1994
Castor canadensis	American beaver	21820.0	combo:ear/hair	1974-1975, 1977-1978	Busher et al. 1983
			ear tag(s) only	1977-1979	Busher 1987
			ear tag(s) only	1985-1994	Smith and Jenkins 1997
			not marked	2003*	Williams et al. 2004
			radio only	1976-1978	Lancia et al. 1982
Cavia aperea	Brazilian guinea pig	549.0	combo:ear/hair	1998-1999	Asher et al. 2004
Chaetodipus baileyi	Bailey's pocket mouse	26.3	combo:ear/toe-clip	1984-1986	Simons 1991
			not indicated	1975	M'Closkey 1983
			toe-clip only	1995-1996	Swann et al. 1997
Chaetodipus fallax	San Diego pocket mouse	18.7	ear tag(s) only	1989-1991	McClenaghan and Taylor 1993
		18.7	either:hair/toe-clip	1991	O'Farrell et al. 1994
Chaetodipus formosus	long-tailed pocket mouse	19.5	not indicated	1970	Smith et al. 1980

Chaetodipus formosus	long-tailed pocket mouse	19.5	other	1978	Bowers 1982
			toe-clip only	1972-1973	O'Farrell 1980
Chaetodipus hispidus	hispid pocket mouse	32.0	not indicated	1970-1973	Grant et al. 1982
			powder only	1984*	Lemen and Freeman 1985
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1996-1997	Cramer and Willig 2002
Chaetodipus intermedius	rock pocket mouse	16.5	not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1993-1994	Ellison and Van Riper 1998
Chaetodipus nelsoni	Nelson's pocket mouse	15.7	combo:hair/toe-clip	1987	Rogovin et al. 1991
Chaetodipus penicillatus	desert pocket mouse	15.0	combo:hair/toe-clip	1987	Rogovin et al. 1991
			not indicated	1975	M'Closkey 1983
Chaetodipus penicillatus	desert pocket mouse	15.0	not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1983	Price et al. 1984
			toe-clip only	1995-1996	Swann et al. 1997
Chinchilla lanigera	chinchilla	485.0	ear tag(s) only	1987-1989	Jimenez et al. 1992
			ear tag(s) only	1988-1991	Torres-Contreras et al. 1997
Chiropodomys gliroides	pencil-tailed tree mouse	21.5	toe-clip only	1997-1998	Adler et al. 1999
Clethrionomys californicus	western red-backed vole	18.3	ear tag(s) only	1998	Manning and Edge 2004
			radio only	1991	Tallmon and Mills 1994
			toe-clip only	1981-1983	Doyle 1990
Clethrionomys gapperi	southern red-backed vole	19.0	combo:ear/toe-clip	1978-1980	Yahner 1982
			ear tag(s) only	1983-1992	McCracken et al. 1999

Clethrionomys gapperi	southern red-backed vole	19.0	ear tag(s) only	1991	Ostfeld et al. 1993
			ear tag(s) only	1996-1997	McShea et al. 2003
			ear tag(s) only	1997-1998	Keinath and Hayward 2003
			ear tag(s) only	1998-2001	Hadley and Wilson 2004
			ear tag(s) only	1999-2000	Glennon et al. 2002
			either:ear/toe-clip	1978-1980	Yahner 1983
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1981-1983	Andersen and MacMahon 1985
			not marked	1964-1971	Vickery and Bider 1981
			toe-clip only	1975-1978	Andersen et al. 1980
			toe-clip only	1986	Belk et al. 1988
			toe-clip only	1998-2000	Smith and Nichols 2004
Clethrionomys glareolus	bank vole	21.2	ear tag(s) only	1990	Tew et al. 1994
			hair dye/bleach/clip only	1976	Gipps 1981
			PIT only	1994-1996	Gockel and Ruf 2001
			toe-clip only	1980-1984	Löfgren 1995
			toe-clip only	1995-1997	Torre et al. 2004
Clethrionomys rufocanus	gray red-backed vole	37.0	toe-clip only	1980-1984	Löfgren 1995
			toe-clip only	1984-1986	Saitoh 1989
Clethrionomys rutilus	northern red-backed vole	27.5	toe-clip only	1972-1973	West 1982
Clyomys laticeps	broad-headed spiny rat	201.0	not indicated	1985	Lacher and Alho 1989
Crocidura flavescens	greater red musk shrew	28.5	toe-clip only	1994-1995, 98	Johnson et al. 2002
Crocidura hirta	lesser red musk shrew	15.8	toe-clip only	1994-1995, 1998	Johnson et al. 2002

Crocidura negrina	Negros shrew	*	not indicated	1982-1984	Heideman et al. 1987
Crocidura russula	white-toothed shrew	8.2	toe-clip only	1995-1997	Torre et al. 2004
Cryptomys mechowi	giant mole-rat	272.0	not indicated	1996	Scharff et al. 2001
Cryptotis parva	least shrew	5.0	not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1990-1994	Loeb 1999
Ctenomys haigi	Patagonian tuco-tuco	164.0	PIT only	1994-1996	Lacey et al. 1998
Ctenomys sociabilis	social tuco-tuco	400.0	PIT only	1993-1995	Lacey et al. 1997
Ctenomys talarum	Talas tuco-tuco	132.3	other	1985-1986	Busch et al. 1989
Cynomys gunnisoni	Gunnison's prairie dog	925.0	combo:ear/hair	1989-1995	Hoogland 1997
			combo:ear/hair	1989-1995	Hoogland 1998
			combo:ear/hair	1989-1995	Hoogland 1999
			combo:ear/hair	1989-1995	Hoogland 2001
			combo:ear/hair	1989-1995	Hoogland 2003
			either:ear/toe-clip	1984-1987	Cully 1997
			not indicated	1979-1981	Rayor 1985
Cynomys leucurus	white-tailed prairie dog	908.5	combo:ear/hair	1974-1976	Hoogland 2003
			ear tag(s) only	1984-1988	Menkens and Anderson 1991
Cynomys ludovicianus	black-tailed prairie dog	1364.0	combo:ear/hair	1975-1980	Foltz and Hoogland 1981
			combo:ear/hair	1975-1988	Hoogland 2001
			combo:ear/hair	1975-1989	Dobson et al. 2004
			combo:ear/hair	1975-1989	Hoogland 2003
			combo:ear/hair	1979-1982	Garrett and Franklin 1988
			combo:ear/hair	1988*	Loughry 1989

Cynomys ludovicianus	black-tailed prairie dog	1364.0	ear tag(s) only	1980-1986	Foltz et al. 1988
			ear tag(s) only	1997-1998	Roach et al. 2001
			ear tag(s) only	1998-1999	Lehmer et al. 2001
			not marked	1982-1984	Adams et al. 1987
			not marked	1983-1984	Devenport 1989
Cynomys mexicanus	Mexican prairie dog	900.0	not marked	1999	Scott-Morales et al. 2004
			toe-clip only	1988	Mellink and Madrigal 1993
Cynomys parvidens	Utah prairie dog	900.0	combo:ear/hair	1991-2001	Hoogland 2003
			combo:ear/hair	1996-2001	Hoogland 2001
Dactylomys dactylinus	Amazon bamboo rat	650.0	hair dye/bleach/clip only	1977-1979	Emmons 1981
Dasyprocta punctata	Central american agouti	2675.0	not marked	1985	Larson and Howe 1987
			toe-clip only	1983-1984	Mares and Ernest 1995
Dendromus mysticalis	chestnut climbing mouse	7.6	toe-clip only	1994-1995, 1998	Johnson et al. 2002
Dipodomys agilis	Pacific kangaroo rat	57.8	ear tag(s) only	1989-1991	McClenaghan and Taylor 1993
Dipodomys deserti	desert kangaroo rat	104.5	combo:ear/toe-clip	1979-1981	Kotler 1985b
			not marked	1980-1982	Kotler 1984
			not marked	1983	Kotler 1985a
Dipodomys heermanni	Heermann's kangaroo rat	72.0	ear tag(s) plus	1996	Shier and Randall 2004
Dipodomys ingens	giant kangaroo rat	133.9	toe-clip only	1981-1982	Braun 1985
Dipodomys merriami	Merriam's kangaroo rat	42.0	combo:ear/toe-clip	1979-1981	Kotler 1985b
			combo:ear/toe-clip	1984-1986	Simons 1991
			combo:hair/toe-clip	1987	Rogovin et al. 1991
			ear tag(s) plus	1979-1982	Jones 1989

Dipodomys merriami	Merriam's kangaroo rat	42.0	ear tag(s) plus	1988-1989	Perri and Randall 1999
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			not indicated	1975	M'Closkey 1983
			not indicated	1981-1982	Thompson 1987
			not indicated	1993-1994	Jorgensen and Demarais 1999
			not marked	1980-1982	Kotler 1984
			not marked	1983	Kotler 1985a
			other	1978	Bowers 1982
			toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1983	Price et al. 1984
			toe-clip only	1986*	Bowers 1988
Dipodomys microps	chisel-toothed kangaroo rat	54.6	combo:ear/toe-clip	1979-1981	Kotler 1985b
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			not marked	1980-1982	Kotler 1984
			toe-clip only	1972-1973	O'Farrell 1980
Dipodomys nelsoni	Nelson's kangaroo rat	88.6	combo:hair/toe-clip	1987	Rogovin et al. 1991
Dipodomys ordii	Ord's kangaroo rat	60.4	combo:ear/toe-clip	1979-1981	Kotler 1985b
			combo:hair/toe-clip	1987	Rogovin et al. 1991
			ear tag(s) only	1981-1982	Longland and Jenkins 1987
			ear tag(s) only	1993-1994	Ellison and Van Riper 1998
			ear tag(s) only	1997	Davidson et al. 1999
			ear tag(s) plus	1988-1989	Perri and Randall 1999
			ear tag(s) plus	1994-1997	Andersen et al. 2000
			not indicated	1970-1973	Grant et al. 1982

Dipodomys ordii	Ord's kangaroo rat	60.4	not indicated	1993-1994	Jorgensen and Demarais 1999
			not marked	1977	Kaufman and Kaufman 1982
			powder only	1984*	Lemen and Freeman 1985
			toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1988	Mellink and Madrigal 1993
			toe-clip only	1996-1997	Cramer and Willig 2002
Dipodomys panamintinus	Panamint kangaroo rat	74.7	toe-clip only	1972-1973	O'Farrell 1980
Dipodomys spectabilis	banner-tailed kangaroo rat	135.9	ear tag(s) only	1979-2001	Waser and Ayers 2003
			ear tag(s) only	1985-1987	Randall 1989
			ear tag(s) only	1997	Davidson et al. 1999
			not indicated	1980-1984	Jones 1988
Dipodomys stephensi	Stephens' kangaroo rat	69.8	combo:ear/PIT	1991	O'Farrell et al. 1994
			ear tag(s) only	1989-1991	McClenaghan and Taylor 1993
			ear tag(s) plus	1990-1991	Price et al. 1994
			PIT only	1997-1999	Brock and Kelt 2004
Eligmodontia typus	highland gerbil mouse	17.3	not indicated	1986-1987	Ojeda 1989
Eliomys quercinus	garden dormouse	115.0	toe-clip only	1995-1997	Torre et al. 2004
Erethizon dorsatum	North American porcupine	7085.3	ear tag(s) only	1988-1990	Sweitzer and Berger 1993
			ear tag(s) plus	1988-1993	Sweitzer 1996
			not indicated	1965-1975	Keith and Cary 1991
			tattoo	2000*	Roze 2002
Geomys attwateri	Attwater's pocket gopher	165.0	not indicated	1978-1980	Williams and Cameron 1984
			radio only	1984	Cameron 1988

Geomys attwateri	Attwater's pocket gopher	165.0	toe-clip only	1992-1994	Rezsutek and Cameron 1998
Geomys bursarius	plains pocket gopher	203.8	other	1984-1985	Sparks and Andersen 1988
Gerbillus allenbyi	Allenby's gerbil	35.3	not marked	1980-1982	Kotler 1984
			other	1987	Brown et al. 1992
			toe-clip only	1986-1988	Kotler et al. 1993
Gerbillus henleyi	pigmy gerbil	8.0	not marked	1980-1982	Kotler 1984
Gerbillus pyramidum	greater Egyptian gerbil	49.4	not marked	1980-1982	Kotler 1984
			toe-clip only	1986-1988	Kotler et al. 1993
Glaucomys sabrinus	northern flying squirrel	166.0	ear tag(s) only	1981-1983	Witt 1992
			ear tag(s) only	1983-1986	Witt 1991
			ear tag(s) only	1992-1993	Ransome and Sullivan 1997
			ear tag(s) only	1996-1998	Pyare and Longland 2001
			ear tag(s) only	1996-1999	Ransome and Sullivan 2004
			ear tag(s) only	1998-2000	Smith and Nichols 2003
			ear tag(s) only	1999-2000	Glennon et al. 2002
			ear tag(s) plus	1996-1997	Cotton and Parker 2000
			not indicated	1965-1975	Keith and Cary 1991
			not indicated	1985	Carey and Witt 1991
			not indicated	1998-2000	Smith et al. 2004
			not indicated	1999-2000	Vernes 2001
			toe-clip only	1981-1983	Doyle 1990
			toe-clip only	1986	Belk et al. 1988
Glaucomys volans	Southern flying squirrel	63.9	ear tag(s) only	1979-1984	Layne and Raymond 1994
			ear tag(s) only	1991	Ostfeld et al. 1993

Glaucomys volans	Southern flying squirrel	63.9	ear tag(s) only	1997-1998	Merritt et al. 2001
			ear tag(s) plus	1984	Bendel and Gates 1987
			not indicated	1992-1996	Nupp and Swihart 2000
			toe-clip only	1990-1994	Loeb 1999
Glirulus japonicus	Japanese dormouse	*	PIT plus	1997-1998	Shibata et al. 2004
Graomys griseoflavus	gray leaf-eared mouse	67.5	not indicated	1986-1987	Ojeda 1989
Heterocephalus glaber	naked mole-rat	55.0	either:toe-clip/PIT	1977-1984, 1987-1995	Sherman et al. 1999
			either:toe-clip/PIT	1994-1995	Braude and Ciszek 1998
Heteromys anomalus	Trinidad spiny pocket mouse	70.0	toe-clip only	1976-1977	O'Connell 1989
Heteromys desmarestianus	Desmarest's spiny pocket mouse	72.5	ear tag(s) only	1999	Caro et al. 2001
			toe-clip only	1998	Mangan and Adler 2000
Heteromys gaumeri	Gaumer's spiny pocket mouse	63.6	ear tag(s) only	1999	Caro et al. 2001
Hodomys alleni	Allen's woodrat	367.6	toe-clip only	1997-1998	Vázquez et al. 2000
Hoplomys gymnurus	armored rat	240.0	toe-clip only	1994-1996	Tomblin and Adler 1998
Hystrix indica	Indian crested porcupine	12435.9	ear tag(s) plus	1982-1983	Alkon and Saltz 1988
Isothrix pagurus	plain brush-tailed mouse	210.0	not indicated	1983-1985	Malcolm 1991
Lagostomus maximus	plains vizcacha	4647.5	ear tag(s) plus	1985-1987	Branch 1993
			ear tag(s) plus	1985-1987	Branch et al. 1993
Lemmiscus curtatus	sagebrush vole	28.3	not indicated	1970-1973	Grant et al. 1982
Lepus americanus	snowshoe hare	1710.0	ear tag(s) only	1981-1983	Litvaitis 1990
			ear tag(s) plus	1995-1996	Gillis and Krebs 1999
			ear tag(s) plus	1999	Burton and Krebs 2003
			radio only	1998-2000	Wirsing et al. 2002

Lepus americanus	snowshoe hare	1710.0	tattoo	1980-1981	Kuvlesky and Keith 1983
Lepus townsendii	white-tailed jackrabbit	1555.0	not indicated	1985-1987	Rogowitz and Wolfe 1991
Liomys pictus	painted spiny pocket mouse	40.0	toe-clip only	1997-1998	Vázquez et al. 2000
Marmota caudata	golden marmot	4350.0	ear tag(s) plus	1988-1993	Blumstein and Arnold 1998
Marmota flaviventris	yellow-bellied marmot	3350.0	combo:ear/hair	1989-1991	Salsbury and Armitage 1994
			combo:ear/hair	1996-2000	Woods and Armitage 2003
			combo:ear/hair	1998-1999	Stallman and Holmes 2002
			combo:ear/hair	2003	Blumstein et al. 2004
Marmota monax	woodchuck	3801.7	combo:ear/hair	1998-2001	Maher 2004
			ear tag(s) plus	1987-1989	Swihart 1992
			radio only	1989	Meier 1991
			radio only	1998-2000	Zervanos and Salsbury 2003
			tattoo	1991-1992	Ferron 1996
Mastomys natalensis	Natal multimammate mouse	60.3	toe-clip only	1994-1995, 1998	Johnson et al. 2002
Maxomys moi	Mo's spiny rat	*	toe-clip only	1997-1998	Adler et al. 1999
Meriones crassus	gentle jird	69.9	not marked	1980-1982	Kotler 1984
Meriones tamariscinus	tamarisk gerbil	120.0	toe-clip only	1995-1999	Tchabovsky and Bazykin 2004
Mesomys hispidus	spiny tree rat	175.0	not indicated	1983-1985	Malcolm 1991
Microdipodops megacephalus	dark kangaroo mouse	10.5	toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1979-1981	Harris 1987
Microdipodops pallidus	pale kangaroo mouse	12.5	combo:ear/toe-clip	1979-1981	Kotler 1985b
			not marked	1983	Kotler 1985a

Microsciurus alfari	Central American dwarf squirrel	87.5	not marked	1984	Giacalone et al. 1987
Microtus agrestis	field vole	42.5	toe-clip only	1980-1984	Löfgren 1995
			toe-clip only	1983-1985	Erlinge et al. 1990
			toe-clip only	1995-1997	Torre et al. 2004
Microtus arvalis	common vole	28.0	radio only	2002*	Briner et al. 2003
Microtus breweri	beach vole	*	not indicated	1976-1977	Keith and Tamarin 1981
Microtus californicus	California vole	57.4	either:hair/toe-clip	1991	O'Farrell et al. 1994
			toe-clip only	1974-1977	Bowen 1982
			toe-clip only	1975-1981	Heske et al. 1984
			toe-clip only	1981-1985	Ostfeld and Klosterman 1986
Microtus californicus	California vole	57.4	toe-clip only	1983	Heske 1987
			toe-clip only	1986	Geissel et al. 1988
Microtus canicaudus	gray-tailed vole	28.4	ear tag(s) only	1992	Manning et al. 1995
			ear tag(s) only	1992-1993	Wolff et al. 1994
			ear tag(s) only	1997	Bond and Wolff 1999
			ear tag(s) only	2000	Wolff et al. 2002
Microtus longicaudus	long-tailed vole	46.7	ear tag(s) only	1986	Douglass 1989
			ear tag(s) only	1997-1998	Keinath and Hayward 2003
			ear tag(s) only	1998	Manning and Edge 2004
			not indicated	1977-1979	Van Horne 1982
Microtus miurus	singing vole	41.0	either:ear/toe-clip	1984-1987	Batzli and Henttonen 1993
Microtus montanus	montane vole	36.3	ear tag(s) only	1981-1982	Longland and Jenkins 1987
			ear tag(s) only	1994-1997	Andersen et al. 2000
			ear tag(s) only	1997-1998	Keinath and Hayward 2003

Microtus montanus	montane vole	36.3	ear tag(s) only	1998-2001	Hadley and Wilson 2004
			not indicated	1970-1973	Grant et al. 1982
			other	1971-1975	Jannett 1982
			toe-clip only	1986	Belk et al. 1988
Microtus ochrogaster	prairie vole	38.0	combo:ear/PIT	1993	Harper and Batzli 1996
			ear tag(s) only	1971-1973	Danielson and Gaines 1987
			ear tag(s) only	1992	Haken and Batzli 1996
			ear tag(s) only	1992-1993	Lin and Batzli 1995
			ear tag(s) only	1995-1996	Lin and Batzli 2004
			ear tag(s) plus	1983-1984	Danielson and Swihart 1987
			ear tag(s) plus	1985	Desy et al. 1989
			ear tag(s) plus	1985-1986	Jike et al. 1988
			either:ear/toe-clip	1973-1983	Sauer and Slade 1986
			either:ear/toe-clip	1976-1995	Slade and Russell 1998
			either:ear/toe-clip	1985-1987	Wood and Slade 1990
			either:ear/toe-clip	1990-1992	Slade et al. 1997
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1973-1988	Slade 1991
			not indicated	1973-1988	Slade and Iskjaer 1990
			not indicated	1979-1981	Danielson et al. 1986
			not indicated	1983-1986	Frase et al. 1990
			not marked	1973-1975	Glass and Slade 1980
			powder only	1995	Jacquot and Solomon 2004
			toe-clip only	1972-1976	Verner and Getz 1985

Microtus ochrogaster	prairie vole	38.0	toe-clip only	1972-1997	Getz et al. 2001
			toe-clip only	1973-1981	Swihart and Slade 1984
			toe-clip only	1973-1984	Swihart and Slade 1989
			toe-clip only	1975-1993	Slade and Blair 2000
			toe-clip only	1978-1999	Brady and Slade 2004
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1981-1987	Getz et al. 1993
			toe-clip only	1984-1988	Mankin and Getz 1994
			toe-clip only	1985-1990	Slade et al. 1993
			toe-clip only	1989-1999	Brady and Slade 2001
			toe-clip only	1994-1995	Cochran and Solomon 2000
			toe-clip plus	1986	Gaulin and FitzGerald 1988
			toe-clip plus	2000	Lin et al. 2004
Microtus oeconomus	tundra vole	37.6	toe-clip plus	1990-1991	Johannesen et al. 1997
Microtus oregoni	creeping vole	20.3	ear tag(s) only	1998	Manning and Edge 2004
			not indicated	1981-1983	Andersen and MacMahon 1985
			toe-clip only	1981-1983	Doyle 1990
Microtus pennsylvanicus	meadow vole	36.8	combo:ear/PIT	1993	Harper and Batzli 1996
			combo:ear/toe-clip	1978-1980	Yahner 1982
			combo:ear/toe-clip	1993-1994	Fortier and Tamarin 1998
			ear tag(s) only	1974-1977	Rose and Dueser 1980
			ear tag(s) only	1978-1981	Reich and Tamarin 1984
			ear tag(s) only	1984	Jett and Nichols 1987

Microtus pennsylvanicus	meadow vole	36.8	ear tag(s) only	1990-1992	Ostfeld and Manson 1996
			ear tag(s) only	1990-1992	Pugh and Ostfeld 1998
			ear tag(s) only	1991	Ostfeld et al. 1993
			ear tag(s) only	1993-1994	Yunger and Randa 1999
			ear tag(s) only	1994-1995	Klaas et al. 1998
			ear tag(s) only	1995-1996	Lin and Batzli 2004
			ear tag(s) plus	1977-1978	Webster and Brooks 1981
			either:ear/toe-clip	1978-1980	Yahner 1983
			not indicated	1974	Baird and Birney 1982
			not indicated	1974-1975	Baker and Brooks 1982
			not indicated	1976-1977	Keith and Tamarin 1981
			radio only	1978	Madison 1981
			radio only	1979-1982	Jones 1990
			toe-clip only	1972-1976	Verner and Getz 1985
			toe-clip only	1972-1997	Getz et al. 2001
			toe-clip only	1984	Brochu et al. 1988
			toe-clip only	1986	Hall et al. 1991
			toe-clip only	1989-1990	Harper et al. 1993
			toe-clip only	1992-1993	Peles and Barrett 1996
			toe-clip only	1992-1993	Peles et al. 1995
			toe-clip plus	1983-1984	McShea and Madison 1989
			toe-clip plus	1986	Gaulin and FitzGerald 1988
Microtus pinetorum	woodland vole	26.3	toe-clip only	1981-1984	Clark et al. 1987
Microtus richardsoni	water vole	85.0	ear tag(s) only	1977-1979	Ludwig 1988

Microtus townsendii	Townsend's vole	64.8	ear tag(s) only	1975-1976	Beacham 1980
			ear tag(s) only	1976-1978	Beacham and Krebs 1980
			ear tag(s) only	1998	Manning and Edge 2004
Mus caroli	Ryukyu mouse	*	toe-clip only	1997-1998	Adler et al. 1999
Mus minutoides	pygmy mouse	6.2	toe-clip only	1994-1995, 1998	Johnson et al. 2002
Mus musculus	house mouse	17.7	combo:ear notch/toe-clip	1990-1993	Drickamer et al. 1999
			combo:hair/toe-clip	1984*	Lenington and Franks 1985
			ear tag(s) only	1996-1997	Chambers et al. 2000
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1977-1983	Grant et al. 1985
			toe-clip only	1976-1977	Maly et al. 1985
			toe-clip only	1979	Humphrey and Barbour 1981
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1982-1983	Gust and Schmidly 1986
			toe-clip only	1983	Coppola and Vandenbergh 1987
			toe-clip only	1986	Geissel et al. 1988
			toe-clip only	1987*	Cox 1989
			toe-clip only	1989	Cittadino et al. 1994
			toe-clip only	1996-1997	Cramer and Willig 2002
Mus pahari	Gairdner's shrewmouse	*	toe-clip only	1997-1998	Adler et al. 1999

Mus spretus	Algerian mouse	12.8	toe-clip only	1995-1997	Torre et al. 2004
Myocastor coypus	nutria	6937.5	combo:ear/hair	1999-2000	Guichón et al. 2003
Myomys verreauxi	Verreaux's mouse	41.0	either:ear/toe-clip	1978-1979	Rickart 1981
Myosorex varius	forest shrew	11.4	toe-clip only	1994-1995, 1998	Johnson et al. 2002
Nannospalax ehrenbergi	Palestine mole rat	*	not indicated	1991*	Rado et al. 1992
Napaeozapus insignis	woodland jumping mouse	22.3	ear tag(s) only	1996-1997	McShea et al. 2003
			ear tag(s) only	1999-2000	Glennon et al. 2002
			not marked	1964-1971	Vickery and Bider 1981
			toe-clip only	1982	Buckner and Shure 1985
Neacomys tenuipes	narrow-footed bristly mouse	19.0	toe-clip only	1976-1977	O'Connell 1989
Nectomys squamipes	South American water rat	190.7	ear notch/punch	1993-1995	Bergallo and Magnusson 1999
			toe-clip only	1983-1984	Mares and Ernest 1995
Neotoma albigula	white-throated woodrat	206.0	combo:ear/toe-clip	1984-1986	Simons 1991
			combo:hair/toe-clip	1987	Rogovin et al. 1991
			ear tag(s) only	1993-1994	Ellison and Van Riper 1998
			ear tag(s) only	1995-1996	Swann et al. 1997
			ear tag(s) only	1997	Davidson et al. 1999
			not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1983	Price et al. 1984
Neotoma cinerea	bushy-tailed woodrat	299.2	ear tag(s) only	1994-1997	Andersen et al. 2000
			ear tag(s) only	1998	Manning and Edge 2004
			other	1987-1989	Moses et al. 1995
			toe-clip only	1975-1978	Andersen et al. 1980

Neotoma floridana	eastern woodrat	244.7	ear tag(s) only	1994-1995	Horne et al 1998
			not indicated	1977-1983	Grant et al. 1985
			not indicated	1979	Barbour and Humphrey 1982
			toe-clip only	1976-1977	Hersh 1981
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1986	Humphrey 1988
			toe-clip only	1990-1994	Loeb 1999
Neotoma fuscipes	dusky-footed woodrat	229.8	either:hair/toe-clip	1991	O'Farrell et al. 1994
			toe-clip only	1967-1972, 1976-1977, 1979-1980	Cranford 1982
Neotoma lepida	desert woodrat	163.7	combo:ear/toe-clip	1979-1981	Kotler 1985b
			ear tag(s) only	1989-1991	McClenaghan and Taylor 1993
			ear tag(s) plus	1975-1976	Thompson 1982
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			other	1976-1978	Vaughan and Schwartz 1980
			toe-clip only	1972-1973	O'Farrell 1980
Neotoma micropus	southern plains woodrat	237.5	ear tag(s) only	1997	Davidson et al. 1999
			not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1996-1997	Cramer and Willig 2002
Neotoma stephensi	Stephens's woodrat	152.5	toe-clip only	1979-1984	Vaughan and Czaplewski 1985
			toe-clip only	1980-1981	Vaughan 1982
Neurotrichus gibbsii	American shrew mole	8.9	ear tag(s) only	1998	Manning and Edge 2004
			not indicated	1981-1983	Andersen and MacMahon 1985

Neurotrichus gibbsii	American shrew mole	8.9	toe-clip only	1981-1983	Doyle 1990
			toe-clip only	1981-1985	Ostfeld and Klosterman 1986
Niviventer fulvescens	Chestnut white-bellied rat	81.8	toe-clip only	1997-1998	Adler et al. 1999
Niviventer langbianis	Lang Bian white-bellied rat	*	toe-clip only	1997-1998	Adler et al. 1999
Nyctomys sumichrasti	vesper rat	60.0	ear notch/punch	1998	Mangan and Adler 2000
Ochotona curzoniae	black-lipped pika	*	ear tag(s) only	1985	Smith and Gao 1991
Ochotona princeps	American pika	157.6	ear tag(s) only	1976-1983	Southwick et al. 1986
			ear tag(s) only	1981-1985	Brown et al. 1989
			not marked	1978	Conner 1982
Ochrotomys nuttalli	golden mouse	22.4	ear tag(s) only	1996-1997	McCay 2000
			radio only	1999-2000	Morzillo et al. 2003
			toe-clip only	1978	Kitchings and Levy 1981
			toe-clip only	1979	Seagle 1985
			toe-clip only	1982	Buckner and Shure 1985
			toe-clip only	1990-1994	Loeb 1999
Octodon degus	degu	210.0	ear tag(s) only	1983-1984	Iriarte et al. 1989
			ear tag(s) only	1987-1989	Jimenez et al. 1992
			hair dye/bleach/clip only	1999	Kenagy et al. 2004
			not indicated	1976	Jaksić et al. 1981
Oecomys bicolor	bicolored arboreal rice rat	34.0	not indicated	1983-1985	Malcolm 1991
			toe-clip only	1976-1977	O'Connell 1989
			toe-clip only	1983-1984	Mares and Ernest 1995
Oecomys concolor	unicolored arboreal rice rat	61.6	not indicated	1985	Lacher and Alho 1989
			toe-clip only	1976-1977	O'Connell 1989

Oecomys concolor	unicolored arboreal rice rat	61.6	toe-clip only	1983-1984	Mares and Ernest 1995
Oecomys paricola	Brazilian arboreal rice rat	73.4	not indicated	1983-1985	Malcolm 1991
Oligoryzomys eliurus	Brazilian pygmy rice rat	30.0	toe-clip only	1983-1984	Mares and Ernest 1995
Oligoryzomys flavescens	yellow pygmy rice rat	21.3	ear tag(s) only	1983-1984	Iriarte et al. 1989
			ear tag(s) only	1987-1989	Jimenez et al. 1992
			either:ear/toe-clip	1980-1985	Kelt et al. 1994
			either:ear/toe-clip	1982-1985	Meserve et al. 1999
			not indicated	1976	Jaksić et al. 1981
			not indicated	1979-1983	González et al. 1989
			other	1981-1982	Murúa et al. 1987
			toe-clip only	1979-1981	Meserve et al. 1982
			toe-clip only	1989	Cittadino et al. 1994
Oligoryzomys vegetus	sprightly pygmy rice rat	*	ear notch/punch	1998	Mangan and Adler 2000
Ondatra zibethicus	muskrat	1065.8	ear tag(s) only	1989-1992	Marinelli et al. 1997
			not indicated	1987	MacArthur 1992
Onychomys arenicola	Mearns's grasshopper mouse	30.0	ear tag(s) only	1997	Davidson et al. 1999
			toe-clip only	1988	Mellink and Madrigal 1993
Onychomys leucogaster	northern grasshopper mouse	27.9	ear tag(s) only	1994	Stapp 1997
			ear tag(s) only	1997	Davidson et al. 1999
			not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1996-1997	Cramer and Willig 2002
Onychomys torridus	southern grasshopper mouse	25.0	combo:ear/toe-clip	1979-1981	Kotler 1985b

Onychomys torridus	southern grasshopper mouse	25.0	combo:ear/toe-clip	1984-1986	Simons 1991
			combo:hair/toe-clip	1987	Rogovin et al. 1991
			ear tag(s) plus	1981-1982, 1988	Frank and Heske 1992
			not indicated	1981-1982	Thompson 1987
			toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1983	Price et al. 1984
Oryctolagus cuniculus	European rabbit	1826.7	ear tag(s) only	1981	Roberts 1978
			hair dye/bleach/clip only	1989	Kunkele 1992
			radio only	1997-1998	Lombardi et al. 2003
			tattoo	1976-1977	Sneddon 1991
Oryzomys alfaroi	Alfaro's rice rat	33.3	ear tag(s) only	1999	Caro et al. 2001
			toe-clip only	1998	Mangan and Adler 2000
Oryzomys argentatus	silver rice rat	*	other	1987-1988	Goodyear 1992
		*	toe-clip plus	1973-1984	Goodyear 1987
Oryzomys capito	large-headed rice rat	57.8	not indicated	1983-1985	Malcolm 1991
			toe-clip only	1976-1977	O'Connell 1989
			toe-clip only	1983-1984	Mares and Ernest 1995
Oryzomys couesi	Coues's rice rat	69.3	ear tag(s) only	1999	Caro et al. 2001
			toe-clip only	1997-1998	Vázquez et al. 2000
Oryzomys devius	Boquete rice rat	*	ear notch/punch	1998	Mangan and Adler 2000
Oryzomys fornesi		*	not indicated	1985	Lacher and Alho 1989
Oryzomys intermedius	intermediate rice rat	60.5	ear notch/punch	1993-1995	Bergallo and Magnusson 1999
Oryzomys macconnelli	MacConnell's rice rat	58.0	not indicated	1983-1985	Malcolm 1991

Oryzomys palustris	marsh rice rat	53.9	not indicated	1972-1979	Cameron and Spencer 1983
			not indicated	1977-1983	Grant et al. 1985
			not indicated	1996-1997	Kruchek 2004
			toe-clip only	1980-1981	Turner and Grant 1987
Oryzomys subflavus	terraced rice rat	50.0	not indicated	1985	Lacher and Alho 1989
Otomys irroratus	vlei rat	101.8	toe-clip only	1994-1995, 1998	Johnson et al. 2002
Ototylomys phyllotis		120.0	ear tag(s) only	1999	Caro et al. 2001
Pappogeomys castanops	yellow-faced pocket gopher	251.8	toe-clip only	1971-1973	Smolen et al. 1980
Perognathus amplus	Arizona pocket mouse	11.7	combo:ear/toe-clip	1984-1986	Simons 1991
			not indicated	1975	M'Closkey 1983
			toe-clip only	1983	Price et al. 1984
Perognathus fasciatus	olive-backed pocket mouse	11.5	ear tag(s) only	1994-1997	Andersen et al. 2000
Perognathus flavescens	plains pocket mouse	8.8	not indicated	1993-1994	Jorgensen and Demarais 1999
			powder only	1984*	Lemen and Freeman 1985
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1996-1997	Cramer and Willig 2002
Perognathus flavus	silky pocket mouse	7.7	combo:hair/toe-clip	1987	Rogovin et al. 1991
			not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1997	Davidson et al. 1999
Perognathus longimembris	little pocket mouse	7.6	combo:ear/toe-clip	1979-1981	Kotler 1985b
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			other	1978	Bowers 1982
			toe-clip only	1972-1973	O'Farrell 1980

Perognathus parvus	Great Basin pocket mouse	21.8	combo:ear/toe-clip	1979-1981	Kotler 1985b
			combo:hair/toe-clip	1982	Verts and Carraway 1986
			ear tag(s) only	1994-1997	Andersen et al. 2000
			not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1980	Small and Verts 1983
Peromyscus attwateri	Texas mouse	27.9	toe-clip only	1986-1987	Etheredge et al. 1989
Peromyscus aztecus	Aztec mouse	40.0	not indicated	1995-1996	Vázquez et al. 2004
			toe-clip only	1997-1998	Vázquez et al. 2000
Peromyscus boylii	brush mouse	21.4	ear tag(s) only	1993-1995	Ribble and Stanley 1998
			ear tag(s) plus	1993-1998	Ribble et al. 2002
			radio only	1996-1998	Kalcounis-Rüppell and Millar 2002
			toe-clip only	1993-1994	Ellison and Van Riper 1998
			toe-clip only	1995-1996	Swann et al. 1997
Peromyscus californicus	California mouse	43.5	radio only	1996-1998	Kalcounis-Rüppell and Millar 2002
			toe-clip only	1967-1972, 1976-1977, 1979-1980	Cranford 1982
Peromyscus crinitus	canyon mouse	18.0	not indicated	1981-1982	Thompson 1987
Peromyscus difficilis	Zacatecan deer mouse	28.0	ear tag(s) only	1986-1988	Galindo-Leal 1997
Peromyscus eremicus	cactus mouse	23.6	combo:ear/toe-clip	1984-1986	Simons 1991
			combo:hair/toe-clip	1987	Rogovin et al. 1991
			either:hair/toe-clip	1991	O'Farrell et al. 1994

Peromyscus eremicus	cactus mouse	23.6	not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1986*	Bowers 1988
			toe-clip only	1993-1994	Ellison and Van Riper 1998
			toe-clip only	1995-1996	Swann et al. 1997
Peromyscus gossypinus	cotton mouse	29.4	ear tag(s) plus	1996-1997	McCay 2000
			not indicated	1979	Barbour and Humphrey 1982
			toe-clip only	1979	Humphrey and Barbour 1981
			toe-clip only	1986	Humphrey 1988
			toe-clip only	1990-1994	Loeb 1999
			toe-clip only	1998-2000	Mabry et al. 2003
Peromyscus keeni	Sitka mouse	28.3	combo:ear/PIT	1992-1995	Hanley and Barnard 1999
			toe-clip only	1998-2000	Smith and Nichols 2004
Peromyscus leucopus	white-footed mouse	21.2	combo:ear notch/toe-clip	1976	Barry and Francq 1980
			combo:ear notch/toe-clip	1980	Barry et al. 1984
			combo:ear/toe-clip	1978-1980	Yahner 1982
			combo:ear/toe-clip	1982-1984	Briggs 1986
			ear tag(s) only	1973-1980	Goundie and Vessey 1986
			ear tag(s) only	1980-1981	Novak 1983
			ear tag(s) only	1980-1981	Parren and Capen 1985
			ear tag(s) only	1980-1982	Krohne and Baccus 1985
			ear tag(s) only	1980-1992	Wolff 1993
			ear tag(s) only	1980-1993	Wolff 1996
			ear tag(s) only	1982-1988	Schug et al. 1991
			ear tag(s) only	1983	Adler et al. 1986

Peromyscus leucopus	white-footed mouse	21.2	ear tag(s) only	1983-1992	McCracken et al. 1999
			ear tag(s) only	1983-2002	Elias et al. 2004
			ear tag(s) only	1984-1985	Wolff and Durr 1986
			ear tag(s) only	1984-1985	Zegers and Merritt 1988
			ear tag(s) only	1987-1988	Xia and Millar 1990
			ear tag(s) only	1991	Ostfeld et al. 1993
			ear tag(s) only	1991-1993	Jacquot and Vessey 1998
			ear tag(s) only	1992-1998	Havelka and Millar 2004
			ear tag(s) only	1992-1998	Yunger 2002
			ear tag(s) only	1993-1994	Yunger and Randa 1999
			ear tag(s) only	1996	Hicks et al. 1998
			ear tag(s) only	1996-1997	McShea et al. 2003
			ear tag(s) only	1997	Davidson et al. 1999
			ear tag(s) only	1997-1998	Wolf and Batzli 2002
			ear tag(s) plus	1989	McShea and Gilles 1992
			either:ear/toe-clip	1973-1993	Lewellen and Vessey 1999
			either:ear/toe-clip	1978-1980	Yahner 1983
			either:ear/toe-clip	1991-1993	Ostfeld et al. 1996
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1977-1983	Grant et al. 1985
			not indicated	1978	Zegers and Ha 1981
			not indicated	1992-1996	Nupp and Swihart 2000
			not indicated	1993-1994	Jorgensen and Demarais 1999
			PIT only	2002	Wilder and Meikle 2004

Peromyscus leucopus	white-footed mouse	21.2	powder only	1989	Manville et al. 1992
			radio only	1981	Wolff and Hurlbutt 1982
			toe-clip only	1973	Smith and Sloan 1988
			toe-clip only	1977-1979	Drickamer 1984
			toe-clip only	1978	Kitchings and Levy 1981
			toe-clip only	1979	Seagle 1985
			toe-clip only	1979-1980	Drickamer 1987
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1982	Buckner and Shure 1985
			toe-clip only	1982	Kaufman et al. 1985
			toe-clip only	1983-1995	Terman and Terman 1999
			toe-clip only	1985-1989	Andersen and Folk 1993
			toe-clip only	1985-1990	Slade et al. 1993
			toe-clip only	1989-1993	Slade and Blair 2000
			toe-clip only	1989-1999	Brady and Slade 2001
			toe-clip only	1989-1999	Brady and Slade 2004
			toe-clip only	1995-1996	Swann et al. 1997
			toe-clip plus	1989-1990	Barnum et al. 1992
Peromyscus maniculatus	deer mouse	21.3	combo:ear notch/toe-clip	1980	Barry et al. 1984
			combo:ear/toe-clip	1979-1981	Kotler 1985b
			combo:ear/toe-clip	1986-1989	Kaufman and Kaufman 1994
			combo:hair/toe-clip	1987	Rogovin et al. 1991

Peromyscus maniculatus	deer mouse	21.3	ear tag(s) only	1996	Hicks et al. 1998
			ear tag(s) only	1998	Manning and Edge 2004
			ear tag(s) only	1980-1981	Parren and Capen 1985
			ear tag(s) only	1980-1993	Wolff 1996
			ear tag(s) only	1981-1982	Longland and Jenkins 1987
			ear tag(s) only	1984-1985	Wolff and Durr 1986
			ear tag(s) only	1984-1985	Zegers and Merritt 1988
			ear tag(s) only	1989-1991	McClenaghan and Taylor 1993
			ear tag(s) only	1990-1992	Havelka and Millar 1997
			ear tag(s) only	1993-1994	Yunger and Randa 1999
			ear tag(s) only	1994-1997	Andersen et al. 2000
			ear tag(s) only	1994-1998	Biggs et al. 2000
			ear tag(s) only	1996-1997	Bowman et al. 2001
			ear tag(s) only	1996-1997	McShea et al. 2003
			ear tag(s) only	1996-1998	Pyare and Longland 2001
			ear tag(s) only	1997-1998	Keinath and Hayward 2003
			ear tag(s) only	1998-2001	Hadley and Wilson 2004
			ear tag(s) only	1999-2000	Glennon et al. 2002
			ear tag(s) plus	1986	Douglass 1989
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1977-1979	Van Horne 1982
			not indicated	1981-1983	Andersen and MacMahon 1985
			not indicated	1989	Millar and Derrickson 1992

Peromyscus maniculatus	deer mouse	21.3	not indicated	1993-1994	Jorgensen and Demarais 1999
			not marked	1964-1971	Vickery and Bider 1981
			not marked	1980-1982	Kotler 1984
			not marked	1983	Kotler 1985a
			powder only	1984-1986	Kaufman 1989
			radio only	1981	Wolff and Hurlbutt 1982
			toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1975-1976	Jenkins and Llewellyn 1981
			toe-clip only	1975-1978	Andersen et al. 1980
			toe-clip only	1977-1979	Drickamer 1984
			toe-clip only	1979-1980	Drickamer 1987
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1982	Kaufman et al. 1988
			toe-clip only	1981-1983	Doyle 1990
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1981-1985	Ostfeld and Klosterman 1986
			toe-clip only	1981-1990	Rehmeier et al. 2004
			toe-clip only	1982	Buckner and Shure 1985
			toe-clip only	1982-1983	Gust and Schmidly 1986
			toe-clip only	1985-1990	Slade et al. 1993
			toe-clip only	1986	Belk et al. 1988
			toe-clip only	1989-1993	Slade and Blair 2000
			toe-clip only	1989-1999	Brady and Slade 2001
			toe-clip only	1989-1999	Brady and Slade 2004

Peromyscus maniculatus	deer mouse	21.3	toe-clip only	1994-1995	Songer et al. 1997
			toe-clip only	1995-1996	Swann et al. 1997
Peromyscus mexicanus	Mexican deer mouse	32.6	ear notch/punch	1998	Mangan and Adler 2000
			ear tag(s) only	1989	Duquette and Millar 1995
Peromyscus oreas	Columbian mouse	21.0	toe-clip only	1994-1995	Songer et al. 1997
Peromyscus pectoralis	white-ankled mouse	39.0	ear tag(s) plus	1988-1989	Mullican and Baccus 1990
			toe-clip only	1986-1987	Etheredge et al. 1989
Peromyscus polionotus	beach mouse	13.0	ear tag(s) only	1976-1979	Extine and Stout 1987
			ear tag(s) only	1996-1997	McCay 2000
			toe-clip only	1979	Humphrey and Barbour 1981
			toe-clip only	1987-1989	Rave and Holler 1992
			toe-clip only	1990-1994	Loeb 1999
			toe-clip only	1994-1997	Swilling and Wooten 2002
			toe-clip only	1998-2000	Mabry et al. 2003
Peromyscus truei	pinyon mouse	27.4	ear tag(s) only	1993-1995	Ribble and Stanley 1998
			ear tag(s) only	1994-1997	Andersen et al. 2000
			ear tag(s) only	1997	Davidson et al. 1999
			ear tag(s) plus	1993-1998	Ribble et al. 2002
			powder only	1984*	Lemen and Freeman 1985
			toe-clip only	1967-1972, 1976-1977, 1979-1980	Cranford 1982
			toe-clip only	1975-1976	Jenkins and Llewellyn 1981
			toe-clip only	1975-1976	Scheibe and O'Farrell 1995

Petaurista leucogenys	Japanese giant flying squirrel	*	not marked	1999	Stafford et al. 2002
			not marked	1999	Stafford et al. 2003
Petaurista philippensis	Indian giant flying squirrel	1676.0	not marked	1997-1998	Kuo and Lee 2003
Phenacomys intermedius	western heather vole	25.2	ear tag(s) only	1997-1998	Keinath and Hayward 2003
			ear tag(s) only	1998-2001	Hadley and Wilson 2004
Phodopus campbelli	Campbell's hamster	23.4	radio only	1988-1990	Wynne-Edwards et al. 1999
Phodopus sungorus	Dzhungarian hamster	23.4	radio only	1988-1990	Wynne-Edwards et al. 1999
Phyllotis darwini	Darwin's leaf-eared mouse	50.8	ear tag(s) only	1983-1984	Iriarte et al. 1989
			ear tag(s) only	1987-1989	Jimenez et al. 1992
			ear tag(s) only	1988-1991	Torres-Contreras et al. 1997
			not indicated	1976	Jaksić et al. 1981
Proechimys sp.	spiny rat	*	not indicated	1983-1985	Malcolm 1991
Proechimys guairae	Guaira spiny rat	400.0	toe-clip only	1976-1977	O'Connell 1989
			toe-clip only	1983-1984	Aguilera 1999
Proechimys iheringi	Ihering's spiny rat	203.0	ear notch/punch	1993-1995	Bergallo and Magnusson 1999
Proechimys longicaudatus	long-tailed spiny rat	205.0	toe-clip only	1983-1984	Mares and Ernest 1995
Proechimys semispinosus	Tome's spiny rat	360.5	toe-clip only	1994-1996	Tomblin and Adler 1998
			toe-clip only	1997-1998	Lambert and Adler 2000
			radio only	1989	Seamon and Adler 1999
Psammomys obesus	fat sand rat	149.6	not indicated	1981-1984	Ilan and Yom-Tov 1990
Pseudomys higginsi	long-tailed mouse	67.0	ear tag(s) only	1989-1990	Luo et al. 1998
			ear tag(s) only	1989-1990	Monamy and Fox 1999
Pteromys volans	Siberian flying squirrel	143.8	ear tag(s) plus	1996-1998	Hanski et al. 2000
Rattus argentiventer	rice-field rat	132.5	radio only	2000	Tristiani et al. 2003

Rattus exulans	Polynesian rat	47.5	combo:ear notch/toe-clip	1972-1974	Koeppl et al. 1981
			not indicated	1982-1984	Heideman et al. 1987
Rattus fuscipes	bush rat	133.0	ear tag(s) only	1978-1980	McDonald et al. 1988
Rattus lutreolus	Australian swamp rat	106.0	ear tag(s) only	1989-1990	Luo et al. 1998
			ear tag(s) only	1989-1990	Monamy and Fox 1999
Rattus nittidus	Himalayan field rat	*	toe-clip only	1997-1998	Adler et al. 1999
Rattus norvegicus	brown rat	338.4	ear tag(s) only	1984-1986	Glass et al. 1988
			toe-clip only	1975-1976	Stroud 1982
Rattus rattus	house rat	229.2	either:hair/toe-clip	1991	O'Farrell et al. 1994
			not indicated	1982-1984	Heideman et al. 1987
			other	1987-1988	Goodyear 1992
			toe-clip only	1975-1976	Stroud 1982
			toe-clip only	1979	Humphrey and Barbour 1981
Rattus sikkimensis	Sikkim rat	*	toe-clip only	1997-1998	Adler et al. 1999
Reithrodontomys fulvescens	fulvous harvest mouse	11.4	not indicated	1970-1973	Grant et al. 1982
			not indicated	1972-1979	Cameron and Spencer 1983
			not indicated	1974-1975	Kincaid and Cameron 1982
			not indicated	1977-1983	Grant et al. 1985
			not indicated	1995-1996	Vázquez et al. 2004
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1982-1983	Gust and Schmidly 1986
			toe-clip only	1995-1996	Swann et al. 1997
			toe-clip only	1997-1998	Vázquez et al. 2000

Reithrodontomys humulis	eastern harvest mouse	8.3	ear tag(s) only	1996-1997	McCay 2000
			toe-clip only	1982-1983	Gust and Schmidly 1986
Reithrodontomys megalotis	western harvest mouse	9.4	combo:ear/toe-clip	1979-1981	Kotler 1985b
			combo:ear/toe-clip	1980-1991	Skupski 1995
			ear tag(s) only	1994-1997	Andersen et al. 2000
			ear tag(s) only	1997	Davidson et al. 1999
			either:hair/toe-clip	1991	O'Farrell et al. 1994
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1974-1975	Blaustein and Fugle 1981
			not indicated	1993-1994	Jorgensen and Demarais 1999
			toe-clip only	1972-1973	O'Farrell 1980
			toe-clip only	1975-1981	Heske et al. 1984
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1982	Kaufman et al. 1988
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1981-1985	Ostfeld and Klosterman 1986
			toe-clip only	1986	Geissel et al. 1988
			toe-clip only	1989-1993	Slade and Blair 2000
			toe-clip only	1989-1999	Brady and Slade 2001
			toe-clip only	1989-1999	Brady and Slade 2004
			toe-clip only	1993-1994	Ellison and Van Riper 1998
			toe-clip only	1996-1997	Cramer and Willig 2002
Reithrodontomys mexicanus	Mexican harvest mouse	16.0	ear notch/punch	1998	Mangan and Adler 2000

Reithrodontomys montanus	plains harvest mouse	10.9	ear tag(s) only	1997	Davidson et al. 1999
			not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1982-1983	Gust and Schmidly 1986
			toe-clip only	1996-1997	Cramer and Willig 2002
Reithrodontomys raviventris	salt-marsh harvest mouse	11.0	ear tag(s) only	1986	Geissel et al. 1988
Reithrodontomys sumichrasti	Sumichrast's harvest mouse	19.0	toe-clip only	1997-1998	Vázquez et al. 2000
Rhabdomys pumilio	four-striped grass mouse	40.7	either:ear/toe-clip	1978-1979	Rickart 1981
			toe-clip only	1994-1995, 1998	Johnson et al. 2002
Rhipidomys mastacalis	Atlantic forest climbing mouse	77.5	not indicated	1983-1985	Malcolm 1991
			toe-clip only	1976-1977	O'Connell 1989
			toe-clip only	1983-1984	Mares and Ernest 1995
Rhombomys opimus	great gerbil	185.0	combo:ear/hair	1996-2001	Rogovin et al. 2004
Saccostomus mearnsi	Mearns's pouched mouse	45.5	not indicated	1995-1996	Keesing 1998
Scapanus orarius	coast mole	61.2	ear tag(s) only	1998	Manning and Edge 2004
Sciurus aberti	Abert's squirrel	624.0	not indicated	1970-1974	Farentinos 1980
Sciurus carolinensis	eastern gray squirrel	506.5	combo:ear/hair	1983	Brown 1986
			combo:ear/toe-clip	1974-1976	Riege 1991
			ear tag(s) plus	1986-1988	Koprowski 1991

Sciurus carolinensis	eastern gray squirrel	506.5	not indicated	1988-1990	Koprowski 1992
			not indicated	1992-1996	Nupp and Swihart 2000
			not marked	1977-1979	Lishak 1982b
			not marked	1978-1979	Lishak 1982a
			not marked	1978-1979	Lishak 1984
			other	1986-1990	Koprowski 1996
			toe-clip only	1979	Humphrey and Barbour 1981
Sciurus granatensis	red-tailed squirrel	250.0	not marked	1977-1978	Glanz 1984
			not marked	1984	Giacalone et al. 1987
			toe-clip only	1976-1977	O'Connell 1989
Sciurus griseus	western gray squirrel	731.0	ear tag(s) plus	1998-1999	Linders et al. 2004
Sciurus niger	eastern fox squirrel	761.9	combo:ear/toe-clip	1968-1986	Koprowski et al. 1988
			ear tag(s) plus	1986-1988	Koprowski 1991
			ear tag(s) plus	1984-1985	Kantola and Humphrey 1990
			not indicated	1988-1990	Koprowski 1992
			not indicated	1992-1996	Nupp and Swihart 2000
			other	1986-1990	Koprowski 1996
			toe-clip only	1990-1994	Loeb 1999
Sciurus variegatoides	variegated squirrel	485.0	not marked	1977-1978	Glanz 1984
			not marked	1984	Giacalone et al. 1987
Sigmodon alleni	Allen's cotton rat	179.0	toe-clip only	1997-1998	Vázquez et al. 2000
Sigmodon alstoni	Alston's cotton rat	55.7	toe-clip only	1976-1977	O'Connell 1989
Sigmodon hispidus	hispid cotton rat	92.4	combo:hair/toe-clip	1987	Rogovin et al. 1991
			ear tag(s) only	1972-1983	Sauer and Slade 1985

Sigmodon hispidus	hispid cotton rat	92.4	ear tag(s) only	1973-1975	Glass and Slade 1980
			ear tag(s) only	1973-1976	Stout and Demmer 1982
			ear tag(s) only	1973-1981	Slade and Swihart 1983
			ear tag(s) only	1973-1981	Swihart and Slade 1984
			ear tag(s) only	1973-1982	Slade et al. 1984
			ear tag(s) only	1973-1990	Campbell and Slade 1993
			ear tag(s) only	1973-1993	Slade and Blair 2000
			ear tag(s) only	1976-1995	Slade and Russell 1998
			ear tag(s) only	1978-1993	Eifler and Slade 1999
			ear tag(s) only	1978-1999	Brady and Slade 2004
			ear tag(s) only	1979-1980	Stafford and Stout 1983
			ear tag(s) only	1985-1990	Slade et al. 1993
			ear tag(s) only	1989-1999	Brady and Slade 2001
			ear tag(s) only	1990-1992	Sulok et al. 2004
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1972-1979	Cameron and Spencer 1983
			not indicated	1973-1988	Slade 1991
			not indicated	1973-1988	Slade and Iskjaer 1990
			not indicated	1974-1975	Kincaid and Cameron 1982
			not indicated	1975-1976	Teska 1980
			not indicated	1977-1983	Grant et al. 1985
			not indicated	1980-1983	Swihart and Slade 1985
			not indicated	1993-1994	Jorgensen and Demarais 1999
			radio only	1981-1982	Cameron 1995

Sigmodon hispidus	hispid cotton rat	92.4	toe-clip only	1979	Humphrey and Barbour 1981
			toe-clip only	1980-1981	Turner and Grant 1987
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1982	Gregory and Cameron 1988
			toe-clip only	1981-1984	Clark et al. 1987
			toe-clip only	1982-1983	Gust and Schmidly 1986
			toe-clip only	1990-1994	Loeb 1999
			toe-clip only	1996-1997	Cramer and Willig 2002
			toe-clip only	1998-2000	Mabry et al. 2003
Sigmodon ochrognathus	yellow-nosed cotton rat	122.0	ear tag(s) only	1995-1996	Swann et al. 1997
Sorex spp.	shrews	*	ear tag(s) only	1998	Manning and Edge 2004
Sorex araneus	Eurasian shrew	10.0	toe-clip only	1995-1997	Torre et al. 2004
Sorex cinereus	cinereus shrew	4.7	combo:ear/toe-clip	1978-1980	Yahner 1982
			ear tag(s) only	1996-1997	McShea et al. 2003
			ear tag(s) only	1997-1998	Keinath and Hayward 2003
			hair dye/bleach/clip only	1999-2000	Glennon et al. 2002
			not marked	1998-2001	Hadley and Wilson 2004
			toe-clip only	1992-1993	Merritt 1995
Sorex fumeus	smoky shrew	7.7	ear tag(s) only	1996-1997	McShea et al. 2003
Sorex hoyi	pygmy shrew	2.6	ear tag(s) only	1996-1997	McShea et al. 2003
Sorex minutus	Eurasian pygmy shrew	4.5	toe-clip only	1995-1997	Torre et al. 2004
Sorex monticolus	montane shrew	5.3	not indicated	1981-1983	Andersen and MacMahon 1985
			not marked	1998-2001	Hadley and Wilson 2004
			toe-clip only	1981-1983	Doyle 1990

Sorex trowbridgii	Trowbridge's shrew	3.8	toe-clip only	1981-1983	Doyle 1990
Sorex vagrans	vagrant shrew	4.4	toe-clip only	1981-1985	Ostfeld and Klosterman 1986
			toe-clip only	1986	Geissel et al. 1988
Spermophilus armatus	Uinta ground squirrel	313.0	toe-clip only	1986	Belk et al. 1988
Spermophilus beecheyi	California ground squirrel	578.5	combo:ear/hair	1977-1978	Dobson 1983
			combo:ear/hair	1987-1988	Boellstorff and Owings 1995
			ear tag(s) only	1977-1978	Dobson 1981
			ear tag(s) only	1977-1978	Dobson and Davis 1986
			not indicated	1987*	Salmon and Marsh 1989
			other	1999*	Muchlinski et al. 2000
Spermophilus beldingi	Belding's ground squirrel	280.5	combo:ear/hair	1993-1994	Nunes and Holekamp 1996
			combo:ear/toe-clip	1986-1987	Trombulak 1989
			tattoo	1975-1976	Verts and Costain 1988
Spermophilus brunneus	Idaho ground squirrel	300.0	ear tag(s) only	1991-1997	Gavin et al. 1999
Spermophilus citellus	European ground squirrel	290.0	combo:hair/PIT	1990-1995	Millesi et al. 1999
			combo:hair/PIT	1992-1999	Hoffmann et al. 2003
Spermophilus columbianus	Columbian ground squirrel	493.0	combo:ear/hair	1972, 1974, 1976-1978	Murie et al. 1980
			combo:ear/hair	1974-1980	Murie and Harris 1982
			combo:ear/hair	1982	Waterman 1984
			combo:ear/hair	1984-1989	Murie 1992
			combo:ear/hair	1989	Hare and Murie 1992
			combo:ear/hair	1994-1998	Neuhaus 2000
			ear tag(s) only	1974-1980	Murie and Boag 1984

Spermophilus columbianus	Columbian ground squirrel	493.0	not indicated	1982-1985	Weddell 1989
			other	1975-1976	Ramirez and Hornocker 1981
Spermophilus elegans	Wyoming ground squirrel	453.6	combo:ear/hair	1977-1979	Pfeifer 1982
			combo:ear/hair	1979-1981	Fagerstone 1988
Spermophilus franklinii	Franklin's ground squirrel	363.0	not indicated	1965-1975	Keith and Cary 1991
Spermophilus lateralis	golden-mantled ground squirrel	191.0	ear tag(s) only	1996-1998	Pyare and Longland 2001
			ear tag(s) only	1998-2001	Hadley and Wilson 2004
			hair dye/bleach/clip only	1999-2000	Eiler and Banack 2004
			not indicated	1974-1976	Bronson 1980
			toe-clip only	1975-1978	Andersen et al. 1980
Spermophilus mohavensis	Mohave ground squirrel	190.0	not marked	1978	Zembal and Gall 1980
			PIT plus	1990, 1994-1997	Harris and Leitner 2004
Spermophilus mollis	Piute ground squirrel	165.4	toe-clip only	1984	Rickart 1986
Spermophilus parryii	arctic ground squirrel	760.0	combo:ear/hair	1993-1995	Buck and Barnes 1999b
			combo:ear/hair/PIT	1993-1995	Buck and Barnes 1999a
Spermophilus richardsonii	Richardson's ground squirrel	406.0	combo:ear/hair	1979-1982	Michener 1984
			combo:ear/hair	1982-1984	Michener 1985
			combo:ear/hair	1983-1986	Michener and Locklear 1990
			combo:ear/hair	1993-1998	Michener 2002
			ear tag(s) only	1979-1986	Michener 1993
			ear tag(s) only	1980-1981	Davis and Murie 1985
Spermophilus saturatus	Cascade golden-mantled ground squirrel	220.0	hair dye/bleach/clip only	1999-2000	Eiler and Banack 2004

Spermophilus saturatus	Cascade golden-mantled ground squirrel	220.0	not indicated	1981-1983	Andersen and MacMahon 1985
			toe-clip only	1980-1982	Trombulak 1987
Spermophilus spilosoma	spotted ground squirrel	89.0	combo:hair/toe-clip	1987	Rogovin et al. 1991
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1996-1997	Cramer and Willig 2002
Spermophilus townsendii	Townsend's ground squirrel	213.0	combo:hair/PIT	1991-1992	Schooley et al. 1993
			combo:hair/PIT	1992-1994	Sharpe and Van Horne 1998
			not indicated	1970-1973	Grant et al. 1982
			not indicated	1982-1983	Johnson et al. 1987
			PIT only	1991-1994	Van Horne et al. 1998
Spermophilus tridecemlineatus	thirteen-lined ground squirrel	131.7	not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1981-1982	Fleharty and Navo 1983
			toe-clip only	1981-1984	Clark et al. 1987
Spermophilus variegatus	rock squirrel	691.6	combo:hair/toe-clip	1983-1987	Ortega 1990b
			combo:hair/toe-clip	1985-1986	Shriner and Stacey 1991
			combo:hair/toe-clip	1986-1987	Ortega 1990a
Stylodipus telum	thick-tailed three-toed jerboa	65.0	combo:ear/hair	1991	Heske et al. 1995
Suncus murinus	Asian house shrew	60.4	not indicated	1982-1984	Heideman et al. 1987
Sylvilagus aquaticus	swamp rabbit	2135.8	ear tag(s) plus	1984-1985	Kjolhaug and Woolf 1988
Sylvilagus floridanus	eastern cottontail	1172.8	ear tag(s) only	1981	Scribner et al. 1983
			ear tag(s) plus	1998*	Mankin and Warner 1999
			radio only	1978-1980	Althoff and Storm 1989

Sylvilagus floridanus	eastern cottontail	1172.8	toe-clip only	1990-1994	Loeb 1999
Sylvilagus nuttallii	mountain cottontail	755.1	not indicated	1972-1981	Verts et al 1984
Synaptomys cooperi	southern bog lemming	31.9	ear tag(s) only	1971-1973	Danielson and Gaines 1987
			ear tag(s) plus	1983-1984	Danielson and Swihart 1987
			toe-clip only	1981-1984	Clark et al. 1987
Synaptomys cooperi (cont.)	southern bog lemming	31.9	toe-clip only	1989-1999	Brady and Slade 2001
			toe-clip only	1989-1999	Brady and Slade 2004
Syntheosciurus brochus	mountain squirrel	*	not marked	1984	Giacalone et al. 1987
Talpa romana	Roman mole	92.5	other	1991-1992	Loy et al. 1994
Tamias sp.	chipmunk	*	not indicated	1981-1983	Andersen and MacMahon 1985
Tamias amoenus	yellow-pine chipmunk	50.5	ear tag(s) only	1986	Douglass 1989
			toe-clip only	1975-1977	Sharples 1983
			toe-clip only	1980-1982	Trombulak 1985
Tamias dorsalis	cliff chipmunk	71.1	ear tag(s) only	1994-1997	Andersen et al. 2000
Tamias minimus	least chipmunk	135.3	ear tag(s) only	1994-1997	Andersen et al. 2000
			ear tag(s) only	1998-2001	Hadley and Wilson 2004
			ear tag(s) plus	1983-1984	Bergstrom 1988
			toe-clip only	1975-1978	Andersen et al. 1980
			toe-clip only	1986	Belk et al. 1988
Tamias quadrimaculatus	long-eared chipmunk	85.2	ear tag(s) only	1996-1998	Pyare and Longland 2001
			toe-clip only	1975-1980	Sharples 1983
Tamias quadrivittatus	Colorado chipmunk	62.2	ear tag(s) plus	1983-1984	Bergstrom 1988
Tamias senex	Allen's chipmunk	89.3	toe-clip only	1975-1979	Sharples 1983
Tamias sibiricus	Siberian chipmunk	85.0	combo:hair/toe-clip	1973-1979	Kawamichi 1996

Tamias sibiricus	Siberian chipmunk	85.0	toe-clip only	1973-1979	Kawamichi 1989
Tamias speciosus	lodgepole chipmunk	62.0	ear tag(s) only	1996-1998	Pyare and Longland 2001
			toe-clip only	1975-1978	Sharples 1983
Tamias striatus	eastern chipmunk	111.9	combo:ear/hair	1990-1991	da Silva et al. 2002
			combo:hair/toe-clip or ear	1977	Getty 1981
			ear tag(s) only	1979	Shaffer 1980
			ear tag(s) only	1980-1993	Wolff 1996
			ear tag(s) only	1988	Bowers 1995
			ear tag(s) only	1991	Ostfeld et al. 1993
			ear tag(s) only	1996-1997	McShea et al. 2003
			ear tag(s) only	1999-2000	Glennon et al. 2002
			not indicated	1977	Lacki et al. 1984
			not indicated	1992-1996	Nupp and Swihart 2000
			toe-clip only	1975-1978	Mares et al. 1980
			toe-clip only	1978	Kitchings and Levy 1981
			toe-clip only	1978-1979	Mares et al. 1981
			toe-clip only	1981-1982	Lacher and Mares 1996
Tamias townsendii	Townsend's chipmunk	74.8	ear tag(s) only	1998	Manning and Edge 2004
			not indicated	1985	Carey and Witt 1991
			toe-clip only	1980-1982	Trombulak 1985
			toe-clip only	1981-1983	Doyle 1990
Tamias umbrinus	Uinta chipmunk	63.0	ear tag(s) plus	1983-1984	Bergstrom 1988
			toe-clip only	1975-1978	Andersen et al. 1980

Tamiasciurus douglasii	Douglas squirrel	225.0	combo:ear/hair	1974-1978	Koford 1982
			ear tag(s) only	1996-1998	Pyare and Longland 2001
			ear tag(s) only	1996-1999	Ransome and Sullivan 2004
			not marked	1985	Carey and Witt 1991
Tamiasciurus hudsonicus	eastern red squirrel	201.2	combo:ear/toe-clip	1974-1976	Riege 1991
			ear tag(s) only	1983-1986	Sullivan 1990
			ear tag(s) only	1990-1991	Dempsey and Keppie 1993
			ear tag(s) only	1992-1993	Ransome and Sullivan 1997
			ear tag(s) only	1995-1996	Wheatley et al. 2002
			ear tag(s) only	1999-2000	Glennon et al. 2002
			ear tag(s) only	2000-2001	Haughland and Larsen 2004
			not indicated	1959-1973	Halvorson and Engeman 1983
			not indicated	1965-1975	Keith and Cary 1991
			not indicated	1992-1996	Nupp and Swihart 2000
			radio only	1978-1980	Lair 1985
			radio only	1998-2000	Wirsing et al. 2002
			toe-clip only	1986	Belk et al. 1988
Tamiops macclellandi	Himalayan striped squirrel	55.5	toe-clip only	1997-1998	Adler et al. 1999
Thallomys nigricauda	black-tailed tree rat	124.7	radio only	2001	Eccard et al. 2004
Thomomys bottae	Botta's pocket gopher	114.7	not indicated	1980-1983	Daly and Patton 1986
			other	1978	Gettinger 1984
			toe-clip only	1975-1976	Bandoli 1981
Thomomys talpoides	northern pocket gopher	130.1	not indicated	1970-1973	Grant et al. 1982
			not indicated	1980-1981	Andersen 1982

Thomomys talpoides	northern pocket gopher	130.1	toe-clip only	1986	Belk et al. 1988
Thrichomys apereoides	punare	275.0	not indicated	1985	Lacher and Alho 1989
Tylomys nudicaudus	Peter's climbing rat	100.0	ear tag(s) only	1999	Caro et al. 2001
Tylomys watsoni	Watson's climbing rat	*	ear notch/punch	1998	Mangan and Adler 2000
Vandeleuria oleracea	Asiatic long-tailed climbing mouse	*	toe-clip only	1997-1998	Adler et al. 1999
Xerus inauris	South African ground squirrel	624.5	combo:ear/hair	1989-1991	Waterman 1996
Zapus hudsonius	meadow jumping mouse	17.1	combo:ear/toe-clip	1975-1976	Nichols and Conley 1982
			ear tag(s) only	1999-2000	Glennon et al. 2002
			toe-clip only	1976-1979	Muchlinski 1988
			toe-clip only	1981-1984	Clark et al. 1987
Zapus princeps	western jumping mouse	29.0	ear tag(s) only	1986	Douglass 1989
			ear tag(s) only	1998-2001	Hadley and Wilson 2004
			not indicated	1970-1973	Grant et al. 1982
			toe-clip only	1975-1978	Andersen et al. 1980
			toe-clip only	1986	Belk et al. 1988
Zapus trinotatus	Pacific jumping mouse	27.5	ear tag(s) only	1998	Manning and Edge 2004
			not indicated	1981-1983	Andersen and MacMahon 1985
			toe-clip only	1981-1983	Doyle 1990
Zygodontomys brevicauda	short-tailed cane mouse	52.2	toe-clip only	1976-1977	O'Connell 1989
Zyzomys argurus	silver-tailed rock rat	36.0	not indicated	1971-1973	Calaby and Taylor 1983
			toe-clip only	1981-1982	Bradley et al. 1988
Zyzomys woodwardi	Kimberly rock rat	136.0	not indicated	1971-1973	Calaby and Taylor 1983

Literature Cited for Appendix 1

Adams, R. A., B. J. Lengas, and M. Bekoff. 1987. Variations in avoidance responses to humans by black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Mammalogy 68:686-689.

Adler, G. H., S. A. Mangan, and V. Suntsov. 1999. Richness, abundance, and habitat relations of rodents in the Lang Bian Mountains of southern Viet Nam. Journal of Mammalogy 80:891-898.

Adler, G. H., M. L. Wilson, and M. J. Derosa. 1986. Influence of island area and isolation on population characteristics of *Peromyscus leucopus*. Journal of Mammalogy 67:406-409.

Aguilera, M. 1999. Population ecology of *Proechimys guairae* (Rodentia: Echimyidae). Journal of Mammalogy 80:487-498.

Alkon, P. U., and D. Saltz. 1988. Influence of season and moonlight on temporal-activity patterns of Indian crested porcupines (*Hystrix indica*). Journal of Mammalogy 69:71-80.

Althoff, D. P., and G. L. Storm. 1989. Daytime spatial characteristics of cottontail rabbits in central Pennsylvania. Journal of Mammalogy 70:820-824.

Andersen, D. C. 1982. Observations on *Thomomys talpoides* in the region affected by the eruption of Mount St. Helens. Journal of Mammalogy 63:652-655.

Andersen, D. C., and M. L. Folk. 1993. *Blarina brevicauda* and *Peromyscus leucopus* reduce overwinter survivorship of acorn weevils in an Indiana hardwood forest. Journal of Mammalogy 74:656-664.

Andersen, D. C., and J. A. MacMahon. 1985. The effects of catastrophic ecosystem disturbance: the residual mammals at Mount St. Helens. Journal of Mammalogy 66:581-589.

Andersen, D. C., J. A. MacMahon, and M. L. Wolfe. 1980. Herbivorous mammals along a montane sere: community structure and energetics. Journal of Mammalogy 61:500-519.

Andersen, D. C., K. R. Wilson, M. S. Miller, and M. Falck. 2000. Movement patterns of riparian small mammals during predictable floodplain inundation. Journal of Mammalogy 81:1087-1099.

Asher, M., E. S. de Oliveira, and N. Sachser. 2004. Social system and spatial organization of wild guinea pigs (*Cavia aperea*) in a natural population. Journal of Mammalogy 85:788-796.

Baird, D. D., and E. C. Birney. 1982. Pattern of colonization in *Microtus pennsylvanicus*. Journal of Mammalogy 63:290-293.

Baker, J. A., and R. J. Brooks. 1982. Impact of raptor predation on a declining vole population. Journal of Mammalogy 63:297-300.

Bandoli, J. H. 1981. Factors influencing seasonal burrowing activity in the pocket gopher, *Thomomys bottae*. Journal of Mammalogy 62:293-303.

Barbour, D. B., and S. R. Humphrey. 1982. Status and habitat of the Key Largo woodrat and cotton mouse (*Neotoma floridana smalli* and *Peromyscus gossypinus allapaticola*). Journal of Mammalogy 63:144-148.

Barnum, S. A., C. J. Manville, J. R. Tester, and W. J. Carmen. 1992. Path selection by *Peromyscus leucopus* in the presence and absence of vegetative cover. Journal of Mammalogy 73:797-801.

Barry, R. E., Jr., M. A. Botje, and L. B. Grantham. 1984. Vertical stratification of *Peromyscus leucopus* and *P. maniculatus* in southwestern Virginia. Journal of Mammalogy 65:145-148.

Barry, R. E., Jr., and E. N. Francq. 1980. Orientation to landmarks within the preferred habitat by *Peromyscus leucopus*. Journal of Mammalogy 61:292-303.

Batzli, G. O., and H. Henttonen. 1993. Home range and social organization of the singing vole (*Microtus miurus*). Journal of Mammalogy 74:868-878.

Beacham, T. D. 1980. Survival of large and small adults in fluctuating populations of *Microtus townsendii*. Journal of Mammalogy 61:551-555.

Beacham, T. D., and C. J. Krebs. 1980. Pitfall versus live-trapping enumeration of fluctuating populations of *Microtus townsendii*. Journal of Mammalogy 61:486-499.

Belk, M. C., H. D. Smith, and J. Lawson. 1988. Use and partitioning of montane habitat by small mammals. Journal of Mammalogy 69:688-695.

Bendel, P. R., and J. E. Gates. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). Journal of Mammalogy 68:243-255.

Bergallo, H. G., and W. E. Magnusson. 1999. Effects of climate and food availability on four rodent species in southeastern Brazil. Journal of Mammalogy 80:472-486.

Bergstrom, B. J. 1988. Home ranges of three species of chipmunks (*Tamias*) as assessed by radiotelemetry and grid trapping. Journal of Mammalogy 69:190-193.

Bertolino, S., P. J. Mazzoglio, M. Vaiana, and I. Currado. 2004. Activity budget and foraging behavior of introduced *Callosciurus finlaysonii* (Rodentia, Sciuridae) in Italy. Journal of Mammalogy 85:254-259.

Biggs, J. R., et al. 2000. Relationship of ecological variables to Sin Nombre Virus antibody seroprevalence in populations of deer mice. Journal of Mammalogy 81:676-682.

Blanchong, J. A., and L. Smale. 2000. Temporal patterns of activity of the unstriped Nile rat, *Arvicanthis niloticus*. Journal of Mammalogy 81:595-599.

Blaustein, A. R., and G. N. Fugle. 1981. Activity of *Reithrodontomys megalotis* in Santa Barbara, California. Journal of Mammalogy 62:195-199.

Blumstein, D. T., and W. Arnold. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). Journal of Mammalogy 79:873-886.

Blumstein, D. T., S. Im, A. Nicodemus, and C. Zugmeyer. 2004. Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. Journal of Mammalogy 85:25-29.

Boellstorff, D. E., and D. H. Owings. 1995. Home range, population structure, and spatial organization of California ground squirrels. Journal of Mammalogy 76:551-561.

Bond, M. L., and J. O. Wolff. 1999. Does access to females or competition among males limit male home-range size in a promiscuous rodent? Journal of Mammalogy 80:1243-1250.

Bowen, B. S. 1982. Temporal dynamics of microgeographic structure of genetic variation in *Microtus californicus*. Journal of Mammalogy 63:625-638.

Bowers, M. A. 1982. Foraging behavior of heteromyid rodents: field evidence of resource partitioning. Journal of Mammalogy 63:361-367.

Bowers, M. A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. Journal of Mammalogy 69:201-204.

Bowers, M. A. 1995. Use of space and habitats by the eastern chipmunk, *Tamias striatus*. Journal of Mammalogy 76:12-21.

Bowman, J., G. J. Forbes, and T. G. Dilworth. 2001. Spatial and temporal patterns of an irrupting population of deer mice. Journal of Mammalogy 82:567-572.

Bradley, A. J., C. M. Kemper, D. J. Kitchener, W. F. Humphreys, R. A. How, and L. H. Schmitt. 1988. Population ecology and physiology of the common rock rat, *Zyzomys argurus* (Rodentia: Muridae) in tropical northwestern Australia. Journal of Mammalogy 69:749-764.

Brady, M. J., and N. A. Slade. 2001. Diversity of a grassland rodent community at varying temporal scales: the role of ecologically dominant species. Journal of Mammalogy 82:974-983.

Brady, M. J., and N. A. Slade. 2004. Long-term dynamics of a grassland rodent community. Journal of Mammalogy 85:552-561.

Branch, L. C. 1993. Intergroup and intragroup spacing in the plains vizcacha, *Lagostomus maximus*. Journal of Mammalogy 74:890-900.

Branch, L. C., D. Villarreal, and G. S. Fowler. 1993. Recruitment, dispersal, and group fusion in a declining population of the plains vizcacha (*Lagostomus maximus*; Chinchillidae). Journal of Mammalogy 74:9-20.

Braude, S., and D. Ciszek. 1998. Survival of naked mole-rats marked by implantable transponders and toe-clipping. Journal of Mammalogy 79:360-363.

Braun, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. Journal of Mammalogy 66:1-12.

Briggs, J. M. 1986. Supplemental food and two island populations of *Peromyscus leucopus*. Journal of Mammalogy 67:474-480.

Briner, T., J-P. Airoldi, F. Dellsperger, S. Eggimann, and W. Nentwig. 2003. A new system for automatic radiotracking of small mammals. Journal of Mammalogy 84:571-578.

Brochu, L., L. Caron, and J-M. Bergeron. 1988. Diet quality and body condition of dispersing and resident voles (*Microtus pennsylvanicus*). Journal of Mammalogy 69:704-710.

Brock, R. E., and D. A. Kelt. 2004. Conservation and social structure of Stephens' kangaroo rat: implications from burrow-use behavior. Journal of Mammalogy 85:51-57.

Bronson, M. T. 1980. Altitudinal variation in emergence time of golden-mantled ground squirrels (*Spermophilus lateralis*). Journal of Mammalogy 61:124-126.

Brown, J. S., Y. Arel, Z. Abramsky, and B. P. Kotler. 1992. Patch use by gerbils (*Gerbillus allenbyi*) in sandy and rocky habitats. Journal of Mammalogy 73:821-829.

Brown, L. N. 1986. Sex-ratio bias among gray squirrels foraging at a single attractive seasonal food source. Journal of Mammalogy 67:582-583.

Brown, R. N., C. H. Southwick, and S. C. Golian. 1989. Male-female spacing, territorial replacement, and the mating system of pikas (*Ochotona princeps*). Journal of Mammalogy 70:622-627.

Buck, C. L., and B. M. Barnes. 1999a. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. Journal of Mammalogy 80:430-442.

Buck, C. L., and B. M. Barnes. 1999b. Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. Journal of Mammalogy 80:1264-1276.

Buckner, C. A., and D. J. Shure. 1985. The response of *Peromyscus* to forest opening size in the southern Appalachian Mountains. Journal of Mammalogy 66:299-307.

Burton, C., and C. J. Krebs. 2003. Influence of relatedness on snowshoe hare spacing behavior. Journal of Mammalogy 84:1100-1111.

Busch, C., A. I. Malizia, O. A. Scaglia, and O. A. Reig. 1989. Spatial distribution and attributes of a population of *Ctenomys talarum* (Rodentia: Octodontidae). Journal of Mammalogy 70:204-208.

Busher, P. E. 1987. Population parameters and family composition of beaver in California. Journal of Mammalogy 68:860-864.

Busher, P. E., R. J. Warner, and S. H. Jenkins. 1983. Population density, colony composition, and local movements in two Sierra Nevadan beaver populations. Journal of Mammalogy 64:314-318.

Calaby, J. H., and J. M. Taylor. 1983. Breeding in wild populations of the Australian rock rats, *Zyzomys argurus* and *Z. woodwardi*. Journal of Mammalogy 64:610-616.

Cameron, G. N. 1995. Temporal use of home range by the hispid cotton rat. Journal of Mammalogy 76:819-827.

Cameron, G. N., and S. R. Spencer. 1983. Field growth rates and dynamics of body mass for rodents on the Texas coastal prairie. Journal of Mammalogy 64:656-665.

Cameron, G. N., S. R. Spencer, B. D. Eshelman, L. R. Williams, and M. J. Gregory. 1988. Activity and burrow structure of Attwater's pocket gopher (*Geomys attwateri*). Journal of Mammalogy 69:667-677.

Campbell, M. T., and N. A. Slade. 1993. Effect of mass on seasonal survivorship of northern cotton rats. Journal of Mammalogy 74:971-981.

Carey, A. B., and J. W. Witt. 1991. Track counts as indices to abundances of arboreal rodents. Journal of Mammalogy 72:192-194.

Caro, T. M., M. J. Kelly, N. Bol, and S. Matola. 2001. Inventorying mammals at multiple sites in the Maya Mountains of Belize. Journal of Mammalogy 82:43-50.

Chambers, L. K., G. R. Singleton, and C. J. Krebs. 2000. Movements and social organization of wild house mice (*Mus domesticus*) in the wheatlands of northwestern Victoria, Australia. Journal of Mammalogy 81:59-69.

Cittadino, E. A., P. DeCarli, M. Busch, and F. O. Kravetz. 1994. Effects of food supplementation on rodents in winter. Journal of Mammalogy 75:446-453.

Clark, B. K., D. W. Kaufman, G. A. Kaufman, and E. J. Finck. 1987. Use of tallgrass prairie by *Peromyscus leucopus*. Journal of Mammalogy 68:158-160.

Cochran, G. R., and N. G. Solomon. 2000. Effects of food supplementation on the social organization of prairie voles (*Microtus ochrogaster*). Journal of Mammalogy 81:746-757.

Conner, D. A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy 63:48-52.

Coppola, D. M., and J. G. Vandenbergh. 1987. Induction of a puberty-regulating chemosignal in wild mouse populations. Journal of Mammalogy 68:86-91.

Cotton, C. L., and K. L. Parker. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. Journal of Mammalogy 81:1071-1086.

Cox, T. P. 1989. Odor-based discrimination between noncontiguous demes of wild *Mus*. Journal of Mammalogy 70:549-556.

Cramer, M. J., and M. R. Willig. 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sand-shinnery-oak landscape. Journal of Mammalogy 83:743-753.

Cranford, J. A. 1982. The effect of woodrat houses on population density of *Peromyscus*. Journal of Mammalogy 63:663-666.

Cully, J. F., Jr. 1997. Growth and life-history changes in Gunnison's prairie dogs after a plague epizootic. Journal of Mammalogy 78:146-157.

da Silva, K. B., C. Mahan, and J. da Silva. 2002. The trill of the chase: eastern chipmunks call to warn kin. Journal of Mammalogy 83:546-552.

Daly, J. C., and J. L. Patton. 1986. Growth, reproduction, and sexual dimorphism in *Thomomys bottae* pocket gophers. Journal of Mammalogy 67:256-265.

Danielson, B. J., and M. S. Gaines. 1987. Spatial patterns in two syntopic species of microtines: *Microtus ochrogaster* and *Synaptomys cooperi*. Journal of Mammalogy 68:313-322.

Danielson, B. J., M. L. Johnson, and M. S. Gaines. 1986. An analysis of a method for comparing residents and colonists in a natural population of *Microtus ochrogaster*. Journal of Mammalogy 67:733-736.

Danielson, B. J., and R. K. Swihart. 1987. Home range dynamics and activity patterns *Microtus ochrogaster* and *Synaptomys cooperi* in syntopy. Journal of Mammalogy 68:160-165.

Davidson, A. D., R. R. Parmenter, and J. R. Gosz. 1999. Responses of small mammals and vegetation to a reintroduction of Gunnison's prairie dogs. Journal of Mammalogy 80:1311-1324.

Davis, L. S., and J. O. Murie. 1985. Male territoriality and the mating system of Richardson's ground squirrels (*Spermophilus richardsonii*). Journal of Mammalogy 66:268-279.

Dempsey, J. A., and D. M Keppie. 1993. Foraging patterns of eastern red squirrels. Journal of Mammalogy 74:1007-1013.

Desy, E. A., G. O. Batzli, and L. Jike. 1989. Comparison of vole movements assessed by live trapping and radiotracking. Journal of Mammalogy 70:652-656.

Devenport, J. A. 1989. Social influences on foraging in black-tailed prairie dogs. Journal of Mammalogy 70:166-168.

Dobson, F. S. 1981. An experimental examination of an artificial dispersal sink. Journal of Mammalogy 62:74-81.

Dobson, F. S. 1983. Agonism and territoriality in the California ground squirrel. Journal of Mammalogy 64:218-225.

Dobson, F. S., R. K. Chesser, J. L. Hoogland, D. W. Sugg, and D. W. Foltz. 2004. The influence of social breeding groups on effective population size in black-tailed prairie dogs. Journal of Mammalogy 85:58-66.

Dobson, F. S., and D. E. Davis. 1986. Hibernation and sociality in the California ground squirrel. Journal of Mammalogy 67:416-421.

Douglass, R. J. 1989. The use of radio-telemetry to evaluate microhabitat selection by deer mice. Journal of Mammalogy 70:648-652.

Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy 71:14-23.

Drickamer, L. C. 1984. Captures of two species of *Peromyscus* at live traps baited with male and female odors. Journal of Mammalogy 65:699-702.

Drickamer, L. C. 1987. Influence of time of day on captures of two species of *Peromyscus* in a New England deciduous forest. Journal of Mammalogy 68:702-703.

Drickamer, L. C., G. A. Feldhamer, D. G. Mikesic, and C. M. Holmes. 1999. Trap-response heterogeneity of house mice (*Mus musculus*) in outdoor enclosures. Journal of Mammalogy 80:410-420.

Duquette, L. S., and J. S. Millar. 1995. Reproductive response of a tropical mouse, *Peromyscus mexicanus*, to changes in food availability. Journal of Mammalogy 76:592-602.

Eccard, J. A., J. Meyer, and J. Sundell. 2004. Space use, circadian activity pattern, and mating system of the nocturnal tree rat *Thallomys nigricauda*. Journal of Mammalogy 85:440-445.

Eifler, M. A., and N. A. Slade. 1999. Effect of weather on individual growth rates in cotton rats, *Sigmodon hispidus*. Journal of Mammalogy 80:1277-1287.

Eiler, K. C., and S. A. Banack. 2004. Variability in the alarm call of golden-mantled ground squirrels (*Spermophilus lateralis* and *S. saturatus*). Journal of Mammalogy 85:43-50.

Elias, S. P., J. W. Witham, and M. L. Hunter, Jr. 2004. *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. Journal of Mammalogy 85:743-747.

Ellison, L. E., and C. Van Riper, III. 1998. A comparison of small-mammal communities in a desert riparian floodplain. Journal of Mammalogy 79:972-985.

Emmons, L. H. 1981. Morphological, ecological, and behavioral adaptations for arboreal browsing in *Dactylomys dactylinus* (Rodentia, Echimyidae). Journal of Mammalogy 62:183-189.

Erlinge, S., I. Hoogenboom, J. Agrell, J. Nelson, and M. Sandell. 1990. Density-related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. Journal of Mammalogy 71:597-603.

Etheredge, D. R., M. D. Engstrom, and R. C. Stone, Jr. 1989. Habitat discrimination between sympatric populations of *Peromyscus attwateri* and *Peromyscus pectoralis* in west-central Texas. Journal of Mammalogy 70:300-307.

Extine, D. D., and I. J. Stout. 1987. Dispersion and habitat occupancy of the beach mouse, *Peromyscus polionotus niveiventris*. Journal of Mammalogy 68:297-304.

Fagerstone, K. A. 1988. The annual cycle of Wyoming ground squirrels in Colorado. Journal of Mammalogy 69:678-687.

Farentinos, R. C. 1980. Sexual solicitation of subordinate males by female tassel-eared squirrels (*Sciurus aberti*). Journal of Mammalogy 61:337-341.

Ferron, J. 1996. How do woodchucks (*Marmota monax*) cope with harsh winter conditions? Journal of Mammalogy 77:412-416.

Fleharty, E. D., and K. W. Navo. 1983. Irrigated cornfields as habitat for small mammals in the sandsage prairie region of western Kansas. Journal of Mammalogy 64:367-379.

Foltz, D. W., and J. L. Hoogland. 1981. Analysis of the mating system in the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. Journal of Mammalogy 62:706-712.

Foltz, D. W., J. L. Hoogland, and G. M. Koscielny. 1988. Effects of sex, litter size, and heterozygosity on juvenile weight in black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Mammalogy 69:611-614.

Fortier, G. M., and R. H. Tamarin. 1998. Movement of meadow voles in response to food and density manipulations: a test of the food-defense and pup-defense hypotheses. Journal of Mammalogy 79:337-345.

Frank, D. H., and E. J. Heske. 1992. Seasonal change in space use patterns in the southern grasshopper mouse, *Onychomys torridus torridus*. Journal of Mammalogy 73:292-298.

Frase, B. A., T. M. Pizzuto, and L. L. Getz. 1990. Survivorship of bled voles measured by recapture. Journal of Mammalogy 71:104-105.

Galindo-Leal, C. 1997. Infestation of rock mice (*Peromyscus difficilis*) by botflies: ecological consequences of differences between sexes. Journal of Mammalogy 78:900-907.

Garrett, M. G., and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy 69:236-250.

Gaulin, S. J. C., and R. W. FitzGerald. 1988. Home-range size as a predictor of mating systems in *Microtus*. Journal of Mammalogy 69:311-319.

Gavin, T. A., P. W. Sherman, E. Yensen, and B. May. 1999. Population genetic structure of the northern Idaho ground squirrel (*Spermophilus brunneus brunneus*). Journal of Mammalogy 80:156-168.

Geissel, W., H. Shellhammer, and H. T. Harvey. 1988. The ecology of the salt-marsh harvest mouse (*Reithrodontomys raviventris*) in a diked salt marsh. Journal of Mammalogy 69:696-703.

Gettinger, R. D. 1984. A field study of activity patterns of *Thomomys bottae*. Journal of Mammalogy 65:76-84.

Getty, T. 1981. Structure and dynamics of chipmunk home range. Journal of Mammalogy 62:726-737.

Getz, L. L. 1989. A 14-year study of *Blarina brevicauda* populations in east-central Illinois. Journal of Mammalogy 70:58-66.

Getz, L. L., J. E. Hofmann, B. McGuire, and T. W. Dolan, III. 2001. Twenty-five years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois. Journal of Mammalogy 82:22-34.

Getz, L. L., B. McGuire, T. Pizzuto, J. Hofmann, and B. Frase. 1993. Social organization of the prairie vole (*Microtus ochrogaster*). Journal of Mammalogy 74:44-58.

Giacalone, J., N. Wells, and G. Willis. 1987. Observations on *Syntheosciurus brochus* (Sciuridae) in Volcán Poás National Park, Costa Rica. Journal of Mammalogy 68:145-147.

Gillis, E. A., and C. J. Krebs. 1999. Natal dispersal of snowshoe hares during a cyclic population increase. Journal of Mammalogy 80:933-939.

Gipps, J. H. W. 1981. Behavior of bank voles, *Clethrionomys glareolus*, in the field. Journal of Mammalogy 62:382-384.

Glanz, W. E. 1984. Food and habitat use by two sympatric *Sciurus* species in central Panama. Journal of Mammalogy 65:342-347.

Glass, G. E., G. W. Korch, and J. E. Childs. 1988. Seasonal and habitat differences in growth rates of wild *Rattus norvegicus*. Journal of Mammalogy 69:587-592.

Glass, G. E., and N. A. Slade. 1980. Population structure as a predictor of spatial association between *Sigmodon hispidus* and *Microtus ochrogaster*. Journal of Mammalogy 61:473-485.

Glennon, M. J., W. F. Porter, and C. L. Demers. 2002. An alternative field technique for estimating diversity of small-mammal populations. Journal of Mammalogy 83:734-742.

Gockel, J., and T. Ruf. 2001. Alternative seasonal reproductive strategies in wild rodent populations. Journal of Mammalogy 82:1034-1046.

González, L., R. Murúa, and C. Jofré. 1989. The effect of seed availability on population density of *Oryzomys* in southern Chile. Journal of Mammalogy 70:401-403.

Goodyear, N. C. 1987. Distribution and habitat of the silver rice rat, *Oryzomys argentatus*. Journal of Mammalogy 68:692-695.

Goodyear, N. C. 1992. Spatial overlap and dietary selection of native rice rats and exotic black rats. Journal of Mammalogy 73:186-200.

Goundie, T. R., and S. H. Vessey. 1986. Survival and dispersal of young white-footed mice born in nest boxes. Journal of Mammalogy 67:53-60.

Grant, W. E., E. C. Birney, N. R. French, and D. M. Swift. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy 63:248-260.

Grant, W. E., P. E. Carothers, and L. A. Gidley. 1985. Small mammal community structure in the postoak savanna of east-central Texas. Journal of Mammalogy 66:589-594.

Gregory, M. J., and G. N. Cameron. 1988. Examination of socially induced dispersal in *Sigmodon hispidus*. Journal of Mammalogy 69:251-260.

Guichón, M. L., M. Borgnia, C. F. Righi, G. H. Cassini, and M. H. Cassini. 2003. Social behavior and group formation in the coypu (*Myocastor coypus*) in the Argentinean pampas. Journal of Mammalogy 84:254-262.

Gust, D. A., and D. J. Schmidly. 1986. Small mammal populations on reclaimed strip-mined areas in Freestone County, Texas. Journal of Mammalogy 67:214-217.

Hadley, G. L., and K. R. Wilson. 2004. Patterns of small mammal density and survival following ski-run development. Journal of Mammalogy 85:97-104.

Haken, A. E., and G. O. Batzli. 1996. Effects of availability of food and interspecific competition on diet of prairie voles (*Microtus ochrogaster*). Journal of Mammalogy 77:315-324.

Hall, A. T., P. E. Woods, and G. W. Barrett. 1991. Population dynamics of the meadow vole (*Microtus pennsylvanicus*) in nutrient-enriched old-field communities. Journal of Mammalogy 72:332-342.

Halvorson, C. H., and R. M. Engeman. 1983. Survival analysis for a red squirrel population. Journal of Mammalogy 64:332-336.

Hanley, T. A., and J. C. Barnard. 1999. Spatial variation in population dynamics of Sitka mice in floodplain forests. Journal of Mammalogy 80:866-879.

Hanski, I. K., P. C. Stevens, P. Ihalempiä, and V. Selonen. 2000. Home-range size, movements, and nest-site use in the Siberian flying squirrel, *Pteromys volans*. Journal of Mammalogy 81:798-809.

Hare, J. F., and J. O. Murie. 1992. Manipulation of litter size reveals no cost of reproduction in Columbian ground squirrels. Journal of Mammalogy 73:449-454.

Harper, S. J., and G. O. Batzli. 1996. Monitoring use of runways by voles with passive integrated transponders. Journal of Mammalogy 77:364-369.

Harper, S. J., E. K. Bollinger, and G. W. Barrett. 1993. Effects of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). Journal of Mammalogy 74:1045-1055.

Harris, J. C. 1987. Variation in the caudal fat deposit of *Microdipodops megacephalus*. Journal of Mammalogy 68:58-63.

Harris, J. H., and P. Leitner. 2004. Home-range size and use of space by adult Mohave ground squirrels, *Spermophilus mohavensis*. Journal of Mammalogy 85:517-523.

Haughland, D. L., and K. W. Larsen. 2004. Ecology of North American squirrels across contrasting habitats: relating natal dispersal to habitat. Journal of Mammalogy 85:225-236.

Havelka, M. A., and J. S. Millar. 1997. Sex ratio of offspring in *Peromyscus maniculatus borealis*. Journal of Mammalogy 78:626-637.

Havelka, M. A., and J. S. Millar. 2004. Maternal age drives seasonal variation in litter size of *Peromyscus leucopus*. Journal of Mammalogy 85:940-947.

Heideman, P. D., L. R. Heaney, R. L. Thomas, and K. R. Erickson. 1987. Patterns of faunal diversity and species abundance of non-volant small mammals on Negros Island, Philippines. Journal of Mammalogy 68:884-888.

Hersh, S. L. 1981. Ecology of the Key Largo woodrat (*Neotoma floridana smalli*). Journal of Mammalogy 62:201-206.

Heske, E. J. 1987. Responses of a population of California voles, *Microtus californicus*, to odor-baited traps. Journal of Mammalogy 68:64-72.

Heske, E. J., R. S. Ostfeld, and W. Z. Lidicker, Jr. 1984. Competitive interactions between *Microtus californicus* and *Reithrodontomys megalotis* during two peaks of *Microtus* abundance. Journal of Mammalogy 65:271-280.

Heske, E. J., G. I. Shenbrot, and K. A. Rogovin. 1995. Spatial organization of *Stylodipus telum* (Dipodidae, Rodentia) in Dagestan, Russia. Journal of Mammalogy 76:800-808.

Hicks, N. G., M. A. Menzel, and J. Laerm. 1998. Biases in the determination of temporal activity patterns of syntopic *Peromyscus* in the southern Appalachians. Journal of Mammalogy 79:1016-1020.

Hoffmann, I. E., E. Millesi, S. Huber, L. G. Everts, and J. P. Dittami. 2003. Population dynamics of European ground squirrels (*Spermophilus citellus*) in a suburban area. Journal of Mammalogy 84:615-626.

Hoogland, J. L. 1997. Duration of gestation and lactation for Gunnison’s prairie dogs. Journal of Mammalogy 78:173-180.

Hoogland, J. L. 1998. Estrus and copulation of Gunnison's prairie dogs. Journal of Mammalogy 79:887-897.

Hoogland, J. L. 1999. Philopatry, dispersal, and social organization of Gunnison's prairie dogs. Journal of Mammalogy 80:243-251.

Hoogland, J. L. 2001. Black-tailed, Gunnison’s, and Utah prairie dogs reproduce slowly. Journal of Mammalogy 82:917-927.

Hoogland, J. L. 2003. Sexual dimorphism of prairie dogs. Journal of Mammalogy 84:1254-1266.

Horne, E. A., M. McDonald, and O. J. Reichman. 1998. Changes in cache contents over winter in artificial dens of the eastern woodrat (*Neotoma floridana*). Journal of Mammalogy 79:898-905.

Humphrey, S. R. 1988. Density estimates of the endangered Key Largo woodrat and cotton mouse (*Neotoma floridana smalli* and *Peromyscus gossypinus allapaticola*), using the nested-grid approach. Journal of Mammalogy 69:524-531.

Humphrey, S. R., and D. B. Barbour. 1981. Status and habitat of three subspecies of *Peromyscus polionotus* in Florida. Journal of Mammalogy 62:840-844.

Ilan, M., and Y. Yom-Tov. 1990. Diel activity pattern of a diurnal desert rodent, *Psammomys obesus*. Journal of Mammalogy 71:66-69.

Iriarte, J. A., L. C. Contreras, and F. M. Jaksić. 1989. A long-term study of a small-mammal assemblage in the central Chilean matorral. Journal of Mammalogy 70:79-87.

Jacquot, J. J., and N. G. Solomon. 2004. Experimental manipulation of territory occupancy: effects of immigration of female prairie voles. Journal of Mammalogy 85:1009-1014.

Jacquot, J. J., and S. H. Vessey. 1998. Recruitment in white-footed mice (*Peromyscus leucopus*) as a function of litter size, parity, and season. Journal of Mammalogy 79:312-319.

Jaksić, F. M., J. L. Yanez, and E. R. Fuentes. 1981. Assessing a small mammal community in central Chile. Journal of Mammalogy 62:391-396.

Jannett, F. J., Jr. 1982. Nesting patterns of adult voles, *Microtus montanus*, in field populations. Journal of Mammalogy 63:495-498.

Jenkins, S. H., and J. B. Llewellyn. 1981. Multiple captures of *Peromyscus*: age, sex, and species differences. Journal of Mammalogy 62:639-641.

Jett, D. A., and J. D. Nichols. 1987. A field comparison of nested grid and trapping web density estimators. Journal of Mammalogy 68:888-892.

Jike, L., G. O. Batzli, and L. L. Getz. 1988. Home ranges of prairie voles as determined by radiotracking and by powdertracking. Journal of Mammalogy 69:183-186.

Jimenez, J. E., P. Feinsinger, and F. M. Jaksić. 1992. Spatiotemporal patterns of an irruption and decline of small mammals in northcentral Chile. Journal of Mammalogy 73:356-364.

Johannesen, E., H. P. Andreassen, and H. Steen. 1997. Effect of radiocollars on survival of root voles. Journal of Mammalogy 78:638-642.

Johnson, D. R., N. C. Nydegger, and G. W. Smith. 1987. Comparison of movement-based density estimates for Townsend ground squirrels in southwestern Idaho. Journal of Mammalogy 68:689-691.

Johnson, R. J., W. H. Ferguson, A. S. van Jaarsveld, G. N. Bronner, and C. T. Chimimba. 2002. Delayed responses of small-mammal assemblages subject to afforestation-induced grassland fragmentation. Journal of Mammalogy 83:290-300.

Jones, E. N. 1990. Effects of forage availability on home range and population density of *Microtus pennsylvanicus*. Journal of Mammalogy 71:382-389.

Jones, W. T. 1988. Variation in sex ratios of banner-tailed kangaroo rats in relation to population density. Journal of Mammalogy 69:303-310.

Jones, W. T. 1989. Dispersal distance and the range of nightly movements in Merriam's kangaroo rat. Journal of Mammalogy 70:27-34

Jorgensen, E. E., and S. Demarais. 1999. Spatial scale dependence of rodent habitat use. Journal of Mammalogy 80:421-429.

Kalcounis-Rüppell, M. C., and J. S. Millar. 2002. Partitioning of space, food, and time by syntopic *Peromyscus boylii* and *P. californicus*. Journal of Mammalogy 83:614-625.

Kantola, A. T., and S. R. Humphrey. 1990. Habitat use by Sherman's fox squirrel (*Sciurus niger shermani*) in Florida. Journal of Mammalogy 71:411-419.

Kaufman, D. W., and G. A. Kaufman. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy 63:309-312.

Kaufman, D. W., M. E. Peak, and G. A. Kaufman. 1985. *Peromyscus leucopus* in riparian woodlands: use of trees and shrubs. Journal of Mammalogy 66:139-143.

Kaufman, G. A. 1989. Use of fluorescent pigments to study social interactions in a small nocturnal rodent, *Peromyscus maniculatus*. Journal of Mammalogy 70:171-174.

Kaufman, G. A., and D. W. Kaufman. 1994. Changes in body mass related to capture in the prairie deer mouse (*Peromyscus maniculatus*). Journal of Mammalogy 75:681-691.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

Kawamichi, M. 1989. Nest structure dynamics and seasonal use of nests by Siberian chipmunks (*Eutamias sibiricus*). Journal of Mammalogy 70:44-57.

Kawamichi, M. 1996. Ecological factors affecting annual variation in commencement of hibernation in wild chipmunks (*Tamias sibiricus*). Journal of Mammalogy 77:731-744.

Keesing, F. 1998. Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. Journal of Mammalogy 79:919-931.

Keinath, D. A., and G. D. Hayward. 2003. Red-backed vole (*Clethrionomys gapperi*) response to disturbance in subalpine forests: use of regenerating patches. Journal of Mammalogy 84:956-966.

Keith, L. B., and J. R. Cary. 1991. Mustelid, squirrel, and porcupine population trends during a snowshoe hare cycle. Journal of Mammalogy 72:373-378.

Keith, T. P., and R. H. Tamarin. 1981. Genetic and demographic differences between dispersers and residents in cycling and noncycling vole populations. Journal of Mammalogy 62:713-725.

Kelt, D. A., P. L. Meserve, and B. K. Lang. 1994. Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. Journal of Mammalogy 75:890-904.

Kenagy, G. J., R. A. Vásquez, B. M. Barnes, and F. Bozinovic. 2004. Microstructure of summer activity bouts of degus in a thermally heterogeneous habitat. Journal of Mammalogy 85:260-267.

Kincaid, W. B., and G. N. Cameron. 1982. Effects of species removal on resource utilization in a Texas rodent community. Journal of Mammalogy 63:229-235.

Kitchings, J. T., and D. J. Levy. 1981. Habitat patterns in a small mammal community. Journal of Mammalogy 62:814-820.

Kjolhaug, M. S., and A. Woolf. 1988. Home range of the swamp rabbit in southern Illinois. Journal of Mammalogy 69:194-197.

Klaas, B. A., B. J. Danielson, and K. A. Maloney. 1998. Influence of pocket gophers on meadow voles in a tallgrass prairie. Journal of Mammalogy 79:942-952.

Koeppl, J. W., N. A. Slade, and R. W. Turner. 1981. Allochronic associations of *Rattus exulans*. Journal of Mammalogy 62:557-567.

Koford, R. R. 1982. Mating system of a territorial tree squirrel (*Tamiasciurus douglasii*) in California. Journal of Mammalogy 63:274-283.

Koprowski, J. L. 1991. Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. Journal of Mammalogy 72:367-372.

Koprowski, J. L. 1992. Removal of copulatory plugs by female tree squirrels. Journal of Mammalogy 73:572-576.

Koprowski, J. L. 1996. Natal philopatry, communal nesting, and kinship in fox squirrels and gray squirrels. Journal of Mammalogy 77:1006-1016.

Koprowski, J. L., J. L. Roseberry, and W. D. Klimstra. 1988. Longevity records for the fox squirrel. Journal of Mammalogy 69:383-384.

Kotler, B. P. 1984. Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents. Journal of Mammalogy 65:91-96.

Kotler, B. P. 1985a. Microhabitat utilization in desert rodents: a comparison of two methods of measurement. Journal of Mammalogy 66:374-378.

Kotler, B. P. 1985b. Owl predation on desert rodents which differ in morphology and behavior. Journal of Mammalogy 66:824-828.

Kotler, B. P., J. S. Brown, and W. A. Mitchell. 1993. Environmental factors affecting patch use in two species of gerbilline rodents. Journal of Mammalogy 74:614-620.

Krohne, D. T., and R. Baccus. 1985. Genetic and ecological structure of a population of *Peromyscus leucopus*. Journal of Mammalogy 66:529-537.

Kruchek, B. L. 2004. Use of tidal marsh and upland habitats by the marsh rice rat (*Oryzomys palustris*). Journal of Mammalogy 85:569-575.

Kunkele, J. 1992. Infanticide in wild rabbits (*Oryctolagus cuniculus*). Journal of Mammalogy 73:317-320.

Kuo, C-C., and L-L. Lee. 2003. Food availability and food habits of Indian giant flying squirrels (*Petaurista philippensis*) in Taiwan. Journal of Mammalogy 84:1330-1340.

Kuvlesky, W. P., Jr., and L. B. Keith. 1983. Demography of snowshoe hare populations in Wisconsin. Journal of Mammalogy 64:233-244.

Lacey, E. A., S. H. Braude, and J. R. Wieczorek. 1997. Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). Journal of Mammalogy 78:556-562.

Lacey, E. A., S. H. Braude, and J. R. Wieczorek. 1998. Solitary burrow use by adult Patagonian tuco-tucos (*Ctenomys haigi*). Journal of Mammalogy 79:986-991.

Lacher, T. E., Jr., and C. J. R. Alho. 1989. Microhabitat use among small mammals in the Brazilian Pantanal. Journal of Mammalogy 70:396-401.

Lacher, T. E., Jr., and M. A. Mares. 1996. Availability of resources and use of space in eastern chipmunks. Journal of Mammalogy 77:833-849.

Lacki, M. J., M. J. Gregory, and P. K. Williams. 1984. Summer activity of *Tamias striatus* in response to supplemented food. Journal of Mammalogy 65:521-524.

Lair, H. 1985. Length of gestation in the red squirrel, *Tamiasciurus hudsonicus*. Journal of Mammalogy 66:809-810.

Lambert, T. D., and G. H. Adler. 2000. Microhabitat use by a tropical forest rodent, *Proechimys semispinosus*, in central Panama. Journal of Mammalogy 81:70-76.

Lancia, R. A., W. E. Dodge, and J. S. Larson. 1982. Winter activity patterns of two radio-marked beaver colonies. Journal of Mammalogy 63:598-606.

Larson, D., and H. F. Howe. 1987. Dispersal and destruction of *Virola surinamensis* seeds by agoutis: appearance and reality. Journal of Mammalogy 68:859-860.

Layne, J. N., and M. A. V. Raymond. 1994. Communal nesting of southern flying squirrels in Florida. Journal of Mammalogy 75:110-120.

Lehmer, E. M., B. Van Horne, B. Kulbartz, and G. L. Florant. 2001. Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Mammalogy 82:551-557.

Lemen, C. A., and P. W. Freeman. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammalogy 66:134-136.

Lenington, S., and P. Franks. 1985. Trappability of wild house mice under conditions of confinement in relation to T-locus genotype and other variables. Journal of Mammalogy 66:145-148.

Lewellen, R. H., and S. H. Vessey. 1999. Estimating densities of *Peromyscus leucopus* using live-trap and nestbox censuses. Journal of Mammalogy 80:400-409.

Lin, Y. K., and G. O. Batzli. 1995. Predation on voles: an experimental approach. Journal of Mammalogy 76:1003-1012.

Lin, Y. K., and G. O. Batzli. 2004. Movement of voles across habitat boundaries: effects of food and cover. Journal of Mammalogy 85:216-224.

Lin, Y. K., L. D. Hayes, and N. G. Solomon. 2004. Effects of female immigrants on demography and social organization of prairie vole (*Microtus ochrogaster*) populations. Journal of Mammalogy 85:781-787.

Linders, M. J., S. D. West, and W. M. Vander Haegen. 2004. Seasonal variability in the use of space by western gray squirrels in southcentral Washington. Journal of Mammalogy 85:511-516.

Lishak, R. S. 1982a. Gray squirrel mating calls: a spectrographic and ontogenic analysis. Journal of Mammalogy 63:661-663.

Lishak, R. S. 1982b. Vocalizations of nestling gray squirrels. Journal of Mammalogy 63:446-452.

Lishak, R. S. 1984. Alarm vocalizations of adult gray squirrels. Journal of Mammalogy 65:681-684.

Litvaitis, J. A. 1990. Differential habitat use by sexes of snowshoe hares (*Lepus americanus*). Journal of Mammalogy 71:520-523.

Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy 80:460-471.

Löfgren, O. 1995. Niche expansion and increased maturation rate of *Clethrionomys glareolus* in the absence of competitors. Journal of Mammalogy 76:1100-1112.

Lombardi, L., N. Fernández, S. Moreno, and R. Villafuerte. 2003. Habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. Journal of Mammalogy 84:26-36.

Longland, W. S., and S. H. Jenkins. 1987. Sex and age affect vulnerability of desert rodents to owl predation. Journal of Mammalogy 68:746-754.

Loughry, W. J. 1989. Discrimination of snakes by two populations of black-tailed prairie dogs. Journal of Mammalogy 70:627-30.

Loy, A., E. Dupré, and E. Capanna. 1994. Territorial behavior in *Talpa romana*, a fossorial insectivore from southcentral Italy. Journal of Mammalogy 75:529-535.

Ludwig, D. R. 1988. Reproduction and population dynamics of the water vole, *Microtus richardsoni*. Journal of Mammalogy 69:532-541.

Luo, J., V. Monamy, and B. J. Fox. 1998. Competition between two Australian rodent species: a regression analysis. Journal of Mammalogy 79:962-971.

Mabry, K. E., E. A. Dreelin, and G. W. Barrett. 2003. Influence of landscape elements on population densities and habitat use of three small-mammal species. Journal of Mammalogy 84:20-25.

MacArthur, R. A. 1992. Foraging range and aerobic endurance of muskrats diving under ice. Journal of Mammalogy 73:565-569.

Madison, D. M. 1981. Time patterning of nest visitation by lactating meadow voles. Journal of Mammalogy 62:389-391.

Maher, C. R. 2004. Intrasexual territoriality in woodchucks (*Marmota monax*). Journal of Mammalogy 85:1087-1094.

Malcolm, J. R. 1991. Comparative abundances of neotropical small mammals by trap height. Journal of Mammalogy 72:188-192.

Maly, M. S., B. A. Knuth, and G. W. Barrett. 1985. Effects of resource partitioning on dispersal behavior of feral house mice. Journal of Mammalogy 66:148-153.

Mangan, S. A., and G. H. Adler. 2000. Consumption of arbuscular mycorrhizal fungi by terrestrial and arboreal small mammals in a Panamanian cloud forest. Journal of Mammalogy 81:563-570.

Mankin, P. C., and L. L. Getz. 1994. Burrow morphology as related to social organization of *Microtus ochrogaster*. Journal of Mammalogy 75:492-499.

Mankin, P. C., and R. E. Warner. 1999. Responses of eastern cottontails to intensive row-crop farming. Journal of Mammalogy 80:940-949.

Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. Journal of Mammalogy 85:87-96.

Manning, T., W. D. Edge, and J. O. Wolff. 1995. Evaluating population-size estimators: an empirical approach. Journal of Mammalogy 76:1149-1158.

Manville, C. J., S. A. Barnum, and J. R. Tester. 1992. Influence of bait on arboreal behavior of *Peromyscus leucopus*. Journal of Mammalogy 73:335-336.

Mares, M. A., and K. A. Ernest. 1995. Population and community ecology of small mammals in a gallery forest of central Brazil. Journal of Mammalogy 76:750-768.

Mares, M. A., K. E. Streilein, and M. R. Willig. 1981. Experimental assessment of several population estimation techniques on an introduced population of eastern chipmunks. Journal of Mammalogy 62:315-328.

Mares, M. A., M. R. Willig, and N. A. Bitar. 1980. Home range size in eastern chipmunks, *Tamias striatus*, as a function of number of captures: statistical biases of inadequate sampling. Journal of Mammalogy 61:661-669.

Marinelli, L., F. Messier, and Y. Plante. 1997. Consequences of following a mixed reproductive strategy in muskrats. Journal of Mammalogy 78:163-178.

Matlack, R. S., D. W. Kaufman, G. A. Kaufman, and B. R. McMillan. 2002. Long-term variation in abundance of Elliot's short-tailed shrew (*Blarina hylophaga*) in tallgrass prairie. Journal of Mammalogy 83:280-289.

McCay, T. S. 2000. Use of woody-debris by cotton mice (*Peromyscus gossypinus*) in a southeastern pine forest. Journal of Mammalogy 81:527-535.

McClenaghan, L. R., and E. Taylor. 1993. Temporal and spatial demographic patterns in *Dipodomys stephensi* from Riverside County, California. Journal of Mammalogy 74:636-645.

McCracken, K. E., J. W. Witham, and M. L. Hunter, Jr. 1999. Relationships between seed fall of three tree species and *Peromyscus leucopus* and *Clethrionomys gapperi* during 10 years in an oak-pine forest. Journal of Mammalogy 80:1288-1296.

McDonald, I. R., A. K. Lee, K. A. Than, and R. W. Martin. 1988. Concentration of free glucocorticoids in plasma and mortality in the Australian bush rat (*Rattus fuscipes* Waterhouse). Journal of Mammalogy 69:740-748.

M'Closkey, R. T. 1983. *Perognathus baileyi* and jojoba (*Simmondsia chinensi*): a test of their association. Journal of Mammalogy 64:499-501.

McShea, W. J., and A. B. Gilles. 1992. A comparison of traps and fluorescent powder to describe foraging for mast by *Peromyscus leucopus*. Journal of Mammalogy 73:218-222.

McShea, W. J., and D. M. Madison. 1989. Measurements of reproductive traits in a field population of meadow voles. Journal of Mammalogy 70:132-141.

McShea, W. J., J. Pagels, J. Orrock, E. Harper, and K. Koy. 2003. Mesic deciduous forest as patches of small-mammal richness within an Appalachian Mountain forest. Journal of Mammalogy 84:627-643.

Meier, P. T. 1991. Response of adult woodchucks (*Marmota monax*) to oral-gland scents. Journal of Mammalogy 72:622-624.

Mellink, E. M., and H. Madrigal. 1993. Ecology of Mexican prairie dogs, *Cynomys mexicanus*, in El Manantial, northeastern Mexico. Journal of Mammalogy 74:631-635.

Menkens, G. E., Jr., and S. H. Anderson. 1991. Population dynamics of white-tailed prairie dogs during an epizootic of sylvatic plague. Journal of Mammalogy 72:328-331.

Merritt, J. F. 1986. Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*) in an Appalachian montane forest. Journal of Mammalogy 67:450-464.

Merritt, J. F. 1995. Seasonal thermogenesis and changes in body mass of masked shrews, *Sorex cinereus*. Journal of Mammalogy 76:1020-1035.

Merritt, J. F., D. A. Zegers, and L. R. Rose. 2001. Seasonal thermogenesis of southern flying squirrels (*Glaucomys volans*). Journal of Mammalogy 82:51-64.

Meserve, P. L., D. R. Martinez, J. R. Rau, R. Murúa, B. K. Lang, and A. Muñoz-Pedreros. 1999. Comparative demography and diversity of small mammals in precordilleran temperate rainforests of southern Chile. Journal of Mammalogy 80:880-890.

Meserve, P. L., R. Murúa, O. Lopetegui, and J. R. Rau. 1982. Observations on the small mammal fauna of a primary temperate rain forest in southern Chile. Journal of Mammalogy 63:315-317.

Michener, G. R. 1984. Sexual differences in body weight patterns of Richardson's ground squirrels during the breeding season. Journal of Mammalogy 65:59-66.

Michener, G. R. 1985. Chronology of reproductive events for female Richardson's ground squirrels. Journal of Mammalogy 66:280-288.

Michener, G. R. 1993. Lethal myiasis of Richardson’s ground squirrels by the sarcophagid fly, *Neobellieria citellivora*. Journal of Mammalogy 74:148-155.

Michener, G. R. 2002. Seasonal use of subterranean sleep and hibernation sites by adult female Richardson’s ground squirrels. Journal of Mammalogy 83:999-1012.

Michener, G. R., and L. Locklear. 1990. Over-winter weight loss by Richardson's ground squirrels in relation to sexual differences in mating effort. Journal of Mammalogy 71:489-499.

Millar, J. S., and E. M. Derrickson. 1992. Group nesting in *Peromyscus maniculatus*. Journal of Mammalogy 73:403-407.

Millesi, E., A. M. Strijkstra, I. E. Hoffmann, J. P. Dittami, and S. Daan. 1999. Sex and age differences in mass, morphology, and annual cycle in European ground squirrels, *Spermophilus citellus*. Journal of Mammalogy 80:218-231.

Monamy, V., and B. J. Fox. 1999. Habitat selection by female *Rattus lutreolus* drives asymmetric competition and coexistence with *Pseudomys higginsi*. Journal of Mammalogy 80:232-242.

Morzillo, A. T., G. A. Feldhamer, and M. C. Nicholson. 2003. Home range and nest use of the golden mouse (*Ochrotomys nuttalli*) in southern Illinois. Journal of Mammalogy 84:553-560.

Moses, R. A., G. J. Hickling, and J. S. Millar. 1995. Variation in sex ratios of offspring in wild bushy-tailed woodrats. Journal of Mammalogy 76:1047-1055.

Muchlinski, A. E. 1988. Population attributes related to the life-history strategy of hibernating *Zapus hudsonius*. Journal of Mammalogy 69:860-865.

Muchlinski, A. E., B. C. Baldwin, and R. Gramajo. 2000. Endotoxin elicits a febrile response in laboratory maintained but not free-living California ground squirrels. Journal of Mammalogy 81:701-708.

Mullican, T. R., and J. T. Baccus. 1990. Horizontal and vertical movements of the white-ankled mouse (*Peromyscus pectoralis*) in central Texas. Journal of Mammalogy 71:378-381.

Murie, J. O. 1992. Predation by badgers on Columbian ground squirrels. Journal of Mammalogy 73:385-394.

Murie, J. O., and D. A. Boag. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. Journal of Mammalogy 65:688-690.

Murie, J. O., D. A. Boag, and V. K. Kivett. 1980. Litter size in Columbian ground squirrels (*Spermophilus columbianus*). Journal of Mammalogy 61:237-244.

Murie, J. O., and M. A. Harris. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (*Spermophilus columbianus*). Journal of Mammalogy 63:431-439.

Murúa, R., P. L. Meserve, L. A. González, and C. Jofré. 1987. The small mammal community of a Chilean temperate rain forest: lack of evidence of competition between dominant species. Journal of Mammalogy 68:729-738.

Neuhaus, P. 2000. Timing of hibernation and molt in female Columbian ground squirrels. Journal of Mammalogy 81:571-577.

Nichols, J. D., and W. Conley. 1982. Active-season dynamics of a population of *Zapus hudsonius* in Michigan. Journal of Mammalogy 63:422-430.

Novak, J. M. 1983. Multiple captures of *Peromyscus leucopus*: social behavior in a small rodent. Journal of Mammalogy 64:710-713.

Nunes, S., and K. E. Holekamp. 1996. Mass and fat influence the timing of natal dispersal in Belding's ground squirrels. Journal of Mammalogy 77:807-817.

Nupp, T. E., and R. K. Swihart. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. Journal of Mammalogy 81:512-526.

O'Connell, M. A. 1989. Population dynamics of neotropical small mammals in seasonal habitats. Journal of Mammalogy 70:532-548.

O'Farrell, M. J. 1980. Spatial relationships of rodents in a sagebrush community. Journal of Mammalogy 61:589-605.

O’Farrell, M. J., W. A. Clark, F. H. Emmerson, S. M. Juarez, F. R. Kay, T. M. O’Farrell, and T. Y. Goodlett. 1994. Use of mesh live trap for small mammals: are results from Sherman live traps deceptive? Journal of Mammalogy 75:692-699.

Ojeda, R. A. 1989. Small-mammal responses to fire in the Monte Desert, Argentina. Journal of Mammalogy 70:416-420.

Ortega, J. C. 1990a. Home-range size of adult rock squirrels (*Spermophilus variegatus*) in southeastern Arizona. Journal of Mammalogy 71:171-176.

Ortega, J. C. 1990b. Reproductive biology of the rock squirrel (*Spermophilus variegatus*) in southeastern Arizona. Journal of Mammalogy 71:448-457.

Ostfeld, R. S., and L. L. Klosterman. 1986. Demographic substructure in a California vole population inhabiting a patchy environment. Journal of Mammalogy 67:693-704.

Ostfeld, R. S., and R. H. Manson. 1996. Long-distance homing in meadow voles, *Microtus pennsylvanicus*. Journal of Mammalogy 77:870-873.

Ostfeld, R. S., M. C. Miller, and K. R. Hazler. 1996. Causes and consequences of tick (*Ixodes scapularis*) burdens on white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 77:266-273.

Ostfeld, R. S., M. C. Miller, and J. Schnurr. 1993. Eartagging increases tick (*Ixodes dammini*) infestation rates of white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 74:651-655.

Packer, C. 1983. Demographic changes in a colony of Nile grassrats (*Arvicanthis niloticus*) in Tanzania. Journal of Mammalogy 64:159-161.

Parren, S. G., and D. E. Capen. 1985. Local distribution and coexistence of two species of *Peromyscus* in Vermont. Journal of Mammalogy 66:36-44.

Peles, J. D., and G. W. Barrett. 1996. Effects of vegetative cover on the population dynamics of meadow voles. Journal of Mammalogy 77:857-869.

Peles, J. D., M. F. Lucas, and G. W. Barrett. 1995. Population dynamics of agouti and albino meadow voles in high-quality grassland habitats. Journal of Mammalogy 76:1013-1019.

Perri, L. M., and J. A. Randall. 1999. Behavioral mechanisms of coexistence in sympatric species of desert rodents, *Dipodomys ordii* and *D. merriami*. Journal of Mammalogy 80:1297-1310.

Pfeifer, S. R. 1982. Variability in reproductive output and success of *Spermophilus elegans* ground squirrels. Journal of Mammalogy 63:284-289.

Price, M. V., P. A. Kelly, and R. L. Goldingay. 1994. Distances moved by Stephen's kangaroo rat (*Dipodomys stephensi* Merriam) and implications for conservation. Journal of Mammalogy 75:929-939.

Price, M. V., N. M. Waser, and T. A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65:353-356.

Pugh, S. R., and R. S. Ostfeld. 1998. Effects of prior population density on use of space by meadow voles, *Microtus pennsylvanicus*. Journal of Mammalogy 79:551-557.

Pyare, S., and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681-689.

Rado, R., Z. Wollberg, and J. Terkel. 1992. Dispersal of young mole rats (*Spalax ehrenbergi*) from the natal burrow. Journal of Mammalogy 73:885-890.

Ramirez, P., Jr., and M. Hornocker. 1981. Small mammal populations in different-aged clearcuts in northwestern Montana. Journal of Mammalogy 62:400-403.

Randall, J. A. 1989. Territorial-defense interactions with neighbors and strangers in banner-tailed kangaroo rats. Journal of Mammalogy 70:308-315.

Ransome, D. B., and T. P. Sullivan. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. Journal of Mammalogy 78:538-539.

Ransome, D. B., and T. P. Sullivan. 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglassii*. Journal of Mammalogy 85:206-215.

Rave, E. H., and N. R. Holler. 1992. Population dynamics of beach mice (*Peromyscus polionotus ammobates*) in southern Alabama. Journal of Mammalogy 73:347-355.

Rayor, L. S. 1985. Dynamics of a plague outbreak in Gunnison's prairie dog. Journal of Mammalogy 66:194-196.

Rehmeier, R. L., G. A. Kaufman, and D. W. Kaufman. 2004. Long-distance movements of the deer mouse in tallgrass prairie. Journal of Mammalogy 85:562-568.

Reich, L. M., and R. H. Tamarin. 1984. Multiple capture trap associations of meadow voles (*Microtus pennsylvanicus*). Journal of Mammalogy 65:85-90.

Rezsutek, M. J., and G. N. Cameron. 1998. Influence of resource removal on demography of Attwater's pocket gopher. Journal of Mammalogy 79:538-550.

Ribble, D. O., and S. Stanley. 1998. Home ranges and social organization of syntopic *Peromyscus boylii* and *P. truei*. Journal of Mammalogy 79:932-941.

Ribble, D. O., A. E. Wurtz, E. K. McConnell, J. J. Buegge, and K. C. Welch, Jr. 2002. A comparison of home ranges of two species of *Peromyscus* using trapping and radiotelemetry data. Journal of Mammalogy 83:260-266.

Rickart, E. A. 1981. Demography and activity patterns of some small mammals from the Cape Province, South Africa. Journal of Mammalogy 62:646-649.

Rickart, E. A. 1986. Postnatal growth of the Piute ground squirrel (*Spermophilus mollis*). Journal of Mammalogy 67:412-416.

Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. Journal of Mammalogy 72:152-162.

Roach, J. L., P. Stapp, B. Van Horne, and M. F. Antolin. 2001. Genetic structure of a metapopulation of black-tailed prairie dogs. Journal of Mammalogy 82:946-959.

Roberts, S. C. 1978. Group-living and consortships in two populations of the European rabbit (*Oryctolagus cuniculus*). Journal of Mammalogy 68:28-38.

Rogovin, K., J. A. Randall, I. Kolosova, and M. Moshkin. 2004. Predation on a social desert rodent, *Rhombomys opimus*: effect of group size. Journal of Mammalogy 85:723-730.

Rogovin, K., G. Shenbrot, and A. Surov. 1991. Analysis of spatial organization of a desert rodent community in Bolsón de Mapimí, Mexico. Journal of Mammalogy 72:347-359.

Rogowitz, G. L., and M. L. Wolfe. 1991. Intraspecific variation in life-history traits of the white-tailed jackrabbit (*Lepus townsendii*). Journal of Mammalogy 72:796-806.

Rose, R. K., and R. D. Dueser. 1980. Lifespan of Virginia meadow voles. Journal of Mammalogy 61:760-763.

Roze, U. 2002. A facilitated release mechanism for quills of the North American porcupine (*Erethizon dorsatum*). Journal of Mammalogy 83:381-385.

Saitoh, T. 1989. Effects of added food on some attributes of an enclosed vole population. Journal of Mammalogy 70:772-782.

Salmon, T. P., and R. E. Marsh. 1989. California ground-squirrel trapping influenced by anal-gland odors. Journal of Mammalogy 70:428-431.

Salsbury, C. M., and K. B. Armitage. 1994. Home-range size and exploratory excursions of adult, male yellow-bellied marmots. Journal of Mammalogy 75:648-656.

Sauer, J. R., and N. A. Slade. 1985. Mass-based demography of a hispid cotton rat (*Sigmodon hispidus*) population. Journal of Mammalogy 66:316-328.

Sauer, J. R., and N. A. Slade. 1986. Field-determined growth rates of prairie voles (*Microtus ochrogaster*): observed patterns and environmental influences. Journal of Mammalogy 67:61-68.

Scharff, A., O. Locker-Grütjen, M. Kawalika, and H. Burda. 2001. Natural history of the giant mole-rat, *Cryptomys mechowi* (Rodentia: Bathyergidae) from Zambia. Journal of Mammalogy 82:1003-1015.

Scheibe, J. S., and M. J. O'Farrell. 1995. Habitat dynamics in *Peromyscus truei*: eclectic females, density dependence, or reproductive constraints? Journal of Mammalogy 76:368-375.

Schooley, R. L., B. Van Horne, and K. P. Burnham. 1993. Passive integrated transponders for marking free-ranging Townsend's ground squirrels. Journal of Mammalogy 74:480-484.

Schug, M. D., S. H. Vessey, and A. I. Korytko. 1991. Longevity and survival in a population of white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 72:360-366.

Scott-Morales, L., E. Estrada, F. Chávez-Ramírez, and M. Cotera. 2004. Continued decline in geographical distribution of the Mexican prairie dog (*Cynomys mexicanus*). Journal of Mammalogy 85:1095-1101.

Scribner, K. T., R. K. Chesser, and R. J. Warren. 1983. Spatial and temporal genetic variability of the eastern cottontail on West Texas playa basins. Journal of Mammalogy 64:287-294.

Seagle, S. W. 1985. Patterns of small mammal microhabitat utilization in cedar glade and deciduous forest habitats. Journal of Mammalogy 66:22-35.

Seamon, J. O., and G. H. Adler. 1999. Short-term use of space by a neotropical forest rodent, *Proechimys semispinosus*. Journal of Mammalogy 80:899-904.

Setoguchi, M. 1990. Food habits of red-bellied tree squirrels on a small island in Japan. Journal of Mammalogy 71:570-578.

Setoguchi, M. 1991. Nest-site selection and nest-building behavior of red-bellied tree squirrels on Tomogashima Island, Japan. Journal of Mammalogy 72:163-170.

Shaffer, L. 1980. Use of scatterhoards by eastern chipmunks to replace stolen food. Journal of Mammalogy 61:733-734.

Shargal, E., N. Kronfeld-Schor, and T. Dayan. 2000. Population biology and spatial relationships of coexisting spiny mice (*Acomys*) in Israel. Journal of Mammalogy 81:1046-1052.

Sharpe, P. B., and B. Van Horne. 1998. Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). Journal of Mammalogy 79:906-918.

Sharples, F. E. 1983. Habitat use by sympatric species of *Eutamias*. Journal of Mammalogy 64:572-579.

Sherman, P. W., S. Braude, and J. U. M. Jarvis. 1999. Litter sizes and mammary numbers of naked mole-rats: breaking the one-half rule. Journal of Mammalogy 80:720-733.

Shibata, F., T. Kawamichi, and K. Nishibayashi. 2004. Daily rest-site selection and use by the Japanese dormouse. Journal of Mammalogy 85:30-37.

Shier, D. M., and J. A. Randall. 2004. Spacing as a predictor of social organization in kangaroo rats (*Dipodomys heermanni arenae*). Journal of Mammalogy 85:1002-1008.

Shriner, W. M., and P. B. Stacey. 1991. Spatial relationships and dispersal patterns in the rock squirrel, *Spermophilus variegatus*. Journal of Mammalogy 72:601-606.

Simons, L. H. 1991. Rodent dynamics in relation to fire in the Sonoran Desert. Journal of Mammalogy 72:518-524.

Skupski, M. P. 1995. Population ecology of the western harvest mouse, *Reithrodontomys megalotis*: a long-term perspective. Journal of Mammalogy 76:358-367.

Slade, N. A. 1991. Loss of body mass associated with capture of *Sigmodon* and *Microtus* from northeastern Kansas. Journal of Mammalogy 72:171-176.

Slade, N. A., and S. M. Blair. 2000. An empirical test of using counts of individuals captured as indices of population size. Journal of Mammalogy 81:1035-1045.

Slade, N. A., M. A. Eifler, N. M. Gruenhagen, and A. L. Davelos. 1993. Differential effectiveness of standard and long Sherman livetraps in capturing small mammals. Journal of Mammalogy 74:156-161.

Slade, N. A., and C. Iskjaer. 1990. Daily variation in body mass of free-living rodents and its significance for mass-based population dynamics. Journal of Mammalogy 71:357-363.

Slade, N. A., and S. A. Russell. 1998. Distances as indices to movements and home-range size from trapping records of small mammals. Journal of Mammalogy 79:346-351.

Slade, N. A., S. A. Russell, and T. J. Doonan. 1997. The impact of supplemental food on movements of prairie voles (*Microtus ochrogaster*). Journal of Mammalogy 78:1149-1155.

Slade, N. A., J. R. Sauer, and G. E. Glass. 1984. Seasonal variation in field-determined growth rates of the hispid cotton rat (*Sigmodon hispidus*). Journal of Mammalogy 65:263-270.

Slade, N. A., and R. K. Swihart. 1983. Home range indices for the hispid cotton rat (*Sigmodon hispidus*) in northeastern Kansas. Journal of Mammalogy 64:580-590.

Small, R. J., and B. J. Verts. 1983. Responses of a population of *Perognathus parvus* to removal trapping. Journal of Mammalogy 64:139-143.

Smith, A. T., and W. X. Gao. 1991. Social relationships of adult black-lipped pikas (*Ochotona curzoniae*). Journal of Mammalogy 72:231-247.

Smith, D. W., and S. H. Jenkins. 1997. Seasonal change in body mass and size of tail of northern beavers. Journal of Mammalogy 78:869-876.

Smith, F. A., et al. 2003. Body mass of Late Quaternary mammals. Ecological Archives E084-094; Ecology 84:3403.

Smith, H. R., and R. J. Sloan. 1988. Estimated effective population size in a wild population of *Peromyscus leucopus*. Journal of Mammalogy 69:176-177.

Smith, M. H., B. G. Maza, and J. G. Wiener. 1980. Social interactions and spatial distribution in a desert rodent. Journal of Mammalogy 61:113-116.

Smith, W. P., and J. V. Nichols. 2003. Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. Journal of Mammalogy 84:1044-1058.

Smith, W. P., and J. V. Nichols. 2004. Demography of two endemic forest-floor mammals of southeastern Alaskan temperate rain forest. Journal of Mammalogy 85:540-551.

Smith, W. P., S. M. Gende, and J. V. Nichols. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. Journal of Mammalogy 85:663-674.

Smolen, M. J., H. H. Genoways, and R. J. Baker. 1980. Demographic and reproductive parameters of the yellow-cheeked pocket gopher (*Pappogeomys castanops*). Journal of Mammalogy 61:224-236.

Sneddon, I. A. 1991. Latrine use by the European rabbit (*Oryctolagus cuniculus*). Journal of Mammalogy 72:769-775.

Songer, M. A., M. V. Lomolino, and D. R. Perault. 1997. Niche dynamics of deer mice in a fragmented, old-growth-forest landscape. Journal of Mammalogy 78:1027-1039.

Southwick, C. H., S. C. Golian, M. R. Whitworth, J. C. Halfpenny, and R. Brown. 1986. Population density and fluctuations of pikas (*Ochotona princeps*) in Colorado. Journal of Mammalogy 67:149-153.

Sparks, D. W., and D. C. Andersen. 1988. The relationship between habitat quality and mound building by a fossorial rodent, *Geomys bursarius*. Journal of Mammalogy 69:583-587.

Stafford, B. J., R. W. Thorington, Jr., and T. Kawamichi. 2002. Gliding behavior of Japanese giant flying squirrels (*Petaurista leucogenys*). Journal of Mammalogy 83:553-562.

Stafford, B. J., R. W. Thorington, Jr., and T. Kawamichi. 2003. Positional behavior of Japanese giant flying squirrels (*Petaurista leucogenys*). Journal of Mammalogy 84:263-271.

Stafford, S. R., and I. J. Stout. 1983. Dispersal of the cotton rat. Journal of Mammalogy 64:210-217.

Stallman, E. L., and W. G. Holmes. 2002. Selective foraging and food distribution of high-elevation yellow-bellied marmots (*Marmota flaviventris*). Journal of Mammalogy 83:576-584.

Stapp, P. 1997. Habitat selection by an insectivorous rodent: patterns and mechanisms across multiple scales. Journal of Mammalogy 78:1128-1143.

Stout, I. J., and R. J. Demmer. 1982. Cotton rat invasion of sand pine scrub habitat. Journal of Mammalogy 63:236-242.

Stroud, D. C. 1982. Population dynamics of *Rattus rattus* and *R. norvegicus* in a riparian habitat. Journal of Mammalogy 63:151-154.

Sullivan, T. P. 1990. Response of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. Journal of Mammalogy 71:579-590.

Sulok, M., N. A. Slade, and T. J. Doonan. 2004. Effects of supplemental food on movements of cotton rats (*Sigmodon hispidus*). Journal of Mammalogy 85:1102-1105.

Swann, D. E., A. J. Kuenzi, M. L. Morrison, and S. DeStefano. 1997. Effects of sampling blood on survival of small mammals. Journal of Mammalogy 78:908-913.

Sweitzer, R. A. 1996. Predation or starvation: consequences of foraging decisions by porcupines (*Erethizon dorsatum*). Journal of Mammalogy 77:1068-1077.

Sweitzer, R. A., and J. Berger. 1993. Seasonal dynamics of mass and body condition in Great Basin porcupines (*Erethizon dorsatum*). Journal of Mammalogy 74:198-203.

Swihart, R. K. 1992. Home-range attributes and spatial structure of woodchuck populations. Journal of Mammalogy 73:604-618.

Swihart, R. K., and N. A. Slade. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. Journal of Mammalogy 65:357-360.

Swihart, R. K., and N. A. Slade. 1985. Seasonal use of brush piles by the hispid cotton rat (*Sigmodon hispidus*). Journal of Mammalogy 66:577-580.

Swihart, R. K., and N. A. Slade. 1989. Differences in home-range size between sexes of *Microtus ochrogaster*. Journal of Mammalogy 70:816-820.

Swilling, W. R., Jr., and M. C. Wooten. 2002. Subadult dispersal in a monogamous species: the Alabama beach mouse (*Peromyscus polionotus ammobates*). Journal of Mammalogy 83:252-259.

Tallmon, D., and L. S. Mills. 1994. Use of logs within home ranges of California red-backed voles in a remnant of forest. Journal of Mammalogy 75:97-101.

Tamura, N. 1993. Role of sound communication in mating of Malaysian *Callosciurus* (Sciuridae). Journal of Mammalogy 74:468-476.

Tamura, N., F. Hayashi, and K. Miyashita. 1988. Dominance hierarchy and mating behavior of the Formosan squirrel, *Callosciurus erythaeus thaiwanensis*. Journal of Mammalogy 69:320-331.

Tchabovsky, A., and G. Bazykin. 2004. Females delay dispersal and breeding in a solitary gerbil, *Meriones tamariscinus*. Journal of Mammalogy 85:105-112.

Terman, C. R., and J. R. Terman. 1999. Early summer reproductive hiatus in wild adult white-footed mice. Journal of Mammalogy 80:1251-1256.

Teska, W. R. 1980. Effects of food availability on trap response of the hispid cotton rat, *Sigmodon hispidus*. Journal of Mammalogy 61:555-557.

Tew, T. E., I. A. Todd, and D. W. Macdonald. 1994. Temporal changes in olfactory preference in muroid rodents revealed by live-trapping. Journal of Mammalogy 75:750-756.

Thompson, S. D. 1982. Spatial utilization and foraging behavior of the desert woodrat, *Neotoma lepida lepida*. Journal of Mammalogy 63:570-581.

Thompson, S. D. 1987. Resource availability and microhabitat use by Merriam's kangaroo rats, *Dipodomys merriami*, in the Mojave Desert. Journal of Mammalogy 68:256-265.

Tomblin, D. C., and G. H. Adler. 1998. Differences in habitat use between two morphologically similar tropical forest rodents. Journal of Mammalogy 79:953-961.

Torre, I., A. Arrizabalaga, and C. Flaquer. 2004. Three methods for assessing richness and composition of small mammal communities. Journal of Mammalogy 85:524-530.

Torres-Contreras, H., E. Silva-Aránguiz, P. A. Marquet, P. A. Camus, and F. M. Jaksić. 1997. Spatiotemporal variability of rodent subpopulations at a semiarid neotropical locality. Journal of Mammalogy 78:505-513.

Tristiani, H., O. Murakami, and H. Watanabe. 2003. Ranging and nesting behavior of the ricefield rat *Rattus argentiventer* (Rodentia: Muridae). Journal of Mammalogy 84:1228-1236.

Trombulak, S. C. 1985. The influence of interspecific competition on home range size in chipmunks (*Eutamias*). Journal of Mammalogy 66:329-337.

Trombulak, S. C. 1987. Life history of the Cascade golden-mantled ground squirrel (*Spermophilus saturatus*). Journal of Mammalogy 68:544-554.

Trombulak, S. C. 1989. Running speed and body mass in Belding's ground squirrels. Journal of Mammalogy 70:194-197.

Turner, C. L., and W. E. Grant. 1987. Effect of removal of *Sigmodon hispidus* on microhabitat utilization by *Baiomys taylori* and *Reithrodontomys fulvescens*. Journal of Mammalogy 68:80-85.

Van Horne, B. 1982. Effective trapped area for live-trap grids. Journal of Mammalogy 63:155-157.

Van Horne, B., R. L. Schooley, and P. B. Sharpe. 1998. Influence of habitat, sex, age, and drought on the diet of Townsend's ground squirrels. Journal of Mammalogy 79:521-537.

Vaughan, T. A. 1982. Stephens' woodrat, a dietary specialist. Journal of Mammalogy 63:53-62.

Vaughan, T. A., and N. J. Czaplewski. 1985. Reproduction in Stephens' woodrat: the wages of folivory. Journal of Mammalogy 66:429-443.

Vaughan, T. A., and S. T. Schwartz. 1980. Behavioral ecology of an insular woodrat. Journal of Mammalogy 61:205-218.

Vázquez, L. B., G. N. Cameron, and R. A. Medellín. 2004. Characteristics of diet of *Peromyscus aztecus* and *Reithrodontomys fulvescens* in montane western Mexico. Journal of Mammalogy 85:196-205.

Vázquez, L. B., R. A. Medellín, and G. N. Cameron. 2000. Population and community ecology of small rodents in montane forest of western Mexico. Journal of Mammalogy 81:77-85.

Verner, L., and L. L. Getz. 1985. Significance of dispersal in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus*. Journal of Mammalogy 66:338-347.

Vernes, K. 2001. Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest of eastern Canada. Journal of Mammalogy 82:1026-1033.

Verts, B. J., and L. N. Carraway. 1986. Replacement in a population of *Perognathus parvus* subjected to removal trapping. Journal of Mammalogy 67:201-205.

Verts, B. J., and D. B. Costain. 1988. Changes in sex ratios of *Spermophilus beldingi* in Oregon. Journal of Mammalogy 69:186-190.

Verts, B. J., S. D. Gehman, and K. J. Hundertmark. 1984. *Sylvilagus nuttalli*: a semiarboreal lagomorph. Journal of Mammalogy 65:131-135.

Vickery, W. L., and J. R. Bider. 1981. The influence of weather on rodent activity. Journal of Mammalogy 62:140-145.

Waser, P. M., and J. M. Ayers. 2003. Microhabitat use and population decline in banner-tailed kangaroo rats. Journal of Mammalogy 84:1031-1043.

Waterman, J. M. 1984. Infanticide in the Columbian ground squirrel, *Spermophilus columbianus*. Journal of Mammalogy 65:137-138.

Waterman, J. M. 1996. Reproductive biology of a tropical, non-hibernating ground squirrel. Journal of Mammalogy 77:134-146.

Webster, A. B., and R. J. Brooks. 1981. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. Journal of Mammalogy 62:738-751.

Weddell, B. J. 1989. Dispersion of Columbian ground squirrels (*Spermophilus columbianus*) in meadow steppe and coniferous forest. Journal of Mammalogy 70:842-845.

West, S. D. 1982. Dynamics of colonization and abundance in central Alaskan populations of the northern red-backed vole, *Clethrionomys rutilus*. Journal of Mammalogy 63:128-143.

Wheatley, M., K. W. Larsen, and S. Boutin. 2002. Does density reflect habitat quality for North American red squirrels during a spruce cone failure? Journal of Mammalogy 83:716-727.

Wilder, S. M., and D. B. Meikle. 2004. Prevalence of deer ticks (*Ixodes scapularis*) on white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 85:1015-1018.

Williams, C. L., S. W. Breck, and B. W. Baker. 2004. Genetic methods improve accuracy of gender determination in beavers. Journal of Mammalogy 85:1145-1148.

Williams, L. R., and G. N. Cameron. 1984. Demography of dispersal in Attwater's pocket gopher (*Geomys attwateri*). Journal of Mammalogy 65:67-75.

Wirsing, A. J., T. D. Steury, and D. L. Murray. 2002. Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. Journal of Mammalogy 83:707-715.

Witt, J. W. 1991. Fluctuations in the weight and trap response for *Glaucomys sabrinus* in western Oregon. Journal of Mammalogy 72:612-615.

Witt, J. W. 1992. Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. Journal of Mammalogy 73:921-929.

Wolf, M., and G. O. Batzli. 2002. Relationship of previous trap occupancy to capture of white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 83:728-733.

Wolff, J. O. 1993. Does the "Chitty Effect" occur in *Peromyscus*? Journal of Mammalogy 74:846-851.

Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy 77:850-856.

Wolff, J. O., and D. S. Durr. 1986. Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 67:409-412.

Wolff, J. O., W. D. Edge, and R. Bentley. 1994. Reproductive and behavioral biology of the gray-tailed vole. Journal of Mammalogy 75:873-879.

Wolff, J. O., W. D. Edge, and G. Wang. 2002. Effects of adult sex ratios on recruitment of juvenile gray-tailed voles, *Microtus canicaudus*. Journal of Mammalogy 83:947-956.

Wolff, J. O., and B. Hurlbutt. 1982. Day refuges of *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 63:666-668.

Wood, M. D., and N. A. Slade. 1990. Comparison of ear-tagging and toe-clipping in prairie voles, *Microtus ochrogaster*. Journal of Mammalogy 71:252-255.

Woods, B. C., and K. B. Armitage. 2003. Effects of food supplementation on juvenile growth and survival in *Marmota flaviventris*. Journal of Mammalogy 84:903-914.

Wynne-Edwards, K. E., A. V. Surov, and A. Y. Telitzina. 1999. Differences in endogenous activity within the genus *Phodopus*. Journal of Mammalogy 80:855-865.

Xia, X., and J. S. Millar. 1990. Infestations of wild *Peromyscus leucopus* by bot fly larvae. Journal of Mammalogy 71:255-258.

Yahner, R. H. 1982. Microhabitat use by small mammals in farmstead shelterbelts. Journal of Mammalogy 63:440-445.

Yahner, R. H. 1983. Population dynamics of small mammals in farmstead shelterbelts. Journal of Mammalogy 64:380-386.

Yunger, J. A. 2002. Response of two low-density populations of *Peromyscus leucopus* to increased food availability. Journal of Mammalogy 83:267-279.

Yunger, J. A., and L. A. Randa. 1999. Trap decontamination using hypochlorite: effects on trappability of small mammals. Journal of Mammalogy 80:1336-1340.

Zegers, D. A., and J. C. Ha. 1981. Niche separation of *Peromyscus leucopus* and *Blarina brevicauda*. Journal of Mammalogy 62:199-201.

Zegers, D. A., and J. F. Merritt. 1988. Adaptations of *Peromyscus* for winter survival in an Appalachian montane forest. Journal of Mammalogy 69:516-523.

Zembal, R., and C. Gall. 1980. Observations on Mohave ground squirrels, *Spermophilus mohavensis*, in Inyo County, California. Journal of Mammalogy 61:347-350.

Zervanos, S. M., and C. M. Salsbury. 2003. Seasonal body temperature fluctuations and energetic strategies in free-ranging eastern woodchucks (*Marmota monax*). Journal of Mammalogy 84:299-310.

Chapter 2: An automatic activity-monitoring system for small mammals under natural conditions.

Abstract

Small mammals spend a majority of their lives in shelter sites such as belowground burrows. Understanding temporal patterns of burrow use would provide valuable information about the influence of physiological and environmental factors on activity patterns. To examine patterns of burrow use, I developed a system that automatically monitors activity of deer mice, *Peromyscus maniculatus*, at artificial burrows in tallgrass prairie. The automatic activity-monitoring system is composed of a passive integrated transponder (PIT)-tag transceiver that reads the identification tags of individuals and an infrared trail monitor that confirms movements in and out of artificial burrows. I PIT-tagged and monitored the nightly activity of more than 100 deer mice on Konza Prairie Biological Station in northeastern Kansas from July 2003 to December 2004. The monitoring system allowed us to examine individual variation in these patterns relative to sex, age, reproductive status, parental status, as well as variation within individuals over time. I also discuss advantages and disadvantages of the system compared to other activity-monitoring techniques, so that researchers might develop similar systems for other study species.

Introduction

Nest boxes and artificial burrows have been used in population studies of small mammals for many years (Goundie and Vessey 1986; Havelka and Millar 2000; Howard 1949; Kaufman and Kaufman 1989; Lewellen and Vessey 1999; Wolff 1994). Manual inspection of shelters can provide a snapshot of which individuals are in an area at a given time and elucidate patterns of cohabitation and individual spacing. Further, information on how individuals use their refuges throughout a diel cycle of activity could provide better insights into the behavioral ecology of a species than data collected under laboratory conditions or from live trapping alone. Although live trapping can detect time of foraging activity of individuals (e.g., Barry et al. 1989), the presence of traps and handling of animals likely influence animal movements (Price et al. 1994; Sheppe 1967) and activity patterns (Gilbert et al. 1986; O'Farrell 1974).

Recent advances in technology used to mark free-living small animals have allowed for creative solutions to questions about previously unobservable phenomena. Initially, passive integrated transponder (PIT) tags were used to simply identify individuals (Prentice and Park 1984). Researchers then began designing systems to recognize tagged individuals and record temporal and spatial data relative to specific individuals without recapturing them. For example, automatic PIT-tag monitoring systems were designed to record use of fish ladders by salmon around hydroelectric dams (Prentice et al. 1990). Subsequently, systems have been developed for terrestrial habitats to identify, for example, individual bats at maternity roosts (Neubaum et al. 2005), birds at nest boxes (Freitag et al. 2001), tortoises at highway culverts (Boarman et al. 1998), and geckos on trees (Gruber 2004). Only 2 automatic-monitoring systems have been designed for small mammals previously; one recorded activity of prairie voles (*Microtus ochrogaster*) and meadow voles (*M. pennsylvanicus*) using aboveground runways (Harper and Batzli 1996), and the second recorded identities of white-footed mice (*Peromyscus leucopus*) at foraging trays (Burns 2005).

Many kinds of small mammals spend the majority of their lives in shelter sites such as belowground burrows. Description and analysis of temporal and spatial patterns of burrow use would provide information that could be used to assess the influence of physiological and environmental factors on activity patterns ["chronoecology;" Halle and Stenseth (2000)], as well as determine residents and visitors at burrow sites. Herein, I describe a system that automatically records the timing of aboveground activity of deer mice (*P. maniculatus*) in tallgrass prairie by monitoring when animals leave and return to artificial burrows. This is the first study to monitor activity patterns remotely at a shelter site, and I highlight ways the system can be used to monitor activity of individuals and groups of deer mice over extended time periods. In addition, I discuss the advantages and disadvantages of this automatic activity-monitoring system, so that researchers might develop or adapt similar systems to answer questions in other study species.

Materials and Methods

Study site

The study was conducted on Konza Prairie Biological Station (Konza Prairie), a 3,487-ha tallgrass prairie preserve in northeastern Kansas, near Manhattan (39°05’N 96°35’W). I studied deer mice in 2 adjacent grassland sites, experimental treatment units 2A and 1B. Unit 1B is burned annually in the spring and was burned in 2003 and 2004, whereas 2A is burned every 2 years in the spring and was burned in 2004. Data were collected between July 2003 and December 2004.

Artificial burrows

I installed 20 artificial burrows (Kaufman and Kaufman 1989), in upland sites and along hillsides. Each artificial burrow had 3 entrance tunnels from the nest chamber, as modified by Kaufman and Kaufman (in review). I also attached a 45° polyvinyl chloride (PVC) elbow to 1 of the 3 entrance tunnels and attached a 20-cm length of 2.5-cm (inside diameter) PVC tubing onto it. The configuration created an extended entrance tunnel parallel to the ground surface. All burrows on the study site were checked systematically for deer mice about once per week in spring, summer, and autumn and biweekly in winter.

Trapping methods

Six traplines were established to sample deer mice. This sampling supplemented weekly manual checking of all artificial burrows and increased the likelihood that all resident deer mice were marked and could be identified by the automatic monitoring system. Trap stations were spaced 15 m apart on each of 6 traplines, which ranged in length from 90 to 210 m. Two large Sherman live traps (7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) were placed at each station. Traps were baited with peanut butter and rolled oats (Kaufman et al. 1988). Polyester fiberfill was provided in traps for insulation during fall trapping. I live-trapped small mammals for 2 consecutive nights once per month in summer and autumn.

Marking methods

Individuals were PIT-tagged at first capture. Young deer mice were PIT-tagged when they attained a body mass of $\geq$ 4.5 g (~7-10 days old). I used implantable, glass-encapsulated PIT tags (Model TX1400L, Biomark, Inc, Boise, Idaho, USA). PIT tags were injected subcutaneously in the interscapular region of the dorsum. After injection, the injected PIT tag was found by palpating the dorsum and pushing the tag backward and laterally to move it away from the site of injection and to minimize tag loss at the insertion site.

I also marked deer mice with ear tags to enable tracking of individual identities if PIT tags were lost or malfunctioned. I used size-1, monel, self-piercing ear tags (style #1005-1, standard stamped; National Band and Tag Co., Newport, Kentucky, USA) to double mark individuals. A single ear tag was applied by using applicator pliers (style 1005s1, National Band and Tag Co.). Young deer mice were ear-tagged when ears had unfolded and grown to sufficient size to retain a tag (mass of ~6 g).

Automatic activity-monitoring system

I used the Destron-Fearing Portable Transceiver System (Model 2001F-ISO; Biomark, Inc.) to read PIT tags of mice entering or exiting the entrance tunnel of a monitored burrow (Fig. 5). The transceiver system recorded both the identity of an individual and time of the event (±1 sec precision) whenever a PIT-tagged individual passed through the electromagnetic field of the ring antenna, which encircled the entrance tunnel. The transceiver had an internal battery that had a life of ≤ 6 h of continuous operation. I increased the amount of time for continuous operation of the transceiver by attaching a 12-volt deep-cycle/marine battery to the transceiver, which provided ≥ 96 h of continuous operation under most conditions. During a trial early in the study, electrical cords were chewed and destroyed by rodents, which resulted in loss of power and the ability to collect data. Subsequently, cords between the antenna and transceiver and the transceiver and external battery were enclosed in 2-cm (inside diameter) PVC tubes, which prevented destruction of wires.

Voltage levels supplied to the antenna affected the shape and size of the reading field around the ring antenna. My goal was to read the tags of those mice that passed directly through the ring via the entrance tunnel. At full power (100%), PIT tags could be detected up to 30 cm from the antenna. At this setting, PIT tags of mice were read when they were inactive inside the burrow or when they were active aboveground and passed nearby the entrance tunnel. Because I wanted a precise location for individual mice, I experimented with a model mouse made of cotton that contained a PIT tag to refine the distance of detection. The model mouse was pulled through a test tunnel outfitted with a ring antenna. After a number of trials at different "mouse" speeds and potential tag orientations, I determined that 30% antenna power was the optimal setting. This setting allowed me to detect all mice passing through the entrance tunnel without

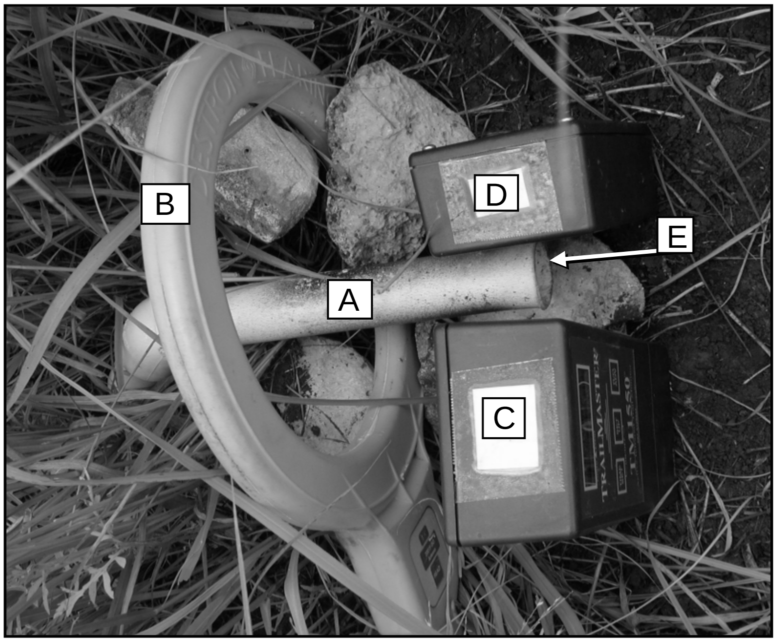

Figure 5. Overhead view of artificial burrow entrance fitted with automatic activity-monitoring system. Components include an aboveground entrance tube (A), a circular ring antenna for detecting and identifying PIT-tagged mice (B), an active infrared (IR) monitoring receiver (C), and an active IR transmitter (D). Mice enter and exit the burrow through a single opening (E).

missing any individuals; therefore, 30% power was used for all subsequent monitoring of artificial burrows. I programmed the transceiver to read continuously so it could identify multiple individuals passing through the reading field simultaneously. The adjustable time delay between successive readings of the same individual was set to a 5-s delay. Thus, if the same individual remained in the reading field (i.e., loitering in the entrance tunnel) for 20 s, the identity of that individual and the time were recorded once every 5 s, for a total of 4 records in this example. This 5-s time delay helped reduce excessive records that provided no new information about activity of that specific individual, but still allowed me to detect brief (≥ 6 s) forays from the entrance/exit tunnel into the environment and then back into the tunnel. Memory storage of the PIT-tag transceiver could hold ~4,200 events.

Although the PIT-transceiver system detected both presence and identity of an individual in the entrance tunnel, loitering behavior by mice in the tunnel (as detected from recorded events) meant that I could not tell if an individual had exited the tunnel or simply moved to the entrance and returned to the interior nest chamber. Therefore, I improved the monitoring system by adding an active infrared (IR) trail monitor (Model TM1550-Bat, TrailMaster, Inc., Lenexa, Kansas, USA) that allowed me to confirm entry or exit movements of an individual at the mouth of the entrance tunnel. This IR system also time stamped each movement event with 1-min precision. This transmitter model was chosen so that I could set the pulse rate (amount of time the IR beam had to be broken to record an event) and intensity, a necessity for use in such a small target species. By using the cotton model mouse, I determined that a pulse-rate setting of 0.012 s was sufficiently sensitive to detect an individual at the mouth of the tunnel entrance. Pulse intensity was set to its low setting, because the transmitter and receiver were within close proximity (~3 cm). The IR receiver was capable of recording up to 1,961 events before onboard memory was filled.

Monitoring activity at artificial burrows

Manual checking of artificial burrows provided known locations of individuals on a given date. When I found deer mice (hereafter, called target mice) in an artificial burrow that I wanted to monitor with the monitoring system, I temporarily covered each of the 3 entrance tunnels with a PVC end cap. Closing off entrances of burrows in which target mice were found allowed me time to finish checking the remaining artificial burrows and ensured that target mice would not escape before the monitoring system could be placed into position. Once all burrows had been inspected, I selected burrows to be monitored, based on goals of the study (i.e., reproductive status, cohabitants, presence of offspring, number of nights of activity previously recorded for each individual).

To set up a monitoring event, the ring antenna was slipped around the aboveground entrance tube (Fig. 5) and the antenna was wedged into place by using limestone rocks, which were ubiquitous on the study site. The antenna-transceiver cord then was passed through its protective PVC pipe and connected at both ends. Next, the transceiver was connected to the 12-volt battery. The PIT-tag reader and IR system then were powered up and time-stamp clocks synchronized. The IR receiver and transmitter were placed on either side of the opening of the aboveground entrance tunnel and secured in place by numerous small limestone rocks. A brief set-up period (1 min) was allowed for the receiver to properly acquire the high-intensity IR beam from the transmitter. Finally, I removed the PVC end cap from the aboveground entrance tunnel, and the monitoring system was ready to monitor activity events. Trials began > 1 h before sunset and lasted for 1-4 consecutive nights.

At the conclusion of a monitoring trial, data were downloaded from the PIT-tag transceiver in the format of a text file to a notebook computer in the field via a RS232 (serial) connection. This output then was read by using terminal emulation software (Terminal 1.3.1, Intensecomp, Pte, Ltd., Singapore; software available at http://www.intensecomp.com/download.html). Events recorded by the IR system were transcribed manually to paper from the memory log of the receiver. Recorded PIT-tag events with no corresponding IR event indicated either that a mouse had not left the burrow entrance or that the mouse was outside the entrance tunnel, near the antenna but had not entered the burrow. These non-movement events were discarded, leaving only records of external movement activity for each individual during a monitoring trial.

I followed guidelines for use of animals set by the Animal Care and Use Committee of the American Society of Mammalogists (1998). Use of animals was approved by the Kansas State University Institutional Animal Care and Use Committee (protocols #2184 and #2184.1).

Results

The monitoring system allowed me to detect continuous activity of numerous types, including nightly initiation of aboveground activity, number and length of activity bouts, time spent attending the burrow, total duration of activity outside the burrow, and total numbers and identities of tagged individuals visiting a burrow in a nighttime. I highlight some of the variation in activity patterns observed among different individuals at different ambient conditions from July to October, within an individual female caring for pups during a 15-d period, and between a female and her offspring during 1 night of activity.

The system showed that variation occurred between the sexes in the initiation and temporal distribution of aboveground activity (Fig. 6). Males emerged from burrows earlier and made more trips of generally shorter duration than females, although the time at which individuals returned for the last time and total time spent away from the burrow each night were similar for each sex (Chapter 3). Variation also occurred in activity among individuals within the same sex. Reproductive status (pregnant or lactating versus nonbreeding) also affected activity patterns of females (Chapter 4).

The monitoring system also recorded variation in the total amount of aboveground activity and temporal distribution of that activity for a female deer mouse that was caring for growing pups (Fig. 7). In fact, females modified their activity patterns slightly over time during the period of parturition and development of young (Chapter 4).

The monitoring system is capable of showing the variation in exploration activity of young deer mice (Fig. 8). Number, spacing, and total duration of activity bouts of young were qualitatively different from the mother (Fig. 8A) and other adults (Figs. 2 and 3; Chapter 3).

Efficacy of monitoring and data logging

On average, the first night of a monitoring trial yielded 100.5 ± 23.9 (1 SE) PIT events. Likewise, IR data logs contained an average of 134.9 ± 18.8 events on the first night of monitoring. After filtering out loitering events from the PIT record, 20.6 ± 3.0 PIT events (20.5%) were retained as valid movements in or out of the burrow.

The onboard memory of the PIT-tag transceiver was filled completely during only 1 trial. In that trial, a juvenile deer mouse spent most of a 7-h period (3,682 consecutive readings) loitering in the tunnel within the reading field of the antenna. The memory on the IR receiver was filled to capacity once, on an afternoon with constant wind speed of 33-37 kph and gusts to ~50 kph. Although the equipment was anchored in place with rocks, winds of this intensity might have shaken the IR receiver sufficiently to record false events on this single occasion.

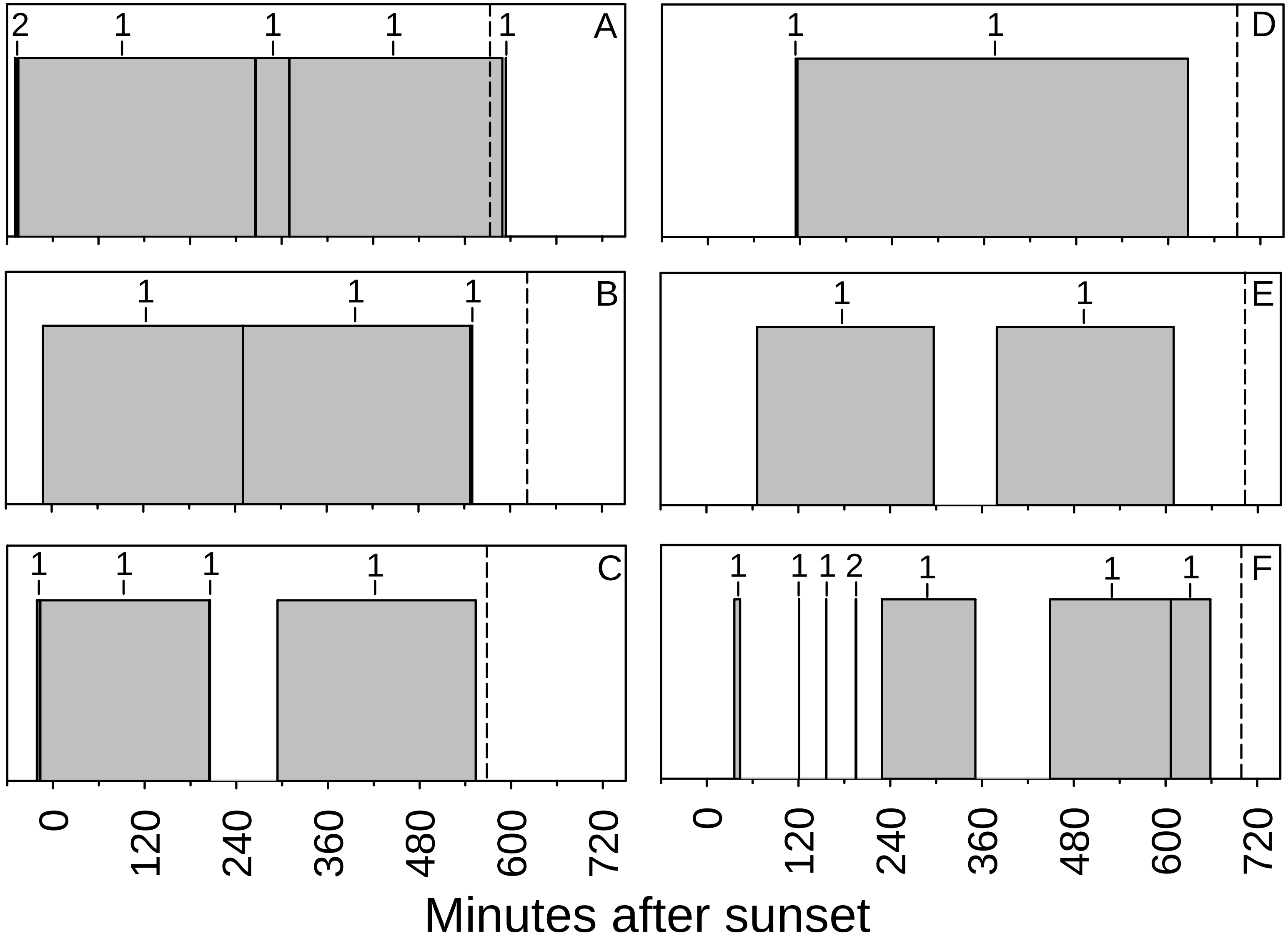

Figure 6. Examples of nightly activity patterns recorded by the automatic activity-monitoring system for male (A-C) and

Figure 6 (cont.) female (D-F) deer mice (*Peromyscus maniculatus*) that used artificial burrows in tallgrass prairie in northeastern Kansas. Time zero denotes sunset, stippled bars indicate activity outside of burrow, and vertical dashed lines denote sunrise. Numbers above plots indicate number of distinct activity bouts within clusters of multiple bouts. Trial dates were 29 July 2003 (A), 14 August 2004 (B), 29 July 2004 (C), 14 September 2004 (D), 18 September 2004 (E), and 2 October 2004 (F).

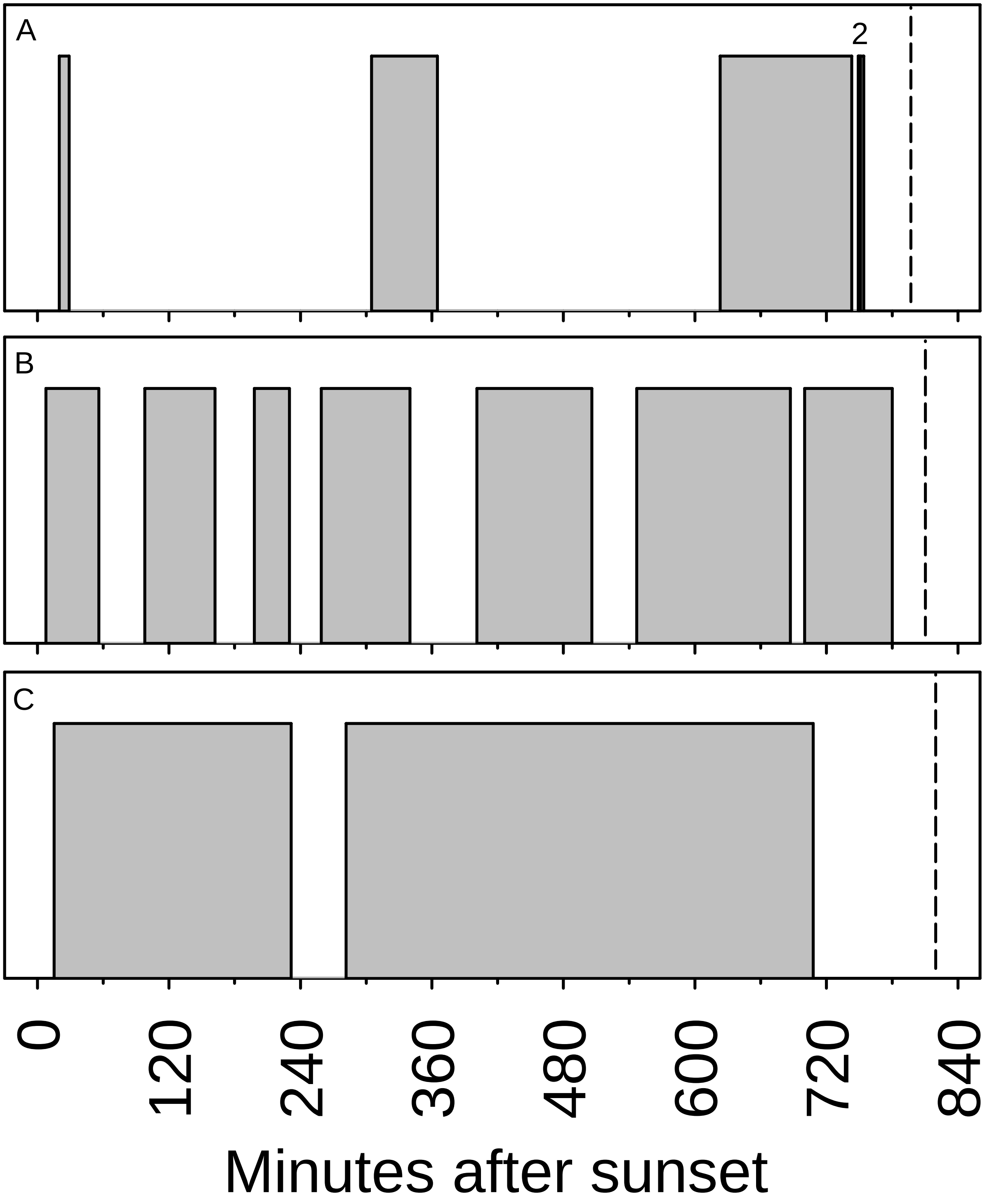

Figure 7. Nightly activity patterns recorded by the automatic activity-monitoring system over a 15-day period for an adult female deer mouse raising a litter of 5 pups in an artificial burrow in

Figure 7 (cont.) tallgrass prairie in northeastern Kansas. Time zero denotes sunset, stippled bars indicate activity outside the burrow, and vertical dashed lines denote sunrise. The "2" above plot (A) denotes a point in the night at which 2 brief, closely spaced activity bouts occurred. Dates of trials were 25 October (young 4 d old; panel A), 2 November (B), and 8 November 2003 (C).

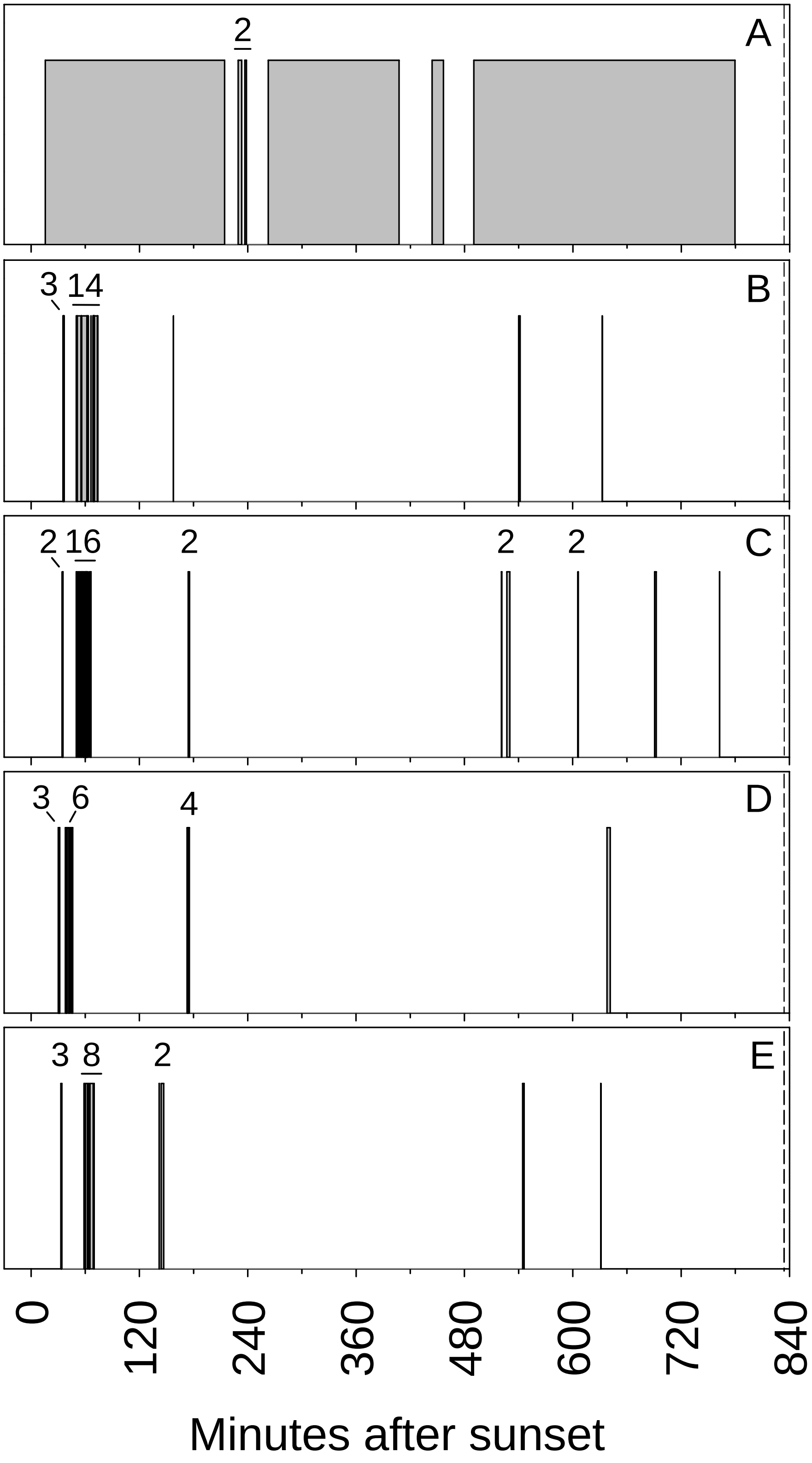

Figure 8. Examples of nighttime activity on 14 November 2004 for an adult female deer

Figure 8 (cont.) mouse (A) and her 4 juvenile pups (B-E; young ~14 d old) on their first night spent exploring outside the natal burrow in tallgrass prairie in northeastern Kansas. Time zero denotes sunset, stippled bars indicate activity outside of burrow, and vertical dashed lines denote sunrise. Numbers above plots indicate number of distinct activity bouts within those clusters of multiple bouts. Ambient conditions were dark (2% moon illumination) and cold (-2.2°C at 2400 h).

Discussion

Enrichment activities available to small mammals influence their patterns of behavior (Kavanau 1962; Yamada et al. 1990). Therefore, when studies are conducted in the laboratory or in enclosures, attempts must be made to emulate natural habitats to maximize the external validity of results. Laboratory and enclosure studies conducted under controlled conditions certainly can aid in the interpretation of patterns observed under natural conditions, but field studies of activity are necessary to better understand how animals behave under natural conditions (Falls 1968).

Advantages of the system

Chronoecological data collected *in situ*, under natural conditions, should yield data that better reflects the normal behavior of small mammals (Halle and Stenseth 2000) than studies conducted under laboratory conditions (Kavanau 1963, 1967, 1969) or in enclosures where movements of individuals were restricted (Wolfe and Summerlin 1989).

The monitoring system can be used to relate aboveground activity of individuals to their identity, sex, age, and reproductive status, whereas studies that use tracking plates, sand trays, or conductance tapes to index activity can resolve neither the number nor identity of individuals responsible for individual tracks (Bider 1968; Blair 1943; Kotler and Brown 1999; Marten 1973). Further, the system provides precise temporal resolution for activity of individuals at a burrow. Studies that use tracking patterns only can resolve the temporal pattern of activity at the level of precision equal to the interval between checking periods of plates, trays, or tapes. For activity patterns as indexed by trapping, precision to the level of minutes or hours requires trap-triggered timers (Barry et al. 1989; Bruseo and Barry 1995) or regular trap checking at set intervals throughout the time of activity (Gilbert et al. 1986; O'Farrell 1974).

A major benefit of the monitoring system is that it can be used to characterize individual differences in behavior (Coleman and Wilson 1998; Wilson et al. 1994). Variation in behaviors among individuals within and between populations (Bell 2005; Bell and Stamps 2004) might help identify correlated behaviors in different contexts, or behavioral syndromes (Sih et al. 2004). These correlations are important because they might lead to trade-offs in different behaviors. Further, these data could allow examination of the developmental stability of individual behaviors and personality types (Bell and Stamps 2004).

Researchers can use this activity-monitoring system to relate activity patterns of individuals to environmental variables, such as weather (Bright et al. 1996; Marten 1973; O'Farrell 1974) or food availability (Rezende and Bozinovic 2001). In contrast, studies conducted in sterile laboratory conditions or in semi-natural enclosures where food is provided *ad libitum* and individuals are protected from predators (Schradin and Pillay 2005), might yield less ecologically realistic results relative to activity.

Presence of researchers constantly checking traps or traversing a study site to collect radiotelemetry data likely causes disturbance that might influence the activity of animals. For example, capture in a trap temporarily restrains mice from their normal activity; subsequently, handling and removing mice from traps could disrupt their behavior and influence their patterns of activity (Sheppe 1967). Radiotelemetry can yield the general location of an individual, but to determine whether the animal is inside or outside of its burrow requires visual contact. Subsequently, the researcher must visit the burrow in which an animal is resting to confirm its presence and this might have a disruptive impact as well. In addition, both techniques, i.e., checking of traps and use of radiotelemetry, are labor intensive. In contrast, the monitoring system runs without disturbance to the animals or input of labor for as long as it is powered by battery or direct electrical connection and onboard memory remains available on the PIT-tag reader and IR receiver. Further, in comparison to use of the monitoring system, use of live trapping does not allow one to determine when an individual actually becomes active. That is, a captured mouse might have emerged from its burrow and traveled directly to the trap or it might have been active for a considerable length of time before entering the trap. Livetrapping reveals the temporal pattern of trappability, which does not necessarily correspond to actual times of activity (Halle and Weinert 2000).

Disadvantages of the monitoring system

The primary difficulty of incorporating the monitoring system into a field research program will be the initial cost of the system components and PIT tags. Currently, the entire monitoring system costs ~US$3,000 (US$2,850 for the PIT-tag transceiver, antenna, and cords; US$410 for the IR system; and ~US$3.90-5.50/PIT tag, depending on number purchased and vendor). However, alternatives, such as radiotelemetry or a large number of live traps, are comparable in cost. In addition, the use of some traditional marking techniques, such as ear tags or toe clipping, are being restricted by some institutional animal care and use committees in favor of the use of PIT tags for individual identifications. I expect the use of PIT tags for identification purposes to increase in the future and, therefore, the application of systems such as the monitoring system would allow researchers to maximize the types of data that could be retrieved each time an animal was detected.

A second disadvantage is that the monitoring system must be installed at a fixed location, in my case, an artificial burrow, during a trial. Once an animal leaves the burrow, I cannot track its behavior without other technology, such as radiotelemetry. However, little is known about the activity patterns of cryptic, nocturnal small mammals at their burrows. In addition, small mammals spend a considerable portion of their lives inside shelter sites, so information regarding use of this important fixed location would prove insightful (Halle and Stenseth 2000).

Last, the deep-cycle battery used to power the monitoring system for extended time periods was bulky (~23 kg). Battery mass may be a limitation in studies where the site of deployment has limited access. However, mobility was important in my study and, despite the mass of the battery, allowed me to move the entire monitoring system among artificial burrows at the tallgrass prairie site and to another site in mixed grass prairie. If a single fixed location were to be used, for instance, in an enclosure study, the monitoring system could be powered for an extended time period by a solar panel or DC electricity source.

Future applications

The monitoring system I designed has provided insights into facets of behavior of deer mice not previously observed under natural conditions. I have highlighted several specific ways in which the monitoring system can be used to collect data on deer mice in tallgrass prairie. However, the same system could be used to monitor activity of any vertebrate that can be marked with a PIT tag and that uses burrows or nest boxes for shelter. On Konza Prairie, I have detected numerous individuals of several species of snakes and amphibians in the artificial burrows, in addition to small mammals, such as white-footed mice (*P. leucopus*), western harvest mice (*Reithrodontomys megalotis*), Elliot's short-tailed shrews (*Blarina hylophaga*), and least shrews (*Cryptotis parva*). It is likely that the monitoring system could be adapted for use in other ecosystems, in concert with artificial burrows or nest boxes modified for the target species. In this way, researchers could expand the understanding of the behavioral ecology of many other species not easily observed by traditional monitoring techniques.

Literature Cited

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416-1431.

Barry, R. E., Jr., A. A. Fressola, and J. A. Bruseo. 1989. Determining the time of capture for small mammals. Journal of Mammalogy 70:660-662.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). Journal of Evolutionary Biology 18:464-473.

Bell, A. M., and J. A. Stamps. 2004. Development of behavioral differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. Animal Behavior 68:1339-1348.

Bider, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecological Monographs 38:269-308.

Blair, W. F. 1943. Activities of the Chihuahua deer-mouse in relation to light intensity. Journal of Wildlife Management 7:92-97.

Boarman, W. I., M. L. Beigel, G. C. Goodlett, and M. Sazaki. 1998. A passive integrated transponder system for tracking animal movements. Wildlife Society Bulletin 26:886-891.

Bright, P. W., P. A. Morris, and N. J. Wiles. 1996. Effects of weather and season on the summer activity of dormice *Muscardinus avellanarius*. Journal of Zoology 238:521-530.

Bruseo, J. A., and R. E. Barry, Jr. 1995. Temporal activity of syntopic *Peromyscus* in the central Appalachians. Journal of Mammalogy 76:78-82.

Burns, C. E. 2005. Behavioral ecology of disturbed landscapes: the response of territorial animals to relocation. Behavioral Ecology 16:898-905.

Coleman, K., and D. S. Wilson. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. Animal Behavior 56:927-936.

Falls, J. B. 1968. Activity. Pp. 543-570 in Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Special Publication, American Society of Mammalogists 2:1-593.

Freitag, A., A. Martinoli, and J. Urzelai. 2001. Monitoring the feeding activity of nesting birds with an autonomous system: case study of the endangered wryneck *Jynx torquilla*. Bird Study 48:102-109.

Gilbert, B. S., C. B. Cichowski, D. Talrico, and C. J. Krebs. 1986. Summer activity patterns of three rodents in the southwestern Yukon. Arctic 39:204-207.

Goundie, T. R., and S. H. Vessey. 1986. Survival and dispersal of young white-footed mice born in nest boxes. Journal of Mammalogy 67:53-60.

Gruber, B. 2004. Monitoring activity of geckos with an automatic movement monitoring system. Herpetological Review 35:245-247.

Halle, S., and N. C. Stenseth, eds. 2000. Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin, Germany.

Halle, S., and D. Weinert. 2000. Recording activity: free choice among drawbacks. Pp. 286-293 in Activity patterns in small mammals: an ecological approach (S. Halle and N. C. Stenseth, eds.). Springer-Verlag, Berlin, Germany.

Harper, S. J., and G. O. Batzli. 1996. Monitoring use of runways by voles with passive integrated transponders. Journal of Mammalogy 77:364-369.

Havelka, M. A., and J. S. Millar. 2000. Use of artificial nest sites as a function of age of litter in *Peromyscus leucopus*. American Midland Naturalist 144:152-158.

Howard, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contributions from the Laboratory of Vertebrate Biology, University of Michigan 43:1-50.

Kaufman, G. A., and D. W. Kaufman. 1989. An artificial burrow for the study of natural populations of small mammals. Journal of Mammalogy 70:656-659.

Kaufman, G. A., and D. W. Kaufman. In Review. Deer mice in artificial burrows: do number of entrances influence use? Prairie Naturalist.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

Kavanau, J. L. 1962. Precise monitoring of drinking behavior in small mammals. Journal of Mammalogy 43:345-351.

Kavanau J. L. 1963. Continuous automatic monitoring of the activities of small captive animals. Ecology 44:95-110.

Kavanau, J. L. 1967. Behavior of captive white-footed mice. Science 155:1623-1639.

Kavanau, J. L. 1969. Influence of light on activity of the small mammals, *Peromyscus* spp., *Tamias striatus*, and *Mustela rixosa*. Experientia 25:208-209.

Kotler, B. P., and J. S. Brown. 1999. Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. Journal of Mammalogy 80:361-374.

Lewellen, R. H., and S. H. Vessey. 1999. Estimating densities of *Peromyscus leucopus* using live trap and nestbox censuses. Journal of Mammalogy 80:400-409.

Marten, G. G. 1973. Time patterns of *Peromyscus* activity and their correlations with weather. Journal of Mammalogy 54:169-188.

Neubaum, D. J., M. A. Neubaum, L. E. Ellison, and T. J. O'Shea. 2005. Survival and condition of big brown bats (*Eptesicus fuscus*) after radiotagging. Journal of Mammalogy 86:95-98.

O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809-823.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. American Fisheries Society Symposium 7:323-334.

Prentice, E. F., and D. L. Park. 1984. Study to determine the biological feasibility of a new fish tagging system. Annual Report, 1983-1984, Project #1983-01900. Portland, OR, Bonneville Power Association Report DOE/BP-348.

Price, M. V., P. A. Kelly, and R. L. Goliday. 1994. Distances moved by Stephens' kangaroo rat (*Dipodomys stephensi* Merriam) and implications for conservation. Journal of Mammalogy 75:929-939.

Rezende, E. L., and F. Bozinovic. 2001. Patterns of daily activity in the leaf-eared mouse (*Phyllotis darwini*): effects of food availability. Journal of Arid Environments 47:95-100.

Schradin, C., and N. Pillay. 2005. The influence of the father on offspring development in the striped mouse. Behavioral Ecology 16:450-455.

Sheppe, W. 1967. The effect of live-trapping on the movements of *Peromyscus*. American Midland Naturalist 78:471-481.

Sih, A., A. M. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology and Evolution 19:372-378.

Wilson, D. S., A. B. Clark, K. Coleman, and T. Dearstyne. 1994. Shyness and boldness in humans and other animals. Trends in Ecology and Evolution 11:442-446.

Wolfe, J. L., and C. T. Summerlin. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. Animal Behavior 37:410-414.

Wolff, J. O. 1994. Reproductive success of solitarily and communally nesting white-footed mice and deer mice. Behavioral Ecology 5:206-209.

Yamada, N., K. Shimoda, K. Takahashi, and S. Takahashi. 1990. Relationship between free-running period and motor activity in blinded rats. Brain Research Bulletin 25:115-119.

Chapter 3: Influence of sex, age, daylight, and season on activity patterns of the deer mouse in tallgrass prairie.

Abstract

Little is known about nightly activity patterns of nocturnal small mammals under natural conditions and how these activity patterns might be affected by photoperiod, season, and sex of individuals. I monitored activity of deer mice, *Peromyscus maniculatus*, at artificial burrows by using an automatic activity-monitoring system in native tallgrass prairie (Konza Prairie Biological Station) from July 2003 though July 2005. I examined how patterns of activity were related to sunset and sunrise in deer mice *in situ*. Second, I assessed whether males and females exhibited different activity patterns, given differences in sex-specific tactics for mating and parental care. Commencement of activity was positively correlated with sunset, whereas time of retirement to the burrow generally was positively correlated with sunrise, with a few unexpected seasonal and sex-specific patterns. Among adults, males and females showed different patterns of activity, as males emerged earlier and made more trips of shorter duration than females, although the total duration of trips was similar. Furthermore, males and females differed in the way they used the burrow during the night. Return visits and subsequent stays typically were shorter for males than females, but total time spent in the burrow and retirement time relative to sunrise were similar for both sexes. Young deer mice emerged significantly later, made more trips of shorter duration, spent less total time outside, and retired to their burrow earlier than adults. Generally, my findings are consistent with results from previous laboratory studies and suggest that a number of ecological and demographic variables are important influences on activity of deer mice in tallgrass prairie.

Introduction

Locomotor activity includes all movements by which small mammals forage for food, socialize with conspecifics, interact with predators, explore their home range, and complete natal or breeding dispersal movements (Falls 1968). The timing of daily activity has ecological consequences, affecting predation risk, interspecific competition, and social organization of populations (Halle and Stenseth 2000). Despite their importance, characterizing these patterns of activity in an ecologically meaningful context for many small mammals can be a complicated task, for logistical reasons.

The daily patterns of activity as well as the cryptic behavior of many small mammals impart particular problems for direct observation of activity patterns. Occasionally, small mammals can be observed under natural conditions, but only if the animal is diurnal (Bacigalupe et al. 2003; Jackson 1998; Koprowski and Corse 2005). Most studies of activity of nocturnal small mammals have been conducted in the laboratory (Kramer and Birney 2001; Rezende and Bozinovic 2001) or in field enclosures (Wolfe and Summerlin 1989). Studies in these environments might not provide sufficient cues for natural behavior. The running wheel most often is used to quantify activity in the laboratory (Blanchong et al. 1999; Dewsbury 1980; Kavanau 1963), but the presence (Yamada et al. 1990) and size (Deboer and Tobler 2000) of the wheel can influence activity of small mammals. Because of an effect of the running wheel on behavior of small mammals, biologically meaningful conclusions from these laboratory studies might be limited (Sherwin 1998). Approaches for measuring activity in the field have included checking live traps multiple times per night (Blanchong and Smale 2000; Gilbert et al. 1986; O’Farrell 1974) or equipping live traps with timers to record the time of capture (Barry et al. 1989). Both techniques require capture and retention of individuals within a trap, which restricts natural movements and activity. Furthermore, removal of individuals from traps may influence subsequent behavior when released.

Radiotelemetry also has been used to quantify activity patterns of nocturnal small mammals in the field (Eccard et al. 2004; Kalcounis-Rüppell and Millar 2002). Radiotelemetry requires that transmitters be attached to individuals and the weight of the transmitter can limit the size of animals that can be monitored. Further, radiotracking of individuals by direct relocation has additional drawbacks that include labor-intensive efforts and observer-presence bias, which might influence individual behavior of nocturnal small mammals. These restrictions and drawbacks make using a fixed, remote-sensing system appealing. The first fixed, remote-sensing system for detecting the presence of nocturnal small mammals at their burrow utilized radiotelemetry (Kalcounis-Rüppell and Millar 2002); however, the temporal resolution and spatial precision of locations might not provide sufficient detail for fine-scale studies of burrow use. Improved methods are necessary to monitor activity under natural conditions and to elucidate decisions made by animals in balancing physiological requirements under ecological pressures in their natural environment (Halle 1995; Halle and Weinert 2000).

The deer mouse (*Peromyscus maniculatus*) might serve as a general model for studying activity of nocturnal small mammals for several reasons. It is the most widespread rodent in North America (Handley 1999) and is abundant in many diverse habitats (forests: Gilbert and Krebs 1991; Harney and Dueser 1987; Silva 2001; Van Horne 1981; grasslands: Kaufman et al. 1988; Kaufman et al. 2000; desert: Heske et al. 1994; sagebrush: Boone and Keller 1993; MacCracken et al. 1985; agricultural lands: Kaufman and Kaufman 1990; Olson and Brewer 2003; oldfield: Brady and Slade 2004). Further, the deer mouse readily inhabits nest boxes and artificial burrows under natural conditions (Howard 1949; Kaufman and Kaufman 1989; Wolff

1994; Wolff and Durr 1986). In addition, a century of studying the biology of deer mice in the field and laboratory provides an extensive background for interpretation of observed patterns (Dewey and Dawson 2001).

For nocturnal small mammals, activity might be influenced by ambient light levels, due to predation pressure by animals using visual cues (Rosenzweig 1974). The effects of natural moonlight on timing and microhabitat shifts in activity have been explored in a number of small mammals, primarily in kangaroo rats inhabiting relatively open habitats (Kaufman and Kaufman 1982; Kenagy 1976; Lockard and Owings 1974; O'Farrell 1974; Wolton 1983). Fewer studies have focused on the relationship between sunset and onset of activity, or between sunrise and ending of activity. The absolute timing of sunset and sunrise change across seasons, so individuals should track seasonal changes in photoperiod and modify their activity accordingly (Kenagy 1976).

Herein, I report on the use of an automatic activity monitoring system to record activity of deer mice, *P. maniculatus*, at artificial burrows in native tallgrass prairie (Chapter 2). My first objective was to examine the relationship between commencement of activity and sunset, as well as termination of activity and sunrise. I hypothesized that activity would be restricted to nighttime to minimize predation risk, and I predicted tight correlations between the beginning and ending of activity and night. Second, I wanted to examine activity patterns for evidence of sex and age differences. I hypothesized that male and female deer mice, which are sexually monomorphic, likely have different strategies for maximizing fitness (Clutton-Brock and Vincent 1991; Emlen and Oring 1977). To address this question, I compared a number of parameters that characterized nightly activity of each sex at the burrow. From the literature on sex-specific activity levels by rodents, I predicted that males would show higher levels of activity than females. To this end, I expected males to make more trips of perhaps longer duration, resulting in longer total duration away from the burrow than females, as female deer mice typically provide all parental care and thus, across the year, females might need to spend more time inside their burrows throughout the night than males. I also hypothesized that mobile but non-independent young likely have little to gain from extensive exploration outside the burrow at a young age. Thus, I predicted that pre-weaned young would make fewer trips and spend less total time outside the burrow than adults. Finally, I described patterns of night-to-night residency in burrows, relative to sex and season, to better understand how deer mice use their nests under natural conditions.

Materials and Methods

Study site

This study was conducted from July 2003 through July 2005 on Konza Prairie Biological Station (Konza Prairie), a 3,487-ha native tallgrass prairie in northeastern Kansas. I installed 20 artificial burrows (Kaufman and Kaufman 1989) across two adjoining treatment units, units 2A and 1B. Unit 1B is burned every spring by prescribed fires (including 2003-2005), whereas unit 2A is burned every second year in the spring (including 2004).

Small mammal sampling

I checked all artificial burrows for deer mice about once per week in spring, summer, and autumn, and biweekly in winter [methods described in Kaufman and Kaufman (1989)]. At first capture, mice were marked uniquely with a numbered monel ear tag and a passive integrated transponder (PIT) tag (Chapter 1). In addition, burrow location, sex, age, reproductive status, and body mass of each deer mouse were recorded at each capture.

I live-trapped small mammals periodically from spring through autumn to ensure that all resident deer mice on the site were marked for monitoring trials (see below). I set multiple lines of Sherman live traps at stations 15 m apart across those portions of the site in which artificial burrows had been installed. I used a mixture of peanut butter and rolled oats for bait. Polyester fiberfill was provided in traps for insulation in spring and autumn. Deer mice were double-marked at first capture (see methods above) and trap location, sex, reproductive status, and body mass were recorded at each capture. Most of the trappable population (99.5%) used artificial burrows; only 1 of 206 PIT-tagged deer mice was captured only in a trap, but never in an artificial burrow.

Monitoring activity

I monitored activity of deer mice at artificial burrows by using a portable, automatic activity-monitoring system (Chapter 2). The monitoring system was comprised of a PIT-tag reader (2001F-ISO, Biomark, Inc., Boise, ID) coupled with an active infrared trail monitor (TM1550-Bat, TrailMaster, Inc., Lenexa, KS), placed at the entrance tunnel of an artificial burrow.

After manually checking the 20 artificial burrows, I selected 1-2 burrows for monitoring on the site. Placement and set-up of monitoring system at an artificial burrow took about 15 min. Subsequently, the activity-monitoring system recorded the time and PIT tag of any individual that entered or left the burrow. Once a trial had begun, deer mice could freely exit from and return to the artificial burrow through its entrance. Behavioral trials began > 1 h before sunset and lasted for 24-96 hours.

Data analysis

Some individuals used the same artificial burrow for multiple day-night periods within the 96-hour trials. To maintain independence among observations, only one night, selected at random from nights in the trial, was used per individual for analysis, unless otherwise noted. I used Shapiro-Wilk procedures and histograms to determine if data met assumptions of parametric statistics. When assumptions were not met, nonparametric statistical procedures were used. I used SAS Ver 8.01 and StatXact-3.0 for statistical analyses. A *P*-value < 0.05 was considered significant in all analyses, unless noted otherwise.

Emergence and retirement times

The time at which an animal first departed the burrow was termed "emergence," whereas the final time an individual returned to the burrow at the end of an activity period was termed "retirement." Any emergence occurring > 30 min. before sunset was considered a daylight emergence, and a retirement > 30 min. after sunrise was considered a daylight retirement. I compared numbers of males and females that emerged from their burrow during daylight with those emerging during nighttime by using log-likelihood tests (G). I used Spearman rank correlation (r_S) analysis to examine the relationship between emergence time and time of sunset and between retirement time and time of sunrise for each sex across seasons.

Analysis of activity patterns

Seven measures were used to characterize activity patterns of the deer mice. These measures were time of first emergence; total number of trips in a night; duration of trips; time of retirement; and total duration of time spent away from the burrow. I also characterized the pattern of return visits and subsequent stays inside the burrow, including duration of visits and total duration of visits inside the burrow. Relative to duration of trips or stays, I was interested in knowing how variable activity was throughout the night, so I further quantified the mean, median, first, shortest, longest trips and visits to the burrow in a night. Only mice that both started and ended the night inside the monitored burrow were used in this analysis. I tested for differences between the sexes within general age classes (adults and pre-weaning young) in the activity variables by using the Wilcoxon rank-sum (W) statistic and pooled within an age class if variables did not differ by sex. I compared each of the activity measures among young mice, adult males, and adult females by using Kruskal-Wallis tests (*H*).

I examined when in the night, relative to the order of all trips made in a night, each individual made its shortest and longest trips. For all individuals that made > 3 trips in a night, I tested whether the duration of the shortest and longest trips were distributed randomly among three categories of trips: first, middle, and last. Females (n = 36) used for this analysis made a total of 272 trips and, therefore, made 36 first trips, 200 middle trips, and 36 last trips. Likewise, males (n = 11) made 121 trips and, therefore, made 11 first trips, 99 middle trips, and 11 last trips. I first tested using a *G* test for seasonal differences between males and females relative to the distribution of trips among these categories. If no significant differences were found, the data were pooled. I then used Pearson's χ^2 test to compare the observed distribution of shortest and longest trips across first, middle, and last trips; the expected frequencies were based on the proportion of trips possible in each category.

I also tested each sex separately to assess what type of emergence tactics were used by males and females. That is, if a mouse emerged when light levels were too bright to initiate activity safely, it would return to the burrow immediately and wait for some period of time before emerging again. If this is the tactic used, then duration of first return visit consistently should exceed duration of the first paired trip outside of the burrow. To test this conjecture, I used a Wilcoxon signed-rank test (SR_+) to test the duration of the first trip to the duration of the first visit within each sex for all individuals that made > 1 trip in a night.

Night-to-night residency in burrows

Using the first night of every trial, I noted whether each mouse that started the night inside the monitored burrow also retired to that same burrow at the end of the night. I used *G* tests to test if the decision to stay in the same burrow over consecutive nights depended on starting status (i.e., in that burrow or not in that burrow). Further, I compared these patterns between sexes and among seasons.

Results

Emergence and retirement times by sexes and across seasons

Visual inspection of emergence and retirement times separated by trial days indicated that every case of daylight emergence (*n* = 30) occurred within the first 24 hours of the initiation of a trial (Fig. 9A) and not during the following day-night periods (Fig. 9B and 1C). Among males, the proportion of daylight emergence as compared to nighttime emergence differed significantly across seasons ($G = 13.6$, *d.f.* = 3, $P = 0.004$); daylight emergence was most common in summer (41% of 22 individuals), followed by autumn (12.5% of 8), spring (9.5% of 21), and winter (0% of 15). For females, proportion of emergences also varied significantly among seasons ($G = 20.4$, *d.f.* = 3, $P < 0.001$); daylight emergence was highest in summer (31.0% of 29 individuals), followed by autumn (7% of 30), spring (2% of 45), and winter (0% of 29). Males and females did not differ significantly in the high proportion of daylight emergence as compared to nighttime emergence in summer ($G = 0.53$, *d.f.* = 1, $P = 0.466$). The extremely low proportions of daylight emergence in other seasons compared to nighttime emergence suggest no differences between males and females in those seasons. The proportion of daylight emergence for adult deer mice (males and females combined) was significantly higher in summer (18 of 51 cases) than in other seasons combined (6 of 48 cases; $G = 30.1$, *d.f.* = 1, $P < 0.001$).

In all but one case, the individual did not return to the monitored burrow after its daylight emergence. I removed all but one of the emergences from subsequent data analyses because I interpreted these daylight emergences as a response by some deer mice to capture and handling by the investigator during the checking of artificial burrows (14 of 137 females; 16 of 60 males).

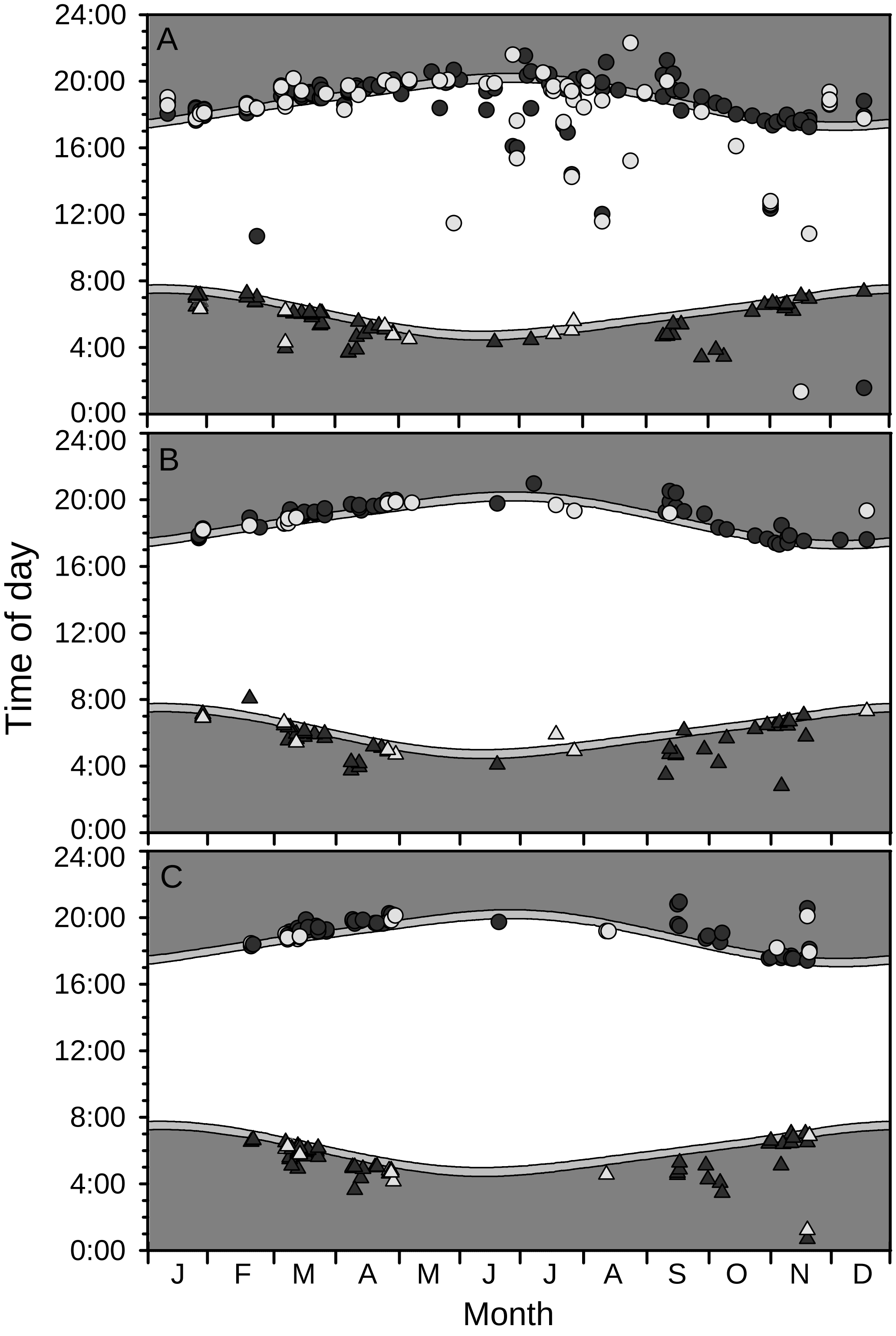

Figure 9. Time (Central Standard Time) of emergence and retirement of deer mice (*Peromyscus maniculatus*) in artificial burrows on Konza Prairie Biological Station relative to length

Figure 9 (cont.) of day, across the year (A: first 24 hours of trial; B: 24-48 hours of trial; C: 48-96 hours of trial; emergence time: circles; retirement time: triangles; males: light symbols; females: dark symbols; daylight hours: white area within each graph; twilight hours: light gray-shaded band within each graph; night hours: dark gray area within each graph).

The one early-emerging individual that was retained in the data set was a male that left 49 min before sunset, returned to the burrow multiple times throughout the night, and subsequently retired in the burrow at the end of the night.

Emergence time of females was correlated positively with timing of sunset across the year ($r_S = 0.88$, $n = 121$, $P < 0.001$), as was that of males ($r_S = 0.73$, $n = 55$, $P < 0.001$; Fig. 10). Females shifted their emergence time to more closely track sunset than did males, as evidenced by significantly different slopes of the best-fit linear regression line for each sex (Fig. 10). Within seasons, female emergence time was correlated with sunset in spring ($r_S = 0.80$, $n = 44$, $P < 0.001$) and autumn ($r_S = 0.86$, $n = 28$, $P < 0.001$), but not in summer ($r_S = 0.23$, $n = 20$, $P = 0.32$) or winter ($r_S = 0.01$, $n = 29$, $P = 0.954$). Male emergence time also was correlated positively with sunset in spring ($r_S = 0.63$, $n = 19$, $P = 0.004$) and autumn ($r_S = 0.79$, $n = 7$, $P = 0.036$), but not in summer ($r_S = 0.28$, $n = 14$, $P = 0.332$). However, emergence time of males in winter was correlated negatively with sunset ($r_S = -0.55$, $n = 15$, $P = 0.033$).

Deer mice typically retired to their burrows during nighttime; only one deer mouse (a male) returned after sunrise and this daylight retirement occurred in summer (Fig. 11). Female retirement time was related directly to time of sunrise across the year ($r_S = 0.84$, $n = 56$, $P < 0.001$), but males did not show this positive relationship ($r_S = 0.46$, $n = 13$, $P = 0.117$; Fig. 11). In contrast to the pattern found for emergence time and sunset, males and females showed similar responsiveness to change in time of sunrise across the year (Fig. 11), as displayed by similar slopes of linear regression lines for each sex. By season, retirement time of females was correlated significantly to sunrise in spring ($r_S = 0.85$, $n = 26$, $P < 0.001$) and autumn ($r_S = 0.66$, $n = 20$, $P = 0.002$), but not in winter ($r_S = 0.17$, $n = 10$, $P = 0.642$). No females retired in the monitored burrow during summer. By season, retirement time of males showed a marginally

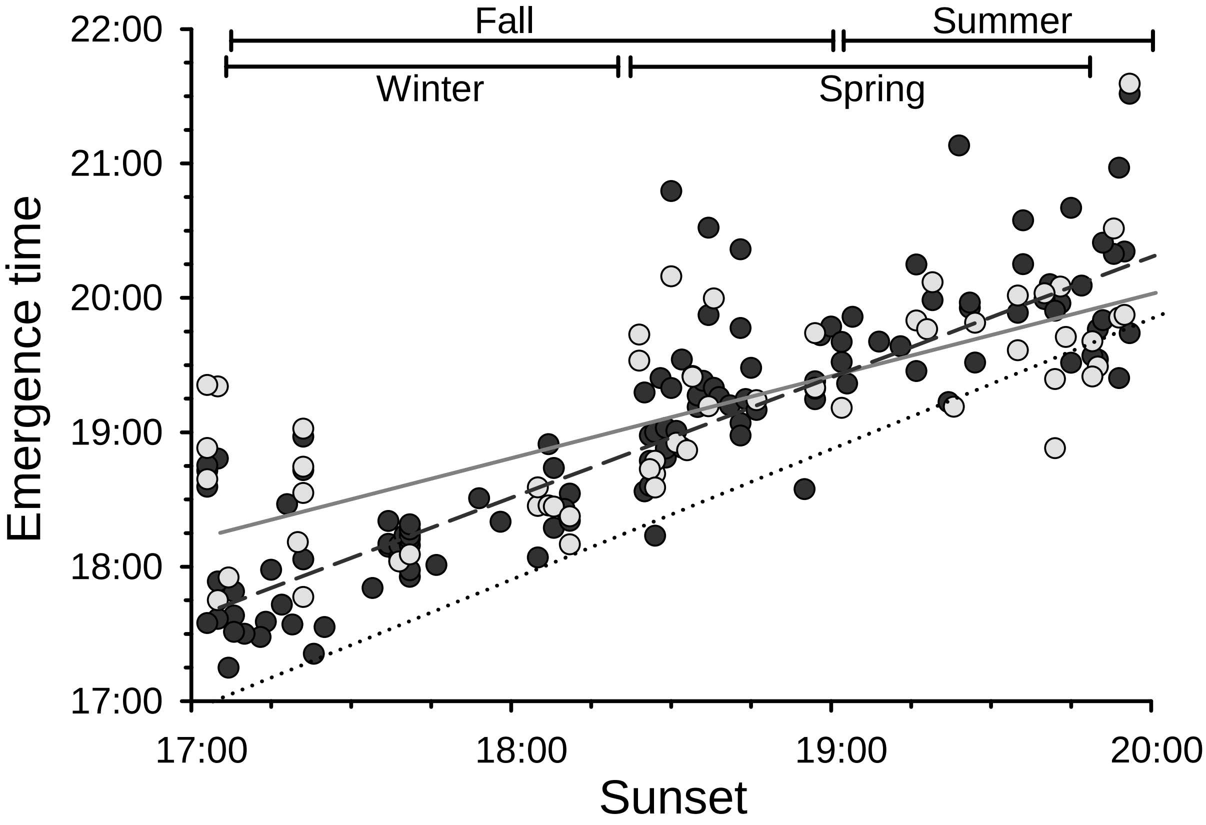

Figure 10. Relationship between time (Central Standard Time) of first emergence of deer mice and sunset. Dark circles and dashed line indicate females (*n* = 121), and light circles and solid line indicate males (*n* = 55). Lines are sex-specific linear regression lines; slopes of the regression lines differed between sexes across the four seasons (*Z* = 2.62, *P* = 0.004). Horizontal lines across top show range in sunset time within each season. Dotted line is line of equality; points above line indicate emergence after sunset.

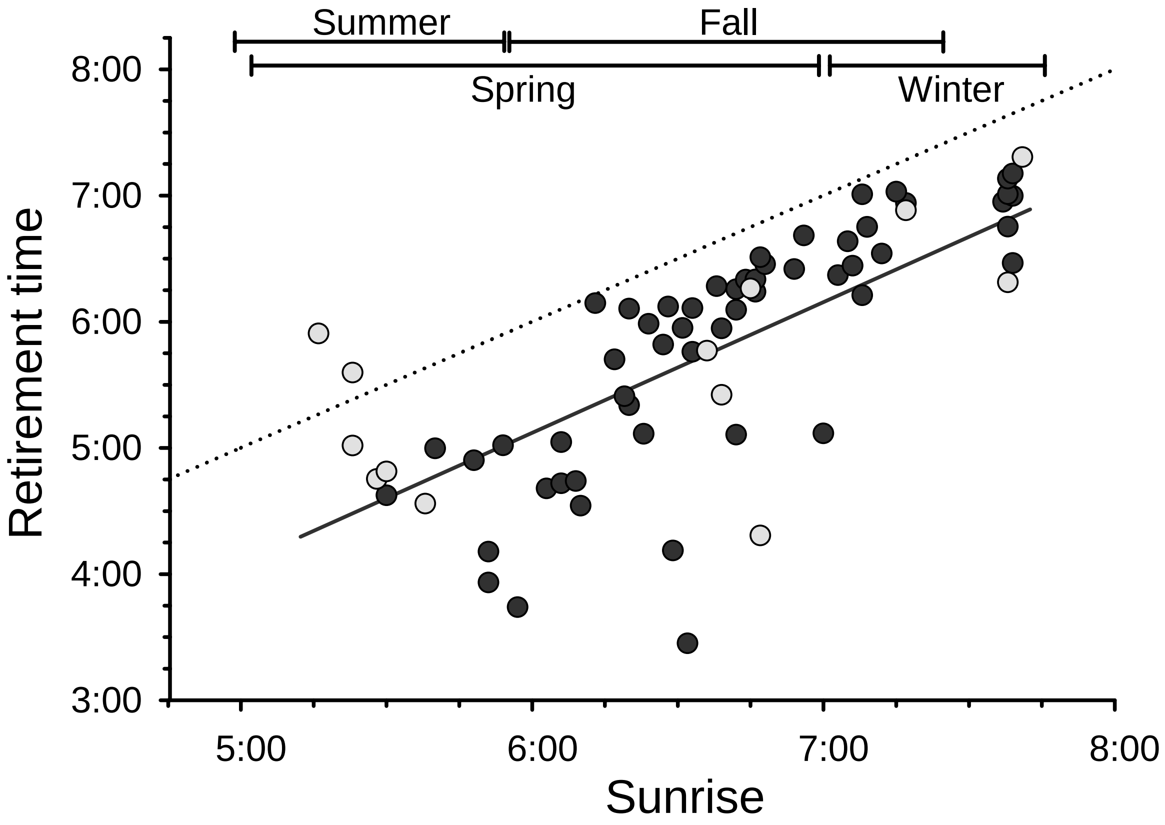

Figure 11. Relationship between time (Central Standard Time) of final retirement to burrows by deer mice and sunrise. Dark circles indicate females (*n* = 56), and light circles indicate males (*n* = 13). Solid dark line is sex-pooled linear regression line, as slopes of regression lines did not differ between sexes (*Z* = 1.14, *P* = 0.127). Horizontal lines at top show range in sunset time within each season. Dotted line is line of equality; points below line indicate retirement before sunrise. Two retirements before 3:00 a.m. are not shown.

negative relationship to time of sunrise in summer ($r_S = -0.95$, $n = 4$, $P = 0.051$), but no relationship to sunrise in spring ($r_S = 0.09$, $n = 6$, $P = 0.872$). Autumn and winter could not be tested, because only one and two males retired to the monitored burrows in those two seasons, respectively.

Nightly activity patterns relative to age and sex

Activity parameters were similar between male and female young mice [number of trips ($W = 51.0$, $P = 0.616$), emergence time ($W = 80.0$, $P = 0.151$), mean trip ($W = 45.0$, $P = 0.367$), median trip ($W = 56.5$, $P = 0.894$), first trip ($W = 64.5$, $P = 0.686$), longest trip ($W = 57.5$, $P = 0.947$), shortest trip ($W = 59.5$, $P = 0.946$), total duration away ($W = 39.0$, $P = 0.193$), retirement time ($W = 76.0$, $P = 0.243$), mean visit ($W = 30.0$, $P = 0.139$), median visit ($W = 14$, $P = 0.007$), first visit ($W = 41.0$, $P = 0.515$), longest visit ($W = 41.0$, $P = 0.518$), shortest visit ($W = 28.5$, $P = 0.100$), total duration of visits ($W = 38.0$, $P = 0.382$)], so sexes were combined for comparison against adults of each sex. Young, adult male, and adult female mice differed in all parameters related to trips outside the burrow (Fig. 12A): emergence time ($H = 19.85$, *d.f. = 2*, $P < 0.001$), average trip ($H = 37.43$, *d.f. = 2*, $P < 0.001$), median trip ($H = 31.53$, *d.f. = 2*, $P < 0.001$), first trip ($H = 29.90$, *d.f. = 2*, $P < 0.001$), longest trip ($H = 20.60$, *d.f. = 2*, $P < 0.001$), shortest trip ($H = 30.62$, *d.f. = 2*, $P < 0.001$), total duration ($H = 23.77$, *d.f. = 2*, $P < 0.001$), and number of trips ($H = 10.65$, *d.f. = 2*, $P = 0.005$). Young emerged later than adult males ($W = 96$, $P < 0.0001$) and adult females ($W = 1223$, $P = 0.0187$); adult males emerged earlier than adult females ($W = 259$, $P = 0.009$). Young took a similar number of trips as adult males ($W = 218.5$, $P = 0.786$), but more trips than adult females ($W = 1248$, $P = 0.004$). Adult males took more trips than adult females ($W = 572.5$, $P = 0.008$). Mean trip duration of young was shorter than that of adult males ($W = 274$, $P = 0.0009$) and adult females ($W = 354$, $P < 0.001$). Mean trip duration of adult males was shorter than adult females ($W = 277$, $P = 0.012$). Median trip duration also was shorter for young than adult males ($W = 241.5$, $P = 0.037$) and adult females ($W = 395$, $P < 0.001$); adult males made shorter median trips than females ($W = 220$, $P = 0.008$). Duration of the first trip of the night was similar for young mice and adult males ($W = 259.5$, $P = 0.383$), but shorter than those of adult females (versus young: $W = 439$, $P < 0.001$; versus adult males: $W = 187$, $P < 0.001$). Duration of longest trip by young was shorter than the longest trips of adults (males: $W = 258$, $P = 0.007$; females: $W = 483$, $P < 0.001$), but adult males and females did not differ ($W = 327$, $P = 0.388$). Shortest trips of young mice and adult males were not different ($W = 208$, $P = 0.418$), but were shorter than those of adult females ($W = 421$, $P < 0.001$). Shortest trips of males were shorter than those of females ($W = 182.5$, $P < 0.001$). Total duration of time spent outside was shorter for young than adult males ($W = 202$, $P = 0.002$) and females ($W = 467$, $P < 0.001$), but adult males and females did not differ ($W = 370$, $P = 0.883$).

Young, adult male, and adult female mice differed in most parameters describing time spent inside the burrow each night, including retirement time ($H = 7.64$, *d.f. = 2*, $P = 0.022$), mean visit ($H = 6.38$, *d.f. = 2*, $P = 0.041$), median visit ($H = 18.66$, *d.f. = 2*, $P < 0.001$), first visit ($H = 17.94$, *d.f. = 2*, $P < 0.001$), shortest visit ($H = 17.68$, *d.f. = 2*, $P < 0.001$), but not in longest visit ($H = 2.96$, *d.f. = 2*, $P = 0.228$) or total time spent inside the burrow ($H = 2.20$, *d.f. = 2*, $P = 0.333$). Young retired to the burrow significantly earlier than adults (males: $W = 171$, $P = 0.032$; females: $W = 1228$, $P = 0.007$; Fig. 12B), but adult males and females retired about the same time ($W = 423.5$, $P = 0.631$). Young were similar to adult males in duration of median visits ($W = 179$, $P = 0.901$), first visits ($W = 176$, $P = 0.999$), and shortest visits ($W = 182$, $P = 0.799$), all of which were significantly shorter than those for adult females (median visit: $W = 416$, $P < 0.001$; first visit: $W = 424$, $P < 0.001$; shortest visit: $W = 421$, $P < 0.001$). Adult males had shorter median ($W = 199.5$, $P = 0.006$), first ($W = 200$, $P = 0.004$), and shortest ($W = 209$,

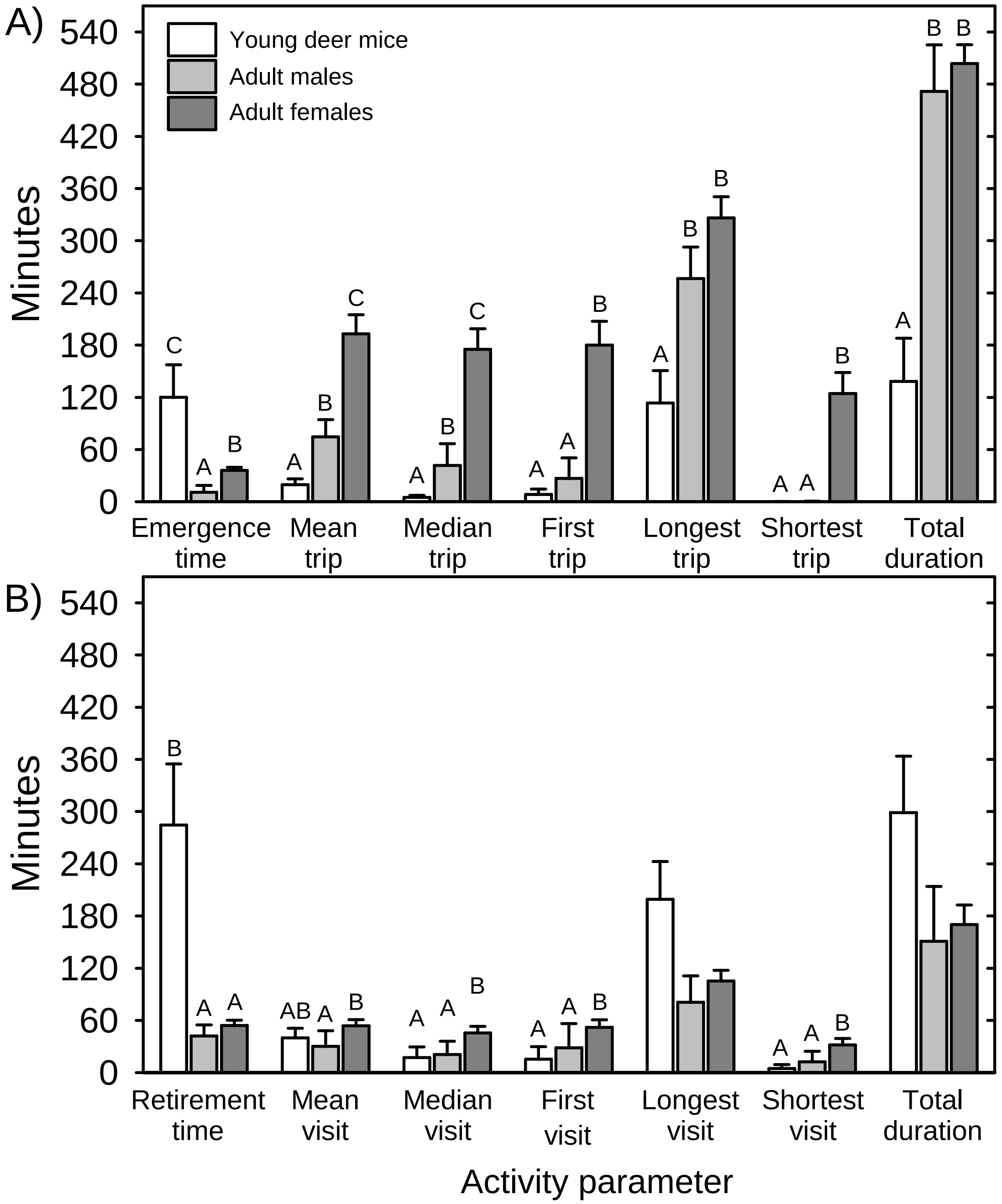

Figure 12. Amount of time spent making A) trips outside and B) return visits inside artificial burrows by deer mice within a single night. Emergence time refers to minutes before sunset, retirement time is minutes before sunrise. White bars are young males and females combined (*n* = 22), light gray bars are adult males (*n* = 11), dark bars are adult females (*n* = 57). Bars represent means ± 1SE. Within each activity parameter, bars sharing the same letter did not differ (Wilcoxon rank-sum pairwise comparisons with *P* > 0.10).

$P = 0.01$) visits than adult females. Mean visits of young were intermediate to and not different from those of adults (young vs. adult males: $W = 152$, $P = 0.322$ young vs. adult females: $W = 603$, $P = 0.135$, but mean visits of adult males were shorter than those of females ($W = 221$, $P = 0.02$). Within each individual, duration of the first trip away from the burrow was consistently longer than duration of the first visit to the burrow for females, but not for males (females: $SR_+ = -3.69$, $P < 0.001$ males: $SR_+ = -0.051$, $P = 0.959$).

Given my sample sizes, no obvious differences were evident between males and females as to when the longest trips occurred during a night (first trips: 9% of males, 14% of females; middle trips: 64% males, 50% females; last trips: 27% males, 36% females). Based on pooled data for males and females, longest trips were more likely to occur during last trips [observed (O): 16, expected (E): 5.6] than during first trips (O: 6, E: 5.6) or middle trips (O: 25, E: 35.7; $\chi^2 = 22.3$, $d.f. = 2$, $P < 0.001$). Likewise, no obvious differences were apparent between males and females for when shortest trips occurred (first trips: 18% of males, 22% of females; middle trips: 55% males, 64% females; last trips: 27% males, 14% females). Based on pooled data for males and females, shortest trips were marginally more likely to occur during first trips (O: 10, E: 5.6) and last trips (O: 8, E: 5.6) than during middle trips (O: 29, E: 35.7; $\chi^2 = 5.6$, $d.f. = 2$, $P = 0.06$).

Night-to-night residency in burrows

Generally, choice of a retirement burrow depended on whether a mouse started the night inside that burrow or visited that burrow during the night ($G = 67.7$, $d.f. = 1$, $P < 0.001$). Mice that started in a burrow retired there 46% of the time (77 of 168 cases), whereas mice that visited a monitored burrow retired there only 5% of the time (6 of 122 cases). Further, this pattern persisted when males and females were examined separately (males: $G = 11.9$, $d.f. = 1$, $P <$

0.001; females: $G = 33.8$, $d.f. = 1$, $P < 0.001$). For males, 24% of 45 mice that started in a burrow retired there, whereas only 4% of 79 mice that visited a burrow retired there. Females were even more likely than males to retire in the burrow in which they started (54% of 123 mice) than in a burrow they visited (7% of 43 mice).

Mice that started in a burrow during a night in spring, summer, or autumn were more likely to retire in that burrow than were mice that only visited a burrow in those seasons (spring: $G = 35.0$, $d.f. = 1$, $P < 0.001$; summer: $G = 9.29$, $d.f. = 1$, $P = 0.002$; autumn: $G = 27.0$, $d.f. = 1$, $P < 0.001$). This difference was greatest in autumn (start: 65% of 31 mice; visit: 6% of 33 mice) followed by spring (start: 59% of 56 mice; visit: 5% of 41 mice), and summer (start: 18% of 33 mice; visit: 0% of 35 mice). In contrast, this pattern, although similar in winter, was not significant ($G = 2.51$, $d.f. = 1$, $P = 0.113$; start: 38% of 48 mice; visit: 15% of 13 mice).

Discussion

PIT-tag readers have monitored visits by small mammals to fixed, target areas, including seed trays for white-footed mice (*Peromyscus leucopus*; Burns 2005) and along aboveground runways of prairie and meadow voles (*Microtus ochrogaster* and *M. pennsylvanicus*, respectively; Harper and Batzli 1996). I expanded the use of this technology to quantify patterns of activity by deer mice at the burrow *in situ* and compared patterns of activity between sexes and ages and across seasons.

Emergence and retirement times

Activity of adult deer mice, undisturbed by an investigator, was nocturnal throughout the year; nearly all mice (98.6 %) emerged soon after sunset and retired before sunrise. This finding was consistent with studies of activity of deer mice in the laboratory (Jaeger 1982; Kavanau 1967, 1969) and with trapping studies completed in the field (Bruseo and Barry 1995; Harling 1971; O’Farrell 1974).

Daylight emergences, recorded most frequently in summer, occurred only on the first day of monitoring trials after deer mice were handled earlier that day. These daylight emergences likely were escape responses to being handled and the greater likelihood of daylight emergence in summer might have been associated with an increased risk of predation in the burrow during summer. Gopher snakes (*Pituophis catenifer*), eastern yellowbelly racers (*Coluber constrictor*), Great Plains rat snakes (*Elaphe emoryi*), milk snakes (*Lampropeltis triangulum*), and speckled kingsnakes (*L. getula*) were present at the study site and active during summer; these snakes readily entered the artificial burrows. In another study conducted in north-central Kansas, I documented a PIT-tagged gopher snake that entered an artificial burrow in the daytime during a monitoring trial and consumed a female deer mouse and her dependent offspring. Further, seasonal patterns of snake activity, which affects the size and composition of breeding groups, has been reported for prairie voles in underground burrows (Getz et al. 1990). It should be noted, however, that many other ecological variables (i.e., food availability, temperature, wind intensity) fluctuate seasonally and could confound my assertion that predation pressure by snakes influences probability of premature evacuation.

Emergence time of deer mice was correlated positively with sunset across the year and within both sexes in spring and autumn. As indexed by capture time in live traps, commencement of foraging in deer mice varied with time of sunset (Bruseo and Barry 1995). Onset of darkness also was an important synchronizer of peak activity of deer mice in the laboratory (Sheffield and Andrews 1980). Spring and autumn are times of peak reproduction and, therefore, periods of larger nutritional demands for prairie deer mice than in non-breeding periods. During these periods of higher nutritional stress, individuals, especially females, might be more attentive to photoperiod and more efficient in their use of time outside the burrow.

Emergence time of males during winter was negatively correlated with time of sunset; cold ambient temperatures might have delayed the emergence of these small endotherms. Environmental temperature has been suggested as the most important abiotic factor affecting time and energy budgets of animals (Huey 1991). Male deer mice maintained at 10°C in the laboratory reduced their activity when compared to males maintained at 21°C (Sheffield and Andrews 1980). Deer mice likely face more extreme winter temperatures in their natural environment. For example, daily minimum and maximum temperatures averaged -4.2°C and 5.6°C, respectively, on Konza Prairie in winter 2005. This range in average daily temperatures is well below temperatures that curtailed activity of male deer mice in the laboratory (Sheffield and Andrews 1980). Alternatively, winter nights might be sufficiently long (i.e., enough hours of darkness) to allow for a delay in commencement of activity. Deer mice in their natural environment on Konza Prairie experience natural light:dark (L:D) cycles of 15:9 L:D on the summer solstice, as compared to 9.5:14.5 L:D on the winter solstice. Male deer mice began activity in the laboratory well after sunset under short day hours that simulated winter, whereas they began activity at or slightly before sunset under long day hours that simulated summer (Underwood et al. 1985).

For the entire sampling period, retirement times of adult deer mice were correlated with sunrise. Deer mice, in the laboratory, immediately stopped running on wheels at simulated dawn, regardless of the real time (Kavanau 1969). Retirement times of females always occurred before sunrise and showed positive relationships with time of sunrise across the year, and during spring and autumn, but not winter. Regardless of patterns of nighttime activity, females were never active outside the burrow after sunrise. Consistent with this observation, lactating deer mice forced to work for their food in the laboratory never extended their activity past simulated sunrise, regardless of their nutritional deficit (Perrigo 1987). Retirement times of male deer mice at Konza Prairie were not correlated with time of sunrise. My research result is similar to a trapping study in southern Yukon where deer mice shifted to earlier activity as hours of daylight increased in summer, whereas termination of their activity remained constant and showed no relationship to photoperiod (Gilbert et al. 1986).

Activity patterns by males and females

Patterns of activity of males and females differed in several ways. Although overall time spent outside of the burrow did not differ between the sexes, on average, males emerged earlier (males: 10.9 ± 7.9 (SE) min, females: 36.1 ± 3.5 min after sunset) and made more trips (males: 10.4 ± 2.8 trips, females: 5.4 ± 0.8 trips) of shorter duration than females (mean trip duration, males: 10.9 ± 7.9 min, females: 36.1 ± 3.5 min; median trip duration, males: 41.8 ± 24.9 min, females: 175.2 ± 23.8 min; first trip duration, males: 26.8 ± 23.6 min, females: 180.0 ± 27.3 min; shortest trip duration, males: 0.4 ± 0.2 min, females: 124.4 ± 24.3 min). Timing of peak activity for leaf-eared mice (*Phyllotis xanthopygus*) in the laboratory was about 50 min. earlier for males than females (Kramer and Birney 2001). Males might become active before females to ensure that they are active when females emerge. This earlier emergence by individual males would allow them to increase their potential reproductive success by finding females in estrus and mating with these available reproductive females before their competitors do. In sagebrush desert in Nevada, male deer mice were captured more often in live traps than females during multiple trapping periods within nights (O'Farrell 1974). If activity can be indexed by numbers of individuals captured through a night, this study would suggest that males are more active than females. An assumption inherent in using captures as a measure of activity is that each individual and both sexes must have equal trappability or catchability in the live traps. Results from my study suggest that this assumption might not be true, as adult males and females, on average, were active for the same length of time during a night (males: 472 ± 53 min; females: 504 ± 22 min). Males and females were active for the same total amount of time, but I found that they differed relative to number of trips made and duration of individual trips during a night.

Although total time spent in burrows during the night was similar for males and females, return visits and subsequent stays by males typically were shorter and more frequent than that by females. The observed pattern of visits by females to the burrows included both reproductive and non-reproductive females. Females with dependent young may be more tied to the burrow than males or non-reproductive females. That is, lactating females likely spend more time in the burrow to huddle with and nurse their growing offspring. My samples of non-reproductive females and males were too few to test whether they differed in their patterns of visits to the burrow during a night.

Duration of the first trip out of the burrow was consistently longer than the first return visit to the burrow for females, but not for males. Why should such a difference occur? Perhaps, males exhibit greater light-sampling behavior than do females (DeCoursey 1986). When a monitored burrow contained a male-female pair, males left from 1 to 20 minutes earlier than the females in the burrow. Further, records from my PIT tag readers showed that deer mice often spent considerable time loitering in the entrance tunnel of the artificial burrow before first emergence. These observations are suggestive that deer mice use light-sampling behavior as a means for photic entrainment of circadian rhythms. Social *zeitgebers* (i.e., external cues for entrainment of rhythms) have received increased attention in studies of entrainment of circadian rhythms in mammals (Mistlberger and Skene 2004). Perhaps, light serves as the primary *zeitgeber* for deer mice, but in the presence of a male, a female may also use his activity for synchronization of circadian rhythms. In the lab, cohabitant deer mice entrain to the activity of others through social interactions (Crowley and Bovet 1980). Finally, males might make more mistakes than females in their efforts to begin nightly activity, but this explanation appears unlikely given the low variability in early emergence of males from burrows, and the likelihood that they do use light-sampling behavior.

For deer mice, shortest trips were most prevalent at the beginning and end of the night, the times at which levels of ambient light are changing most rapidly. Flying squirrels (*Glaucomys volans*) also increased the number of trips made and, therefore, decreased trip length at the end of their active period (DeCoursey 1986). Longest trips of deer mice, on the other hand, occurred last more often than expected; a pattern that is consistent with results from a food-deprivation study of deer mice (Jaeger 1982). In that laboratory study, individual mice, allowed access to food only in the final six hours of darkness, ate more food, lost less weight, and experienced higher survival than those allowed access to food only in the initial six hours of darkness. These patterns suggested that deer mice likely have a temporal routine of early-night foraging and hoarding, but fill their stomach in late-night hours in anticipation of daytime fasting. Under natural conditions, mice that are unsuccessful in obtaining enough food items in the early night likely are forced to use the latter portion of the nocturnal period to find food to support them through the next diurnal period, when they do not leave their burrow to forage.

Night-to-night residence in a burrow

Generally, choice of a retirement burrow depended on whether the mouse started the night inside that burrow. Mice that were inside a burrow at dusk chose to retire there much more frequently than mice that visited the burrow during the night. However, of those mice that were inside the monitored burrow at the start of a night, only 46% of them retired there. Thus, residency in any one burrow seemed to be rather transient over the short term. The finding that deer mice use multiple nests over consecutive nights is not surprising. Shifting from one nest site to another while raising young is common in lactating *Peromyscus* (Havelka and Millar 2000; Howard 1949; Sharpe and Millar 1990). Further, lactating deer mice also move their offspring between successive nests, possibly as a tactic to avoid predation of the young (Sharpe and Millar 1990).

Within sexes, the odds of a mouse retiring to the burrow in which it started were higher for females (54% of cases) than males (24%), a pattern that might have been influenced by some females caring for dependent young. These sex-specific patterns are expected if males maximize their reproductive success by patrolling and searching their home ranges for available females and visiting multiple burrows within a night in search of mates. In my study, breeding typically peaked in spring and fall, but breeding can occur in every month in Kansas (G. A. Kaufman, personal communication), so males could be using this strategy throughout the year. In contrast, females would be more likely to be sedentary if they maximize their reproductive success by maintaining access to resources (e.g., a nest) for reproduction (Clutton-Brock 1989).

In all seasons except winter, mice were more likely to retire to a burrow if they started there than if they only visited there during the night. Group size in occupied burrows increased from typically one or two adults in warmer months up to 13 adults in a burrow in winter. This is similar to deer mice in artificial burrows in mixed-grass prairie in Kansas in which numbers of deer mice occupying a single burrow ranged from 1 to 12 (Kaufman and Kaufman 1989). The larger numbers of deer mice occupying a single burrow occurred in winter and not in summer. Deer mice likely huddle together in colder months for thermoregulatory purposes. Huddles of conspecifics would reduce thermal conductance and allow individuals to reduce metabolic rates to conserve energy (Andrews and Belknap 1986; Vickery and Millar 1984). This conservation of energy during periods of cold ambient temperatures might be more important than maintenance of "ownership" ties to specific burrows.

Literature Cited

Andrews, R. V., and R. W. Belknap. 1986. Bioenergetic benefits of huddling by deer mice (*Peromyscus maniculatus*). Comparative Biochemistry and Physiology A: Comparative Physiology 85:775-778.

Bacigalupe, L. D., E. L. Rezende, G. J. Kenagy, and F. Bozinovic. 2003. Activity and space use by degus: a trade-off between thermal conditions and food availability. Journal of Mammalogy 84:311-318.

Barry, Jr., R. E., A. A. Fressola, and J. A. Bruseo. 1989. Determining the time of capture for small mammals. Journal of Mammalogy 70:660-662.

Blanchong, J., T. McElhinny, M. Mahoney, and L. Smale. 1999. Nocturnal and diurnal rhythms in the unstriped Nile grass rat, *Arvicanthus niloticus*. Journal of Biological Rhythms 14:364-377.

Blanchong, J. A., and L. Smale. 2000. Temporal patterns of activity of the unstriped Nile rat, *Arvicanthus niloticus*. Journal of Mammalogy 81:595-599.

Boone, J. D., and B. L. Keller. 1993. Temporal and spatial patterns of small mammal density and species composition on a radioactive waste disposal area: the role of edge habitat. Great Basin Naturalist 53:341-349.

Brady, M. J., and N. A. Slade. 2004. Long-term dynamics of a grassland rodent community. Journal of Mammalogy 85:552-561.

Bruseo, J. A., and R. E. Barry, Jr. 1995. Temporal activity of syntopic *Peromyscus* in the central Appalachians. Journal of Mammalogy 76:78-82.

Burns, C. E. 2005. Behavioral ecology of disturbed landscapes: the response of territorial animals to relocation. Behavioral Ecology 16:898-905.

Clutton-Brock, T. H. 1989. Mammalian mating systems. Proceedings of the Royal Society of London Series B 236:339-372.

Clutton-Brock, T. H., and A. C. J. Vincent. 1991. Sexual selection and potential reproductive rates of males and females. Nature 351:58-60.

Crowley, M., and J. Bovet. 1980. Social synchronization of circadian rhythms in deer mice (*Peromyscus maniculatus*). Behavioral Ecology and Sociobiology 7:99-105.

Deboer, T., and I. Tobler. 2000. Running wheel size influences circadian rhythm period and its phase shift in mice. Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology 186:969-973.

DeCoursey, P. J. 1986. Light-sampling behavior in photoentrainment of a rodent circadian rhythm. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 159: 161-169.

Dewey, M. J., and W. D. Dawson. 2001. Deer mice: "The *Drosophila* of North American mammalogy". Genesis 29:105-109.

Dewsbury, D. A. 1980. Wheel-running behavior in 12 species of muroid rodents. Behavioral Processes 5:271-280.

Eccard, J. A., J. Meyer, and J. Sundell. 2004. Space use, circadian activity pattern, and mating system of the nocturnal tree rat *Thallomys nigricauda*. Journal of Mammalogy 85:440-445.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Falls, J. B. 1968. Activity. Pp. 543-570 in Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Special Publication 2, American Society of Mammalogists.

Getz, L. L., N. G. Solomon, and T. M. Pizzuto. 1990. The effects of predation of snakes on social organization of the prairie vole, *Microtus ochrogaster*. American Midland Naturalist 123: 365-371.

Gilbert, B. S., C. B. Cichowski, D. Talrico, and C. J. Krebs. 1986. Summer activity patterns of three rodents in the southwestern Yukon. Arctic 39:204-207.

Gilbert, B. S., and C. J. Krebs. 1991. Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon 1973-1989. Holarctic Ecology 14:250-259.

Halle, S. 1995. Diel pattern of locomotor activity in populations of root voles, *Microtus oeconomus*. Journal of Biological Rhythms 10:211-224.

Halle, S., N. C. Stenseth, eds. 2000. Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin.

Halle, S., D. Weinert. 2000. Recording activity: free choice among drawbacks. Pp. 286-293 in Activity patterns in small mammals: an ecological approach (S. Halle and N. C. Stenseth, eds.). Springer-Verlag, Berlin.

Handley, C. O. 1999. Deer mouse, *Peromyscus maniculatus*. Pp. 575-577 in The Smithsonian book of North American mammals (D. E. Wilson and S. Ruff, eds.). Smithsonian Institution, Washington, DC.

Harling, J. 1971. A technique for precisely timing captures of *Peromyscus maniculatus*. Canadian Journal of Zoology 49:1275-1277.

Harney, B. A., and R. D. Dueser. 1987. Vertical stratification of activity of two *Peromyscus* species: an experimental analysis. Ecology 68:1084-1091.

Harper, S. J., and G. O. Batzli. 1996. Monitoring use of runways by voles with passive integrated transponders. Journal of Mammalogy 77:364-369.

Havelka, M. A., and J. S. Millar. 2000. Use of artificial nest sites as a function of age of litter in *Peromyscus leucopus*. American Midland Naturalist 144:152-158.

Heske, E. J., J. H. Brown, and S. Mistry. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology 75:438-445.

Howard, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contributions from the Laboratory of Vertebrate Biology, University of Michigan 43:1-50.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91-S115.

Jackson, T. P. 1998. The diurnal activity of Brants' whistling rat (*Parotomys brantsii*): the effect of seasonal and physical conditions. Transactions of the Royal Society of South Africa 53:227-236.

Jaeger, M. M. 1982. Feeding pattern in *Peromyscus maniculatus*: the response to periodic food deprivation. Physiology & Behavior 28:83-88.

Kalcounis-Rüppell, M. C., and J. S. Millar. 2002. Partitioning of space, food, and time by syntopic *Peromyscus boylii* and *P. californicus*. Journal of Mammalogy 83:614-625.

Kaufman, D. W., and G. A. Kaufman. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). Journal of Mammalogy 63:309-312.

Kaufman, D. W., and G. A. Kaufman. 1990. Small mammals of wheat fields and fallow wheat fields in north-central Kansas. Transactions of the Kansas Academy of Science 93:28-37.

Kaufman, D. W., G. A. Kaufman, and B. K. Clark. 2000. Small mammals in native and anthropogenic habitats in the Lake Wilson area of north-central Kansas. Southwestern Naturalist 45:45-60.

Kaufman, G. A., and D. W. Kaufman. 1989. An artificial burrow for the study of natural populations of small mammals. Journal of Mammalogy 70:656-659.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

Kavanau, J. L. 1963. Continuous automatic monitoring of the activities of small captive animals. Ecology 44:95-110.

Kavanau, J. L. 1967. Behavior of captive white-footed mice. Science 155:1623-1639.

Kavanau, J. L. 1969. Influence of light on activity of the small mammals, *Peromyscus* spp., *Tamias striatus*, and *Mustela rixosa*. Experientia 25:208-209.

Kenagy, G. J. 1976. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia 24:105-140.

Koprowski, J. L., and M. C. Corse. 2005. Time budgets, activity periods, and behavior of Mexican fox squirrels. Journal of Mammalogy 86:947-952.

Kramer, K. M., and E. C. Birney. 2001. Effect of light on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. Journal of Mammalogy 82:535-544.

Lockard, R. B., and D. H. Owings. 1974. Moon related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. Animal Behavior 22:262-273.

MacCracken, J. G., D. W. Uresk, and R. M. Hansen. 1985. Rodent-vegetation relationships in southeastern Montana. Northwest Science 59:272-278.

Mistlberger, R. E., and D. J. Skene. 2004. Social influences on mammalian circadian rhythms: animal and human studies. Biological Reviews 79:533-556.

O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. Journal of Mammalogy 55:809-823.

Olson, R. A., and M. J. Brewer. 2003. Small mammal populations occurring in a diversified winter wheat cropping system. Agriculture, Ecosystems & Environment 95:311-319.

Perrigo, G. 1987. Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. Animal Behavior 35:1298-1316.

Rezende, E. L., and F. Bozinovic. 2001. Patterns of daily activity in the leaf-eared mouse (*Phyllotis darwini*): effects of food availability. Journal of Arid Environments 47:95-100.

Rosenzweig, M. L. 1974. On the optimal aboveground activity of bannertail kangaroo rats. Journal of Mammalogy 55:193-199.

Sharpe, S. T., and J. S. Millar. 1990. Relocation of nest sites by female deer mice, *Peromyscus maniculatus borealis*. Canadian Journal of Zoology 68:2364-2367.

Sheffield, Jr., M. V. 1980. Interactions of ambient temperature and photoperiod on deer mouse *Peromyscus maniculatus* energetics. Comparative Biochemistry and Physiology A: Comparative Physiology 67:103-116.

Sherwin, C. M. 1998. Voluntary wheel-running: a review and novel interpretation. Animal Behavior 56:11-27.

Silva, M. 2001. Abundance, diversity, and community structure of small mammals in forest fragments in Prince Edward Island National Park, Canada. Canadian Journal of Zoology 79:2063-2071.

Underwood, H., J. M. Whitsett, and T. G. O'Brien. 1985. Photoperiodic time measurement in the male deer mouse, *Peromyscus maniculatus*. Biology of Reproduction 32:947-956.

Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska, USA. Canadian Journal of Zoology 59:1045-1061.

Vickery, W. L., and J. S. Millar. 1984. The energetics of huddling by endotherms. Oikos 43:88-93.

Wolfe, J. L., and C. T. Summerlin. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. Animal Behavior 37:410-414.

Wolff, J. O. 1994. Reproductive success of solitarily and communally nesting white-footed mice and deer mice. Behavioral Ecology 5:206-209.

Wolff, J. O., and D. S. Durr. 1986. Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 67:409-412.

Wolton, R. J. 1983. The activity of free ranging wood mice *Apodomys sylvaticus*. Journal of Animal Ecology 52:781-794.

Yamada, N., K. Shimoda, K. Takahashi, and S. Takahashi. 1990. Relationship between free-running period and motor activity in blinded rats. Brain Research Bulletin 25:115-119.

Chapter 4: Reproduction and female activity patterns in the deer mouse in tallgrass prairie.

Abstract

Reproduction imposes high energetic costs on female small mammals. Growth rates of developing neonates are maximized by constant provisioning of warmth and nourishment, but in species with uniparental female care, the mother is obligated to leave the nest to acquire food resources if she cannot utilize body reserves or cached food items. In addition, energetic costs of reproduction may vary with the changing thermal and nutritional needs of growing young throughout the period of lactation. I examined activity of female deer mice (*Peromyscus maniculatus*) at shelter sites under natural conditions in native tallgrass prairie from July 2003 though July 2005. First, I compared reproductive females (i.e., in late pregnancy or lactating) and non-reproductive, adult females (i.e., non-lactating, and not in late pregnancy) relative to a suite of parameters describing trips away from and visits to the burrow. Second, I examined whether activity of females changed from late pregnancy through the first 20 days of lactation reflect needs of developing offspring. Reproductive females emerged later, made fewer trips of generally longer duration, and spent shorter total amounts of time away from the burrow each night than non-reproductive females. Return visits of reproductive females were of longer duration than non-reproductives, but total time spent inside and time of retirement for the night did not differ relative to reproductive status. From parturition through lactation, activity of mothers tended to increase and peak as the young grew larger and gained improved homeothermic and sensory capabilities associated with weaning. My results provide evidence that, in the wild, reproduction forces females to modify their activity in several important ways, which may influence survival of both mothers and offspring.

Introduction

Small mammals typically operate near the physiological limits of homeotherms (Hayes 1989; Ochocinska and Taylor 2005; Weiner 2000), making reproduction a costly endeavor. For example, a female *Peromyscus* (Rodentia: Muridae) has only a small buffer (1.2-1.7 days of fat reserves) against restricted daily foraging (Caldwell and Connell 1968). Lactation further reduces this buffer, leaving only 0.7-1.2 days of fat reserves (Caldwell and Connell 1968); therefore, suggesting that lactating females must forage every night. Short-term costs of reproduction often are quantified by means of increased nutritional intake required above non-reproductive levels (Liu et al. 2003). To strictly monitor amounts of food consumed, studies typically are conducted under controlled laboratory conditions where food is provided *ad libitum*. In contrast, food typically is not available *ad libitum* in natural environments; therefore, females might need to take risks to search for food to meet the increased energetic needs generated by reproduction, especially lactation.

Although numerous studies have quantified energetic costs of reproduction in rodents (Antinuchi and Busch 2001; Degen et al. 2002; Künkele 2000; Liu et al. 2003; Migula 1969; Millar 1975; Sadleir et al. 1973; Sikes 1995; Zenuto et al. 2002), little has been done to consider these costs in an ecological context (Bronson 1985; Halle and Stenseth 2000; Weiner 2000). Activity patterns of small mammals likely reflect immediate nutritional and physiological requirements of an individual and its offspring. This is because most small mammals typically are income breeders rather than capital breeders (Jönsson 1997). Income breeders rely on current ingested food to pay the cost of reproduction, whereas capital breeders rely on stored body reserves. A lactating small mammal has two energy-related priorities, which are foraging for food to maintain her body condition and produce milk and providing warmth to ensure rapid development of her nestlings. In income breeders with uniparental female care, these two priorities cannot be met simultaneously. Therefore, females might balance the tradeoff between time spent foraging and time spent huddling with their nestlings.

Reproduction is expected to influence the pattern of activity if time away from the burrow can be used as an index of foraging. I chose to examine the effect that reproduction has on activity levels of small mammals by studying the deer mouse (*Peromyscus maniculatus*) under natural conditions. I selected the deer mouse because it is widely distributed (Handley 1999) and abundant in a variety of habitats (Gilbert and Krebs 1991; Harney and Dueser 1987; Heske et al. 1994; Kaufman et al. 1988, 2000; Kaufman and Kaufman 1990; MacCracken et al. 1985) and can serve as a model for many small mammals. I expected patterns of activity to differ between reproductive and non-reproductive females. If the acquisition of food energy is the most important factor influencing female activity, then reproductive females should leave their burrows earlier (or retire later), should spend more time away from their burrow, and should spend less time on return visits to their burrow than do non-reproductive females. Alternatively, if the short-term thermal-energy needs of nestlings are most important, then reproductive females should make shorter trips, should spend less time away from their burrow, should make longer individual visits, and should spend more total time in their burrows than non-reproductive females.

Although reproduction places major energy demands on female mammals, demand should not remain constant throughout the period from late pregnancy through weaning of the young (Stebbins 1977; Perrigo 1987; Millar 1978, 1979). In the laboratory, adult female deer mice worked harder for food as energy demands peaked in late lactation (Perrigo 1987). It is unknown whether these patterns translate to deer mice in their natural environment. However, adult female meadow voles (*Microtus pennsylvanicus*) decreased their total activity period under natural conditions, decreased time spent in the nest on each visit, and decreased the regularity of visits over time from the beginning of lactation to the end (Madison 1981). So, do changing demands of a growing litter impose changes in the activity of their mother?

In this study, I used a recently designed automatic activity-monitoring system (Chapter 2) to record activity of reproductive and non-reproductive deer mice at artificial burrows in native tallgrass prairie. First, I examined whether reproductive females differed in their nightly activity patterns as compared to non-reproductive females in the natural environment. Second, I tested the hypothesis that activity of lactating females would change over the period of lactation, mirroring changing thermal and nutritional needs of their developing offspring. To address these objectives, I compared a number of activity variables between reproductive and non-reproductive females. Further, I compared values for each of these activity variables across late stages of pregnancy and advancing stages of lactation.

Materials and Methods

Study site

I conducted this study from July 2003 through July 2005 on Konza Prairie Biological Station, a 3,487-ha tallgrass prairie preserve near Manhattan, in northeastern Kansas. Twenty artificial burrows (Kaufman and Kaufman 1989) were installed in adjoining watershed treatment units 2A (burned biennially, including 2004) and 1B (burned annually).

Small mammal sampling

I inspected all artificial burrows for occupants approximately weekly from spring through autumn and biweekly in winter. On first capture, deer mice were double-marked with a monel ear tag and a passive integrated transponder (PIT) tag. Burrow location, sex, relative age, reproductive status, and body mass were recorded at each capture. Relative age was based on pelage characteristics; juveniles were entirely gray, subadults had begun their post-juvenile molt, and adults had completed the post-juvenile molt (Layne 1968). Nestling deer mice were PIT-tagged when they attained a body mass of ≥ 4.5 g (~7-10 days old; Layne 1968) and ear-tagged when external pinnae had unfolded and were large enough to retain a tag (body mass of ~6 g).

I used monthly live-trapping from spring through autumn to ensure that all resident deer mice were marked before monitoring trials (see below). I set multiple lines of Sherman live traps at stations 15 m apart. Traps were baited with a mixture of peanut butter and rolled oats and polyester fiberfill was provided for insulation in spring and fall. Deer mice were marked uniquely (see methods above), and trap location, sex, age, reproductive status, and body mass were recorded.

Monitoring activity

I monitored activity of deer mice at artificial burrows by using an automatic activity-monitoring system (Chapter 2) placed at the entrance tunnel of a burrow. After inspection of all artificial burrows, I chose 1-2 burrows for monitoring trials. Selection was based on the reproductive status of adults or the presence of offspring. Trials began > 1 h before sunset and lasted 24-96 h.

Data analysis

If a deer mouse returned to the same burrow for multiple nights within a 96-h trial, a single night was selected at random from the 2-4 nights in a trial for that individual for use in analysis. I used StatXact-3.0 for nonparametric statistical analyses when assumptions of parametric statistics were not met and SAS Ver 9.1 for parametric analyses. A P-value of ≤ 0.10 was considered significant in my analyses.

Reproduction and activity patterns

I grouped lactating females with females in late stages of pregnancy, hereafter termed "reproductive" females, and compared their activity patterns against those of non-reproductive females (i.e., adults that were non-lactating and not in late stages of pregnancy). I selected these two categories of females because one group of females (i.e., reproductive) should experience higher energy costs associated with reproduction than the other group (i.e., non-reproductive). For each individual, I calculated time of first emergence; total number of trips; duration of the mean, median, first, longest, and shortest trips; time of final retirement to burrow; and total duration of time spent outside the burrow during that night. I also characterized return visits and stays inside the burrow by calculating duration of the mean, median, first, longest, and shortest visits and total duration of visits throughout the night. Mice had to start and finish the night inside the same burrow to be included in analyses. I also tried a second approach, where I grouped non-reproductive with pregnant females (representing non-lactating females) and compared them with lactating females for each activity variable by using the Wilcoxon rank-sum (W) statistic.

Time since parturition

I included all activity trials in which a female was pregnant or lactating and caring for young. For each trial, I estimated the age of young from body mass and appearance of pelage, eyes (closed or open), and pinnae (folded or unfolded; Layne 1968). Nestlings that were pink and hairless and weighed ≤ 1.9 g were termed "newborns" and were < 24-h old. From detailed observations on known-age individuals, I was able to estimate age (in days) of other young, for which I did not know birthdate for certain.

I grouped trial periods for reproductive females by the presence of fetuses or by the age of the litter. The 6 litter-age categories were mother in late stage of pregnancy (fetuses perceived by palpation of the abdominal region), 1-4, 5-8, 9-12, 13-16, or 17-20 days old. In prairie deer mice, young are capable of maintaining or gaining weight in isolation from the mother at 17-18 days (King et al. 1963). In fact, young also start taking brief trips outside the burrow as early as

14-15 days of age (Fig. 4 in Chapter 2). For an individual female, I averaged all nights within a litter-age category within a single-trial period (maximum of 96 hours). Further, I calculated all activity variables (time of first emergence; total number of trips; duration of the mean, median, first, longest, and shortest trips; time of final retirement to burrow; total duration of trips outside; duration of the mean, median, first, longest, and shortest visits and total duration of visits inside burrow) by litter-age category. I tested for differences among litter-age groups for each activity variable by using a mixed-effects model in SAS (PROC MIXED), with individual mother as a random effect and litter-age group as a fixed effect. Least-squares means (LSMEANS) are reported for responses by mothers within time categories for each activity variable in these mixed-effects models in my unbalanced experimental design. If the mixed-effects model detected a significant overall effect of time since parturition, pair-wise comparisons were made between all litter-age groups for that activity variable.

Results

Reproduction and activity patterns

The direction and general strength of relationships for most activity variables did not change whether I compared reproductive versus non-reproductive females or lactating versus non-lactating females. Hereafter, I will present results for reproductive versus non-reproductive females only.

Reproductive females emerged from the burrow later ($W = 308$, $P = 0.069$) and made fewer trips (mean ± 1 SE for reproductive females: 2.5 ± 0.4 trips; non-reproductives: 10.1 ± 2.7 trips; $W = 511.5$, $P = 0.006$) of longer mean ($W = 307$, $P = 0.067$) and median durations ($W = 245$, $P = 0.003$) than non-reproductive females (Fig. 13A). Reproductive females also had shortest trips of the night that were longer ($W = 239$, $P = 0.002$) than those for non-reproductive females. In addition, both the longest trip of the night ($W = 512$, $P = 0.049$) and total time spent away from the burrow in a night (*W* = 507, *P* = 0.061) were shorter for reproductive than non-reproductive females. Duration of the first trip outside was not different between reproductive and non-reproductive females.

Return visits and subsequent stays by reproductive females typically were longer in duration (mean visit: *W* = 219, *P* = 0.010; median visit: *W* = 153, *P* < 0.001; first return visit: *W* = 171, *P* < 0.001; longest visit: *W* = 318, *P* = 0.666; shortest visit: *W* = 181, *P* < 0.001) than visits by non-reproductive females (Fig. 13B). Total time spent in the burrow throughout the night (*W* = 319, *P* = 0.681), longest visit (*W* = 318, *P* = 0.665), and retirement time relative to sunrise (*W* =312, *P* = 0.256) were similar for reproductive and non-reproductive females.

Time since parturition

Twenty litters could be aged and were included in the time-since-parturition analysis. Sample sizes of mothers according to time categories were before parturition or pregnant (*n* = 3), 1-4 days (*n* = 10), 5-8 days (*n* = 12), 9-12 days (*n* = 9), 13-16 days (*n* = 7), and 17-20 days (*n* = 5). A number of interesting trends were apparent (Fig. 14). Time since parturition influenced the number of trips (*F* = 2.70, *d.f.* = 5, 23, *P* = 0.046) and duration of the longest trip (*F* = 2.76, *d.f.* = 5, 23, *P* = 0.042) of pregnant and lactating females. No other activity parameters showed significant relationships with time since parturition [total duration of trips (*F* = 1.0, *d.f.* = 5, 23, *P* = 0.441), emergence time (*F* = 0.36, *d.f.* = 5, 23, *P* = 0.873), first trip (*F* = 1.43, *d.f.* = 5, 23, *P* = 0.250), mean trip (*F* = 2.02, *d.f.* = 5, 23, *P* = 0.114), median trip (*F* = 2.16, *d.f.* = 5, 23, *P* = 0.094), and shortest trip (*F* = 0.66, *d.f.* = 5, 23, *P* = 0.659).

No significant differences were found in patterns of time spent visiting the burrow (Fig. 15; total duration of visits: *F* = 0.58, *d.f.* = 5, 22, *P* = 0.712, retirement time: *F* = 0.72, *d.f.* = 5, 22, *P* = 0.616, first visit: *F* = 0.28, *d.f.* = 5, 22, *P* = 0.921, mean visit: *F* = 0.70, *d.f.* = 5, 22, *P* =0.628, median visit: *F* = 1.53, *d.f.* = 5, 22, *P* = 0.221, shortest visit: *F* = 1.02, *d.f.* = 5, 22,

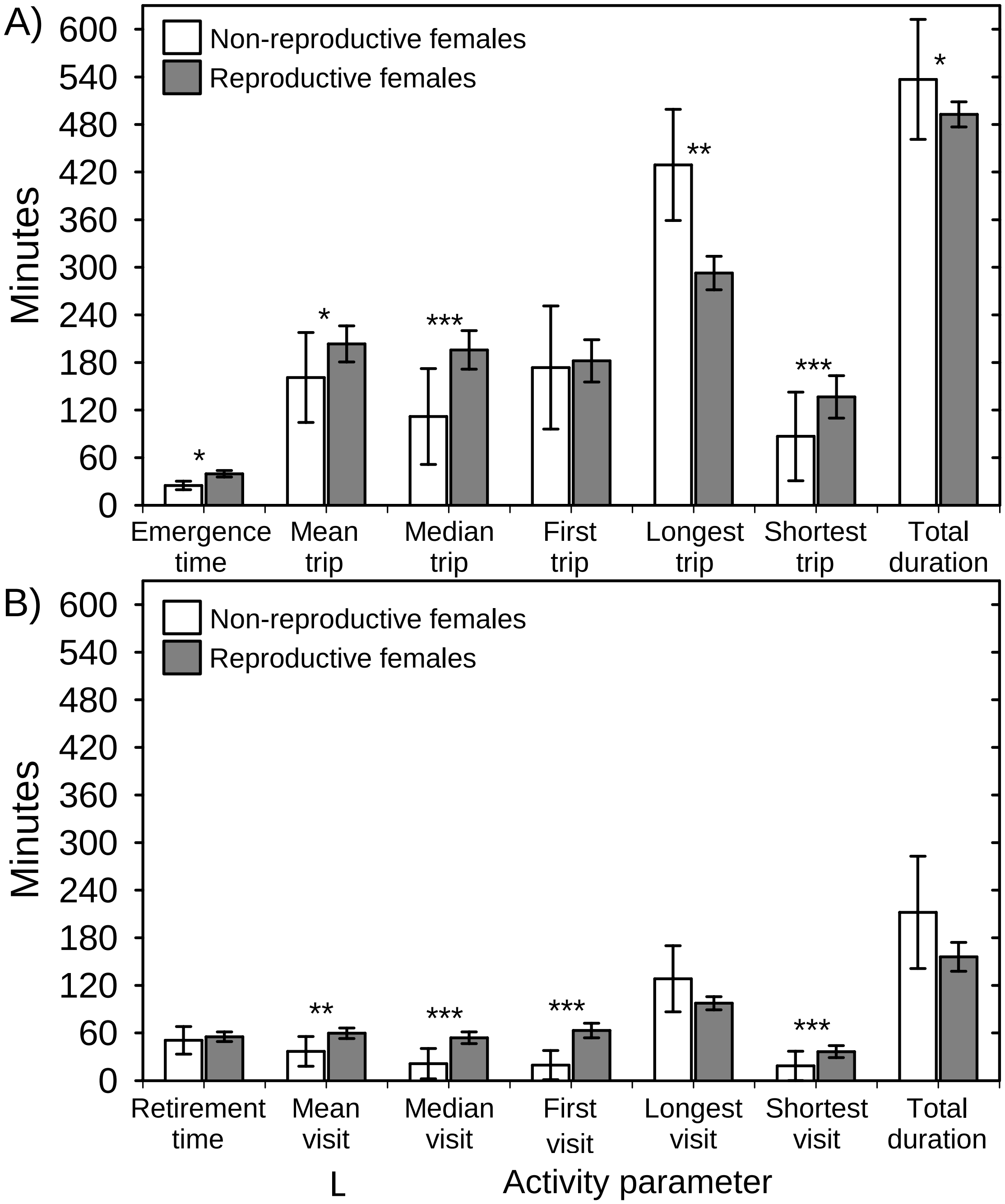

Figure 13. Nightly activity parameters related to trips outside of (A) and return visits to (B) artificial burrows by deer mice within a single night. Emergence time refers to minutes after sunset; retirement time is minutes before sunrise. Bars represent means ±1SE for non-reproductive females (open bars; $n = 14$) and reproductive females (filled bars; $n = 43$). Asterisks indicate P-values from Wilcoxon rank-sum tests (* $P < 0.10$, ** $P < 0.05$, and *** $P < 0.01$) for within-parameter measures between non-reproductive and reproductive females.

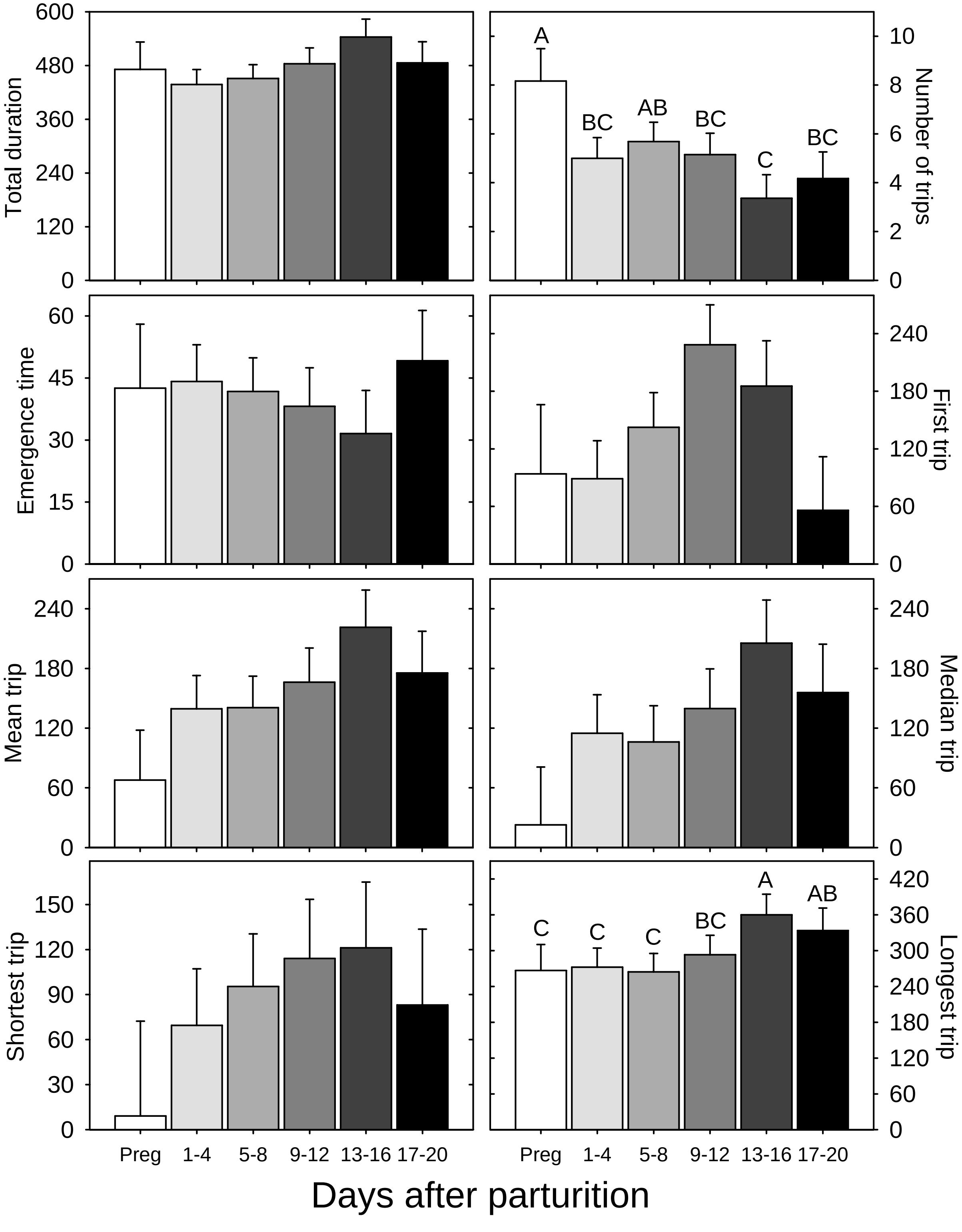

Figure 14. Activity parameters related to trips outside artificial burrows by lactating deer mice across the period of lactation. Bars represent least squares means ± 1 SE for each of successive 4-day intervals, from late pregnancy (Preg) through 17-20 days after parturition. Units for all

Figure 14 (cont.) y-axes are minutes, except "Number of trips". Emergence time refers to minutes after sunset. Sample sizes follow: $n_{\text{Preg}} = 3$, $n_{1\text{-}4\text{ days}} = 10$, $n_{5\text{-}8\text{ days}} = 12$, $n_{9\text{-}12\text{ days}} = 9$, $n_{13\text{-}16\text{ days}} = 7$, $n_{17\text{-}20\text{ days}} = 5$. A significant overall effect of time since parturition was found for number of trips ($F = 2.70$, *d.f.* = 5, 23, $P = 0.046$) and duration of longest trip ($F = 2.76$, *d.f.* = 5, 23, $P = 0.042$); bars sharing the same letters were not significantly different in these 2 parameters.

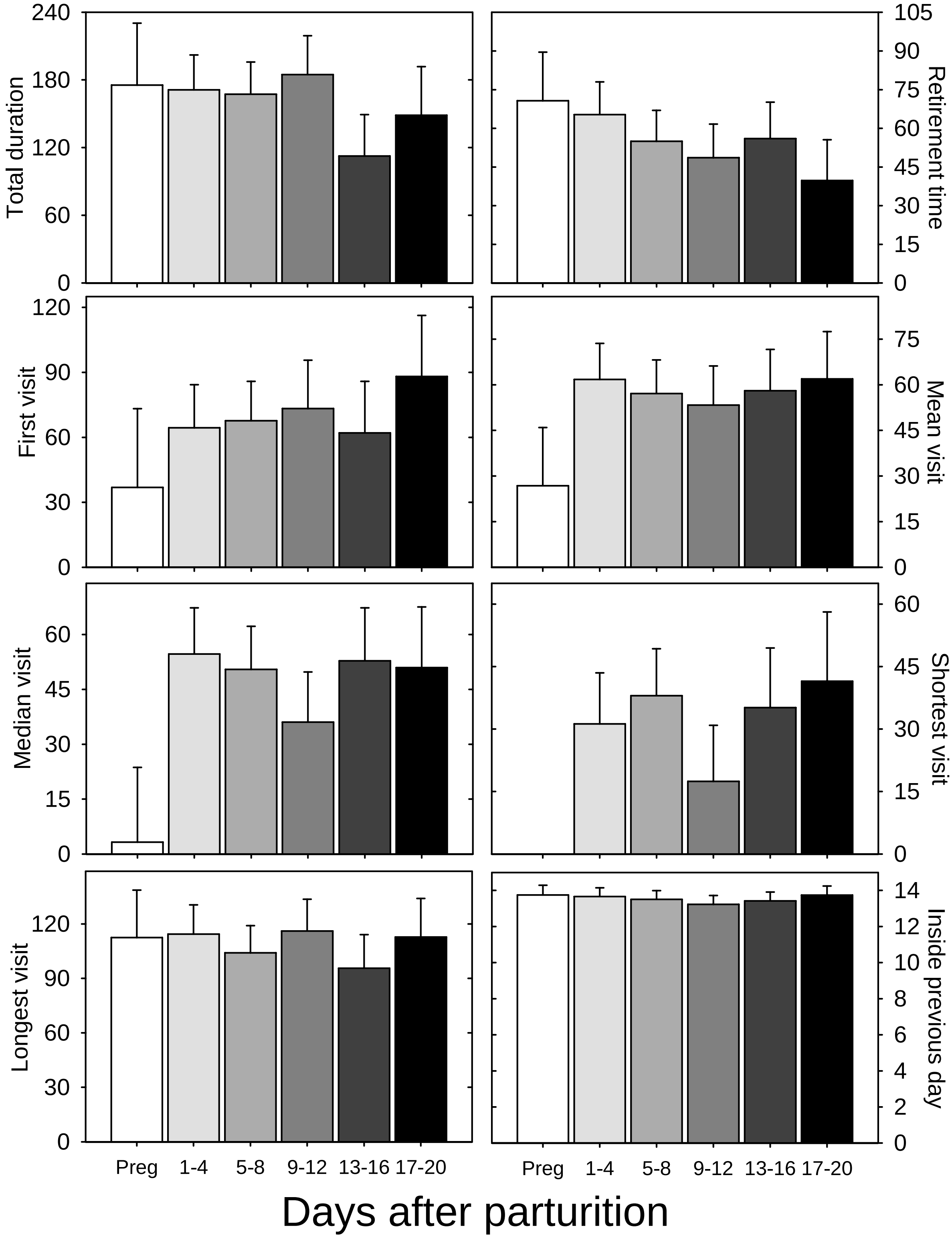

Figure 15. Activity parameters related to visits and time spent inside artificial burrows each night by lactating deer mice across the period of lactation. Bars represent least squares

Figure 15 (cont.) means ±1 SE for each successive 4-day interval, from late pregnancy (Preg) through 17-20 days after parturition. Units for all y-axes are minutes, except "Inside previous day", which is in hours. Retirement time is minutes before sunrise. Sample sizes were as follow: $n_{\text{Preg}} = 3$, $n_{\text{1-4 days}} = 10$, $n_{\text{5-8 days}} = 12$, $n_{\text{9-12 days}} = 8$, $n_{\text{13-16 days}} = 7$, $n_{\text{17-20 days}} = 5$; except for retirement time, where $n_{\text{9-12 days}} = 9$, and inside previous day, where $n_{\text{1-4 days}} = 8$, $n_{\text{5-8 days}} = 11$, and $n_{\text{9-12 days}} = 7$. No significant overall effect of time since parturition was found for any of the activity parameters. Duration of shortest visit for pregnant females was non-estimable because of large variance and small sample size.

$P = 0.430$, longest visit: $F = 0.30$, *d.f.* = 5, 22, $P = 0.909$, and total time spent inside the burrow the previous day: $F = 1.13$, *d.f.* = 5, 20, $P = 0.386$.

Discussion

Reproduction and activity patterns

The energetic cost of pregnancy over non-reproductive levels is reflected by a slight (~15%) increase in daily ingestion of food in *Peromyscus* (Millar 1989). Lactation further increases energetic demands and food intake by *Peromyscus* (Hammond and Kristan 2000; Millar 1978, 1979). Some evidence suggests lactating *Peromyscus* might use rather limited fat reserves for supporting offspring (Stebbins 1977), but as income breeders, the majority of energy for supporting offspring must come from increased food intake (Millar 1975, 1978, 1979). Thus, from a caloric-intake maximization perspective, I expected reproductive females to emerge earlier, take more trips of longer duration, and spend more total time away from the burrow, capped by a later retirement, than non-reproductive females. In contrast to this expected pattern, I observed that reproductive females emerged from the burrow later, made fewer trips of longer durations, and had shortest trips that were longer than those of non-reproductive females. Further, the longest trips of the night were shorter for reproductive females, and they spent slightly less total time away from their burrows than did non-reproductive females. If caloric requirements for maintenance of body condition and production of milk truly increase the amount of food that must be consumed, then reproductive females must be using their time outside the burrow differently than their non-reproductive counterparts. Although their typical trip was longer, reproductive females took fewer trips and spent no more total time outside of the burrow than did non-reproductive females. I suggest that these reproductive females must be more efficient in their foraging and reduce time spent on other activities, such as exploration or social interaction, which might consume greater amounts of time for the less nutritionally stressed non-reproductive females. Considering return visits to the burrow, those made by reproductive females were consistently longer in duration (e.g., mean, median, first, and shortest trips) than those of non-reproductive females, but total duration of time in the burrow did not differ owing to reproductive status.

My results suggest that increased caloric needs do not explain fully the differences in activity patterns of reproductive as compared to non-reproductive females. Like many small-bodied endotherms, *Peromyscus* have altricial young that are hairless and unable to thermoregulate at a very young age (Chew and Spencer 1967). Individual neonates of white-footed mice (*P. leucopus*) were unable to maintain homeothermy from birth to 4 days of age, but thermoregulatory performance improved slowly up to 10 days of age, followed by rapid maturation of abilities from day 10 to 14 (Hill 1976). The number of days of complete reliance on body heat from a parent probably is lower under natural conditions, as the ability of nestlings to maintain their body temperature was greatly enhanced by the presence of littermates in a nest (Hill 1976). Similar estimates of ~13 days for maturation of homeothermic abilities have been observed in deer mice in the laboratory (Chew and Spencer 1967).

Rates of growth and morphological development are increased in nestling *Peromyscus* that are kept warm (Dudley 1974; Hill 1983); cooling requires young to divert energy away from development and growth to an inefficient thermoregulatory process. Because of this relationship between body temperature and growth rate, parental investment through huddling with nestlings can be important (Dudley 1974; Schradin and Pillay 2005). Further, defenseless nestlings undoubtedly have lower survivorship rates than juveniles that can move around in response to their environment. So, selection should favor maximization of growth rates, facilitated by brooding, through these vulnerable early stages of life (Shine 1978). More rapid development has other fitness benefits, as it increases the likelihood that young of the year will breed in their first year of life especially those born in the spring of the year (Kaufman 1990). In contrast, those deer mice that are born in the autumn must survive through winter (~50% survival, Millar and Teferi 1993) to the following spring before they can reproduce.

In addition to food and warmth, nest attendance by a mother likely serves to provide defense against infanticide by conspecifics, especially females (Wolff 1985; Wolff and Peterson 1998).

Time since parturition

Increased ingestion of food has been observed for deer mice throughout lactation under semi-natural and laboratory conditions (Stebbins 1977; Millar 1979; Perrigo 1987). Average daily food intake of lactating female deer mice under laboratory conditions approximately doubled between days 1-4 and days 16-19 (Millar 1979). Similarly, daily energy consumption of lactating deer mice under semi-natural conditions increased from 96% to 194% over non-reproductive females in the first three weeks after parturition (Stebbins 1977). Thus, I expected female deer mice to adjust their nightly activity to mirror changing energetic needs of their offspring. Females in late pregnancy took more trips away from the burrow than did lactating females, and the number of nightly trips made remained fairly constant across the period of lactation. In addition, the duration of the longest trip of the night was affected by stage of lactation, with an increase over time, peaking in the 13th-16th day after parturition interval. Trends in activity indexed by the other activity parameters I considered were not statistically significant, but given my relatively small sample sizes, it is possible these patterns are biologically important and worthy of consideration. Emergence time of mothers tended to shift closer to sunset as lactation progressed (Fig. 14), until days 17-20, when young prairie deer mice may begin ingesting some solid foods and be functionally weaned (King et al. 1963). Further, retirement time tended to occur closer to time of sunrise later in lactation (Fig. 15). Taken together, earlier emergence, later retirement, and longer total duration away from the burrow reflects a temporal shift by females, perhaps to allow sufficient time to collect food to meet the increasing nutritional needs of dependent young. Similarly, the mean and median duration of trips away generally increased across the period of lactation, with peaks in the penultimate interval (13-16 days). Generally, the activity patterns I observed in the wild agree with results from the laboratory, where lactating females increased foraging effort when challenged to work for their food (Perrigo 1987).

After parturition, the number of trips made per night away from the burrow remained fairly constant across lactating periods in deer mice, whereas meadow voles decreased the regularity of visits (Madison 1981). Total duration of nightly activity outside of the burrow for deer mice increased slightly from parturition through 16 days, after which total duration outside of the burrow decreased. Juvenile prairie deer mice start making trips outside the burrow as early as 14-15 days of age (Fig. 4 in Chapter 2). Thus, energetic demands on the mother might begin to decline in the final period of lactation that I considered. This finding contrasts to results for lactating meadow voles that decreased the duration of activity throughout lactation (Madison 1981).

Many variables related to return visits to the burrow show inconsistent responses from parturition through late stages of lactation, but the shape of the curve for total duration of visits is intriguing. The decrease in total duration spent inside the burrow in days 13-16 corresponds to a time of rapid improvement of homeothermic ability of nestlings (Chew and Spencer 1967). Thus, females might be able to spend less time inside the burrow with nestlings than was required earlier in their life. This finding is similar to results for meadow voles, where mothers shortened the duration of each visit to the nest (Madison 1981). My results suggest that a shift occurs in the tradeoff between thermoregulation and energetic demands of developing young. That is, development of young primarily is limited by thermal constraints in the early stages of life, and then, upon nestlings gaining the ability to maintain body temperature on their own, the limiting factor shifts primarily to maximizing the nutritional input via milk production to developing young.

Total body mass of a litter of five deer mice ranged from ~8 g at parturition to ~42 g at weaning; this litter mass corresponds to ~40-180% of the mass of the mother (~24 g) from parturition through lactation (Millar 1979). Therefore, the total energy available to young from milk must increase over time. In some mammalian taxa, females modify the quantity and composition of milk produced during lactation, to match the energy requirements of rapidly growing offspring (Clutton-Brock 1991). In fact, many rodents that have altricial young show an increase in the energy concentration of their milk across the period of lactation (Baverstock et al. 1976; Nicholas and Hartmann 1991; Veloso et al. 2003). Perhaps, the trends I observed in nightly activity from parturition through lactation were similar because lactating females were able to modify caloric content of milk, thus obscuring expected behavioral changes in visitation to the burrow. However, I am unaware of any studies in *Peromyscus* that examined the composition of milk for temporal variation during the period of lactation. Any increase in milk production or enhanced energy levels must have an additional cost for females, and if these costs were met from body reserves, this would be contrary to the idea that deer mice are income breeders, and not capital breeders (Millar 1979; Perrigo 1987; Stebbins 1977). Because lactating females were not weighed daily, I cannot confirm or refute whether females are sacrificing body condition over the lactation period to meet these additional costs.

Finally, my observations suggest that lactating females must find a way to increase the quantity or quality of food ingested while spending the same amount of time outside of the burrow as non-reproductive females. Perhaps, lactating females shift their diet to ingest more energy-dense food during late lactation as compared to early lactation. Stomach or fecal analysis is necessary to document any shifts in nutritional content of food items during lactation.

My findings confirm that, under natural conditions, the increased energetic demands of reproduction are accompanied by changes in nightly activity of females. For a nocturnal small mammal, amount of time spent outside the relatively safe confines of a burrow could influence risk of predation by visual or auditory predators. Automatic monitoring systems adapted for use at burrows and foraging trays (Burns 2005) could reveal the ways reproductive females are utilizing their time away from their young. This information could help provide more information about the complex relationship between activity, foraging, and predation, which together play an important role in survival of mothers and offspring.

Literature Cited

Antinuchi, C. D., and C. Busch. 2001. Reproductive energetics and thermoregulatory status of nestlings in Pampas mice *Akodon azarae* (Rodentia: Sigmodontinae). Physiological and Biochemical Zoology, PBZ 74:319-324.

Baverstock, P., and L. Spencer, and C. Pollard. 1976. Water balance of small lactating rodents-II. Concentration and composition of females on ad libitum and restricted water intakes. Comparative Biochemistry and Physiology - Part A: Comparative Physiology 53:47-52.

Bronson, F. H. 1985. Mammalian reproduction: an ecological perspective. Biology of Reproduction 32:1-26.

Burns, C. E. 2005. Behavioral ecology of disturbed landscapes: the response of territorial animals to relocation. Behavioral Ecology 16:898-905.

Caldwell, L. D., and C. E. Connell. 1968. A précis on energetics of the old field mouse. Ecology 49:542-548.

Chew, R. M., and E. Spencer. 1967. Development of metabolic response to cold in young mice of four species. Comparative Biochemistry and Physiology 22:873-888.

Clutton-Brock, T. H. 1991. Incubation, gestation, and lactation. Pp. 85-99 in The evolution of parental care. Princeton University Press, Princeton, NJ.

Degen, A. A., I. S. Khokhlova, M. Kam, and I. Snider. 2002. Energy requirements during reproduction in female common spiny mice (*Acomys cahirinus*). Journal of Mammalogy 83:645-651.

Dudley, D. 1974. Contribution of paternal care to the growth and development of the young in *Peromyscus californicus*. Behavioral Biology 11:155-166.

Gilbert, B. S., and C. J. Krebs. 1991. Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon: 1973-1989. Holarctic Ecology 14:250-259.

Halle, S., and N. C. Stenseth, eds. 2000. Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin.

Hammond, K. A., and D. M. Kristan. 2000. Responses to lactation and cold exposure by deer mice (*Peromyscus maniculatus*). Physiological and Biochemical Zoology, PBZ 73:547-556.

Handley, C. O. 1999. Deer mouse, *Peromyscus maniculatus*. Pp. 575-577 in The Smithsonian book of North American mammals (D. E. Wilson and S. Ruff, eds.). Smithsonian Institution, Washington, DC.

Harney, B. A., and R. D. Dueser. 1987. Vertical stratification of activity of two *Peromyscus* species: an experimental analysis. Ecology 68:1084-1091.

Hayes, J. P. 1989. Field and maximal metabolic rates of deer mice (*Peromyscus maniculatus*) at low and high altitudes. Physiological Zoology 62:732-744.

Heske, E. J., J. H. Brown, and S. Mistry. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology 75:438-445.

Hill, R. W. 1976. The ontogeny of homeothermy in neonatal *Peromyscus leucopus*. Physiological Zoology 49:292-306.

Hill, R. W. 1983. Thermal physiology and energetics of *Peromyscus*; ontogeny, body temperature, metabolism, insulation, and microclimatology. Journal of Mammalogy 64:19-37.

Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57-66.

Kaufman, D. W., and G. A. Kaufman. 1990. Small mammals of wheat fields and fallow wheat fields in north-central Kansas. Transactions of the Kansas Academy of Science 93:28-37.

Kaufman, D. W., G. A. Kaufman, and B. K. Clark. 2000. Small mammals in native and anthropogenic habitats in the Lake Wilson area of north-central Kansas. Southwestern Naturalist 45:45-60.

Kaufman, G. A. 1990. Population ecology, social organization, and mating systems in the deer mouse (*Peromyscus maniculatus bairdii*) in mixed-grass prairie in Kansas. Ph.D. dissertation, Kansas State University, Manhattan.

Kaufman, G. A., and D. W. Kaufman. 1989. An artificial burrow for the study of natural populations of small mammals. Journal of Mammalogy 70:656-659.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

King, J. A., J. C. Deshaies, and R. Webster. 1963. Age of weaning in two subspecies of deer mice. Science 139:483-484.

Künkele, J. 2000. Energetics of gestation relative to lactation in a precocial rodent, the guinea pig (*Cavia porcellus*). Journal of Zoology 250:533-539.

Layne, J. N. 1968. Ontogeny. Pp. 148-253 in Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Special Publication 2, American Society of Mammalogists.

Liu, H., D.-H. Wang, and Z.-W. Wang. 2003. Energy requirements during reproduction in female Brandt's voles (*Microtus brandtii*). Journal of Mammalogy 84:1410-1416.

MacCracken, J. G., D. W. Uresk, and R. M. Hansen. 1985. Rodent-vegetation relationships in southeastern Montana. Northwest Science 59:272-278.

Madison, D. M. 1981. Time patterning of nest visitation by lactating meadow voles. Journal of Mammalogy 62:389-391.

Migula, P. 1969. Bioenergetics of pregnancy and lactation in the European common vole. Acta Theriologica 14:167-179.

Millar, J. S. 1975. Tactics of energy partitioning in breeding *Peromyscus*. Canadian Journal of Zoology 53:967-976.

Millar, J. S. 1978. Energetics of reproduction in *Peromyscus leucopus*: the cost of lactation. Ecology 59:1055-1061.

Millar, J. S. 1979. Energetics of lactation in *Peromyscus maniculatus*. Canadian Journal of Zoology 57:1015-1019.

Millar, J. S. 1989. Reproduction and development. Pp. 169-232 in Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock, TX.

Millar, J. S., and T. Teferi. 1993. Winter survival in northern *Peromyscus maniculatus*. Canadian Journal of Zoology 71:125-129.

Nicholas, K. R., and P. E. Hartmann. 1991. Milk secretion in the rat: progressive changes in milk composition during lactation and weaning and the effect of diet. Comparative Biochemistry and Physiology - Part A: Comparative Physiology 98:535-542.

Ochocinska, D., J. R. E. Taylor. 2005. Living at the physiological limits: field and maximum metabolic rates of the common shrew (*Sorex araneus*). Physiological and Biochemical Zoology, PBZ 78:808-818.

Perrigo, G. 1987. Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. Animal Behavior 35:1298-1316.

Rehmeier, R. L., G. A. Kaufman, and D. W. Kaufman. In press. An automatic activity-monitoring system for small mammals under natural conditions: Journal of Mammalogy.

Sadleir, R. M. F. S., K. D. Casperson, and J. Harling. 1973. Intake and requirements of energy and protein for the breeding of wild deermice, *Peromyscus maniculatus*. Journal of Reproduction and Fertility, Supplement 19:237-252.

Schradin, C., and N. Pillay. 2005. The influence of the father on offspring development in the striped mouse. Behavioral Ecology 16:455-460.

Shine, R. 1978. Propagule size and parental care: The "safe harbor" hypothesis. Journal of Theoretical Biology 75:417-424.

Sikes, R. S. 1995. Costs of lactation and optimal litter size in northern grasshopper mice (*Onychomys leucogaster*). Journal of Mammalogy 76:348-357.

Stebbins, L. L. 1977. Energy requirements during reproduction of *Peromyscus maniculatus*. Canadian Journal of Zoology 55:1701-1704.

Veloso, C., N. J. Place, and G. J. Kenagy. 2003. Milk composition of free-living yellow-pine chipmunks (*Tamias amoenus*): temporal variation during lactation. Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology 134:387-392.

Weiner, J. 2000. Activity patterns and metabolism. Pp. 49-65 in Activity patterns in small mammals: an ecological approach (S. Halle, and N. C. Stenseth, eds.). Springer-Verlag, Berlin.

Wolff, J. O., and J. A. Peterson. 1998. An offspring-defense hypothesis for territoriality in female mammals. Ethology, Ecology & Evolution 10:227-239.

Wolff, J. O. 1985. Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. Animal Behavior 33:117-123.

Zenuto, R. R., C. D. Antinuchi, and C. Busch. 2002. Bioenergetics of reproduction and pup development in a subterranean rodent (*Ctenomys talarum*). Physiological and Biochemical Zoology, PBZ 75:469-478.