

HABITAT DYNAMICS IN *PEROMYSCUS TRUEI*: ECLECTIC FEMALES, DENSITY DEPENDENCE, OR REPRODUCTIVE CONSTRAINTS?

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We evaluate several hypotheses concerning differential use of habitats by males and females based on data from live-trapping *Peromyscus truei* for 1 year. Multivariate statistical techniques revealed differential use of habitats by males and females during autumn and winter and different levels of habitat specificity throughout the year. Habitat use by males was less variable in autumn and winter, whereas habitat use of females was less variable in spring and summer. Niche breadth and overlap were density-dependent. Males shift use of habitat in response to reproductive condition of females, whereas females show little change in use of habitat throughout the year. Although the data do not falsify the eclectic-female hypothesis, they are most consistent with the reproductive-constraints hypothesis.

Key words: *Peromyscus truei*, habitat use, reproductive constraints, habitat dynamics

Few studies have explored temporal niche dynamics in rodents (Brown and Heske, 1990; Kitchings and Levy, 1981; Llewellyn and Jenkins, 1987; Morris, 1990) or intersexual differences in use of habitat (Bowers and Smith, 1979; Cockburn and Lidicker, 1983; Jones, 1990; Morris, 1984; Seagle, 1985). This is surprising for two reasons. First there is little reason to expect populations of small mammals to be temporally static. Llewellyn and Jenkins (1987) illustrated clearly that niche metrics in *Peromyscus truei* and *Peromyscus maniculatus* are dynamic seasonally. Certainly, foraging economics, physiological tolerance, and the cost of predator avoidance (Price, 1984) are not static and may underlie shifts in habitat usage. Second, a comprehensive understanding of interspecific competition seems unlikely without first understanding intraspecific variation in use of habitat. Those studies of intersexual differences in habitat use have revealed the potential importance of reproductive strategy on niche metrics (Bowers and Smith, 1979; Jones,

1990; Morris, 1984). Temporal changes in niche breadth and overlap between males and females that result from reproductive processes could have a dramatic effect on overall community structure.

Bowers and Smith (1979), Morris (1984), and Seagle (1985) advanced several hypotheses to explain intersexual differences in habitat use by *Peromyscus*. These include the eclectic-female hypothesis (Bowers and Smith, 1979), which states that intersexual differences in habitat use are a consequence of female use of preferred habitats to support reproduction. Use of preferred habitat is achieved through dominance by females and should result in reduced overlap with males and less variation in use of habitat. Morris (1984) rejected the eclectic-female hypothesis and offered two alternatives: density-dependence; reproductive constraints of females. The reproductive-constraints hypothesis attributes intersexual differences in habitat use to males in search of females and to restricted movements by lactating and preg-

nant females. Under this hypothesis, home range and habitat breadth of females should be small, especially during periods of reproduction, but overlap may be large. The density-dependence hypothesis argues that habitat differences are a consequence of demography. Intraspecific competition increases with population size. Thus, niche breadth and overlap should correlate negatively with population density. The objective of our study was to evaluate these hypotheses as they pertain to differences in habitat use between male and female *P. truei*.

METHODS AND STUDY SITE

A 12- by 12-station grid with 15-m spacing between traps was established in pinyon woodland habitat, 1,650 m elev., on the west-facing slope of Walker Pass, Scodie Mountains, California. The site was located in T26S, R37E, NE¼ Sec. 28, Kern Co. Eight 21-station assessment lines, also with 15-m spacing between traps, and following the design of O'Farrell et al. (1977), radiated from the center of the grid and across the pinyon woodland. Joshua tree, scrub, and grassland habitats.

Small mammals were sampled from August 1975 to July 1976 and during October 1976. Animals were live-trapped on the grid for 3 consecutive nights each month, followed by 3 nights of live-trapping on the assessment lines. All trapping took place between the last and first lunar quarter of each month to avoid the activity depression associated with the full moon. Traps were baited with a mixture of bird seed and crushed apples and were supplied with cotton for insulation during the winter. Traps on the grid were checked at 2-h intervals throughout the night from 2 h after sunset to sunrise; traps on assessment lines were checked each morning and evening. Captured animals were identified to gender, weighed, toe-clipped, and released at the point of capture.

Vegetation at each trap station was sampled using four 9-m transects oriented in the cardinal directions. Transects were used to determine relative cover, relative frequency, and relative dominance (Mueller-Dombois and Ellenberg, 1974) of 11 major species of plants on the study site. These values were summed to form an importance value (Mueller-Dombois and Ellenberg,

1974) for each species of plant at each trap station. Because each component of the importance value was binomially distributed, the sum of these components produces a random variable, which has a distribution that approaches the normal distribution (Hoel et al., 1971).

A principal-components analysis (SAS Institute, Inc., 1985) of plant-species importance values of each trap station was used to reduce the dimensionality of the dataset and to provide a series of orthogonal (independent) variables for use in analysis of habitat breadth. Principal components were computed using the correlation matrix. Orthogonality of the principal components resulted in additive habitat axes (Pianka, 1975). Habitat breadth was computed as the sum of the variances of factor scores on each principal axis. Only those principal components with eigenvalues greater than one were retained for analysis. Monthly habitat breadths were computed separately for adult males and females.

Habitat overlap between adult male and female *P. truei* was computed using the technique of Harner and Whitmore (1977) and Whitmore and Harner (1980). This technique uses the overlap formula within discriminant space of MacArthur and Levins (1967) to provide an index of niche overlap. It is based on mahalanobis distances and, thus, reduces potential bias resulting from unequal group variances. A single discriminant function was used to discriminate between sexes and monthly captures of *P. truei* using plant-species importance values. This produced maximal dispersion between groups defined by sex and month of capture. Mahalanobis distances between the sexes for each month were then used in the model of Harner and Whitmore (1977) and Whitmore and Harner (1980) to calculate habitat overlap. Because overlaps are computed within discriminant space, they are minimum overlaps.

Canonical-discriminant-function analysis (SAS Institute, Inc., 1985) was used to detect and follow habitat shifts during the entire year. Captures of adult mice were grouped by sex and month, and discrimination was based on the plant-species importance values associated with each capture site.

Habitat specificity on a seasonal basis was determined with stepwise-multiple-regression models, using the default-stepwise-selection procedure of SAS (SAS Institute, Inc., 1985) and by evaluating coefficients of determination

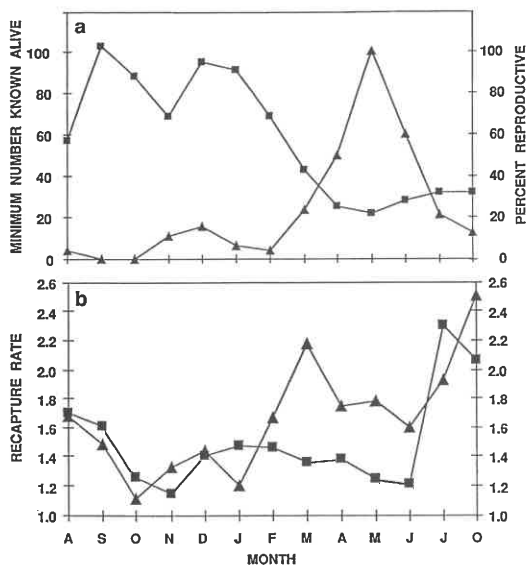


FIG. 1.—Demographic characteristics of *Peromyscus truei*. a, Minimum number known alive (closed squares) and proportion of females in reproductive condition (closed triangles). Perforate vaginas, vaginal plugs, lactation, or pregnancy were used to assess reproductive condition. b, Mean monthly recapture rates for males (closed squares) and females (closed triangles).

associated with each model. In each model, number of captures of each sex at a particular trap station was the dependent variable, and independent variables were the principal components of plant-species importance values and an indicator variable (Neter and Wasserman, 1974) to distinguish between trap stations of the grid and assessment lines. The indicator variable was included in an effort to remove potential biases resulting from different trapping intensities on the two configurations. Use of principal components assured independence of the predictor variables. Only trap stations with captures were used in seasonal regressions. Significance level for entry and retention in the model was 0.15.

Some bias may exist in discrimination and regression results as a consequence of multiple captures of individuals. Resident animals do not move about the grid independently. However, the average number of animals recaptured within a month was only 35%. Large samples resulting from inclusion of all captures reduced the im-

portance of the bias and improved the robustness of the statistical techniques.

RESULTS

Seven species of rodents (*Ammospermophilus leucurus*, *Tamias merriami*, *Perognathus parvus*, *Dipodomys panamintinus*, *Neotoma lepida*, *Peromyscus maniculatus*, and *Peromyscus truei*) were captured on the study site. Only the 875 captures of *P. truei* (pinyon mouse) were used to evaluate the eclectic-female, reproductive-constraints, and density-dependence hypotheses. The demographic attributes of this species, including the minimum number known alive and proportion of reproductive females, exhibit considerable temporal variation (Fig. 1).

Throughout most of the year, *P. truei* was the predominant species at the study site. Only during summer did captures of heteromyid species exceed those of the pinyon mouse. Abundance of *P. truei* declined during spring and summer; recruitment of young was insufficient for significant growth of the population. Although some reproduction was evident throughout most of the year, a peak in reproduction by females (perforate vaginas, vaginal plugs, lactation, or pregnancy) occurred from April through June (Fig. 1a). This corresponded with a general increase in body weights of females from March through May and an increase in recapture rates for females from February through October (Fig. 1b).

The first seven principal components accounted for 74.5% of the variation among sites based on importance values of plant species. *Pinus monophylla* (pinyon pine) and *Haplopappus cooperi* (Cooper goldenbush) had highest factor loadings on the first principal component, and *Artemisia tridentata* (basin sagebrush) was the predominant species of plants on the second principal component. *Pinus* and *Artemisia* loaded negatively on the principal axes. Most variation along the third component was explained by *Fremontodendron* (flannel bush) and *Cercocarpus* (curl-leaf moun-

TABLE 1.—Regression coefficients from step-wise multiple regression analyses of number of captures of *Peromyscus truei* (sexes and seasons were analyzed separately) as a function of principal components for importance values of 13 categories of vegetation, with grid-type configuration as an indicator variable. The significance level to enter and stay in the model was 0.15. Each regression was significant, with $P \leq 0.01$.

Variable	Autumn		Winter		Spring		Summer	
	Male	Female	Male	Female	Male	Female	Male	Female
Intercept	2.675	2.650	2.423	1.873	1.548	2.035	1.019	1.744
Principal-component 1	0.363			0.167 ^a				
Principal-component 2	-0.443	-0.330				-0.417	0.105	
Principal-component 3	0.208 ^a			-0.140 ^a		-0.569		0.342
Principal-component 4	-0.791	-0.513	-0.714		0.141			
Principal-component 5			-0.168 ^a	-0.447				
Principal-component 6			0.223	-0.861				
Principal-component 7	-0.452		-0.453					
Grid	-1.306	-1.037	-1.018			-0.773	0.172	
r^2	0.621	0.337	0.701	0.280	0.098	0.270	0.357	0.188
n	161	162	93	110	61	83	35	50

^aNot significant at $P \leq 0.05$.

tain-mahogany), whereas the fourth axis was composed primarily of *Ephedra viridis* (Mormon tea) and *Tetradimia* sp. (box-thorn). The remaining three axes were comprised primarily of *Quercus*, *Ceanothus*, and miscellaneous annual species, respectively. Most variation in the vegetative habitat was due to *Pinus*, *Haplopappus*, and *Artemisia*.

Stepwise multiple regression (Table 1) revealed differences in use of habitat between sexes. During autumn, males were positively associated with principal-axis one, while females were not. During winter, males and females differed with respect to principal-axes four, six, and seven, and, during spring, they differed with respect to axes two, three, and four. Captures of males in summer were positively associated with principal-axis two, whereas captures of females showed no significant association with any of the principal components.

During autumn and winter, coefficients of determination (Neter and Wasserman, 1974) for males were >0.620 , whereas those for females were 0.337 and 0.280, respectively. During spring and summer, coefficients of females were 0.270 and 0.188, while values for males decreased to 0.098

and 0.357, respectively. Habitat specificity of males was considerably greater than that of females during autumn, winter, and summer, but the situation was reversed during spring.

Two canonical axes provided discrimination between the sex and month groups, but only the first was significant at the 0.05 level. The first axis had a strong positive correlation with the importance value for pinyon pine, whereas the second axis had a strong positive correlation with oak (Table 2). Distribution of males and females in canonical-discriminant space (Fig. 2) revealed that females were remarkably similar in their use of habitat from month to month. However, males shifted their use of habitat in spring and autumn.

Habitat breadth of female *P. truei* remained relatively constant throughout the study and was significantly smaller than habitat breadth of males (Wilcoxon paired sample test, $P < 0.05$). However, habitat breadth of males increased dramatically during summer and contributed strongly to this difference. Habitat breadth had a significant positive relationship with population size in females (product-moment correlation, $r = 0.63$, $P < 0.05$, $d.f. = 11$), but

TABLE 2.—Correlation coefficients of importance values of plant species on each of the first two canonical-discriminant functions for *Peromyscus truei*. The functions discriminate groups defined by month and sex.

Variable	Canonical-discriminant function	
	1	2
<i>Pinus</i>	0.828	-0.021
<i>Artemisia</i>	-0.363	-0.110
<i>Haplopappus</i>	-0.578	-0.209
<i>Ephedra</i>	0.177	-0.056
<i>Fremontodendron</i>	-0.188	0.325
<i>Eriogonum</i>	-0.426	-0.170
<i>Quercus</i>	-0.106	0.704
<i>Yucca</i>	-0.311	-0.340
<i>Cercocarpus</i>	-0.229	-0.007
<i>Ceanothus</i>	0.029	0.250
<i>Tetradimnia</i>	0.047	0.400
Miscellaneous	-0.029	-0.169

not in males ($r = -0.24$, $P > 0.05$, $d.f. = 11$). Although not significant, the relationship was negative for males. However, if habitat breadths for April through July are removed from the analysis, the relationship becomes positive ($r = 0.82$, $P < 0.01$, $d.f. = 7$). Habitat overlap between sexes of *P. truei* was positively related to the minimum number known alive ($r = 0.55$, $P = 0.05$, $d.f. = 11$). Periods of lowest minimum number known alive occurred during the late spring and summer, when food resources were abundant.

DISCUSSION

Bowers and Smith (1979) attributed differential use of habitat by *Peromyscus maniculatus* to eclectic behavior of females. That is, females were hypothesized to be dominant over males and to select higher-quality microhabitats as a consequence of their greater size. Bowers and Smith (1979) argued that high energetic demands of reproduction by females necessitate ecological compensation, survival of altricial young is improved by female use of lush, thickly vegetated microhabitats (high quality habitats in their study), and intersexual

TABLE 3.—Niche breadths and overlaps for male and female *Peromyscus truei* by month.

Month	Male	Female	Overlap
August	7.0	6.6	85.8
September	14.1	11.2	90.2
October	11.7	10.8	75.1
November	6.1	8.3	91.3
December	11.9	5.0	79.8
January	19.4	6.1	86.1
February	13.4	10.0	84.8
March	11.4	7.9	74.9
April	26.9	2.8	30.1
May	90.2	4.8	71.4
June	63.1	4.7	70.8
July	70.0	14.0	70.6
October	6.2	7.5	85.0

partitioning of habitat results in reduced competition between sexes, thus, increasing availability of energy for reproduction and survival. In addition, high-quality habitats occupied by females may be interpreted as a form of parental investment on the part of males.

Females of *P. truei* were heavier than males during periods of reproduction. Large size of female *P. maniculatus* led Bowers and Smith (1979) to hypothesize dominance by females and acquisition of preferred habitats. However, the increased weights of females in this study were due to pregnancy and, consequently, may not have conferred a dominance rank. No study suggests behavioral dominance as a consequence of pregnancy in *P. truei*.

Intersexual partitioning of habitat to reduce competition should result in reduced habitat overlap. In this study, intersexual overlap was high with only a slight reduction during months of peak reproduction (Table 3). Use of high-quality habitat should result in reduced habitat breadth. Habitat breadth of females was small relative to that of males only during months of reproduction. Also, habitat breadth of females varied little from month to month while that of males increased dramatically during spring and summer.

We infer from the eclectic-female hy-

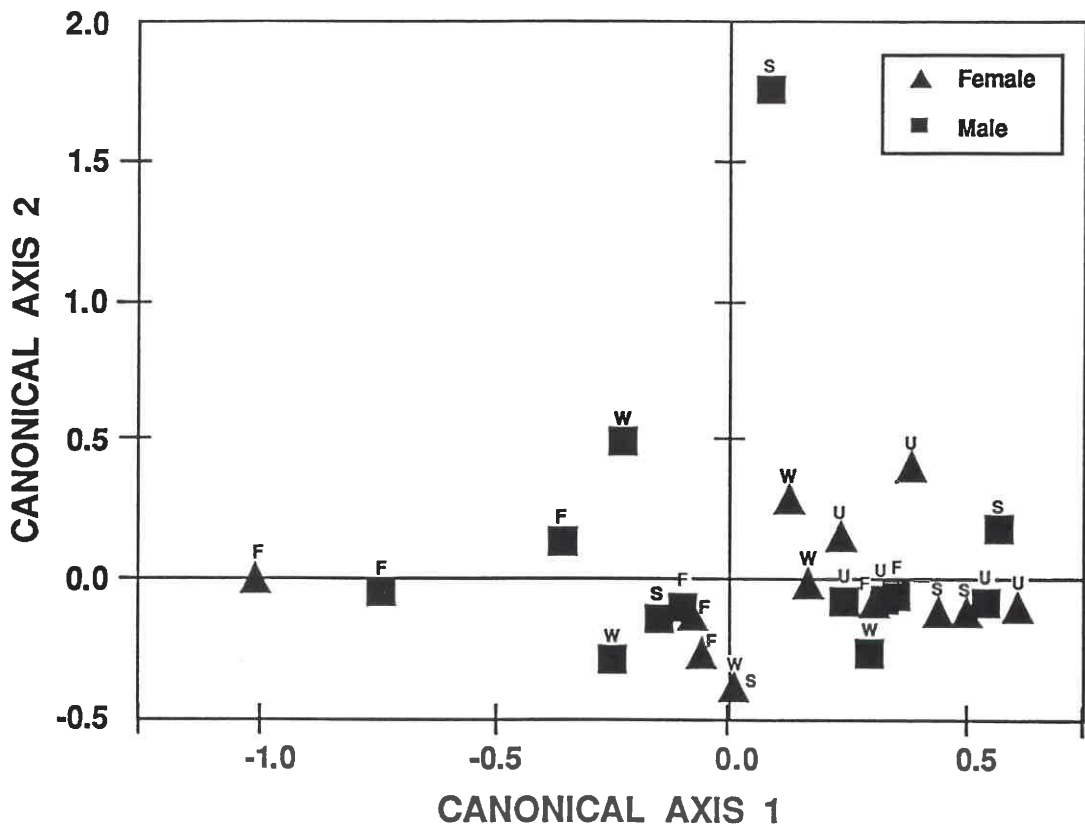


FIG. 2.—Distribution of male (closed squares) and female (closed triangles) *Peromyscus truei* in canonical-discriminant space. Season of capture is indicated by F (autumn), W (winter), S (spring), and U (summer).

pothesis that use of high-quality habitat results in greater predictability of habitat use. In fact, the coefficients of determination for regressions based on females generally are small. Coefficients for females are greater than those for males only during spring when males become more variable in use of habitat.

Lack of evidence for dominance by females, patterns of habitat breadth and overlap, and low predictability of use of habitat by females relative to males casts doubt on the veracity of the eclectic-female hypothesis. Instead, the data suggest a male response to female reproductive condition.

Morris (1984) re-evaluated the eclectic-female hypothesis based on data for *Peromyscus leucopus* and *Microtus pennsylvan-*

icus. He found sexual differences in microhabitat use for *Peromyscus* in some habitats, but, in his study, males occupied higher-quality habitats. His analysis suggested density-dependent effects as a partial explanation for differential use of habitat. Additionally, he suggested an alternative explanation for the results of Bowers and Smith (1979); namely, females select nest sites that are safe for nurturing young and, because of lactation, spend considerable time in the nest and have smaller home ranges. The negligible role of males during parental care enables them to select habitats on the basis of resource availability and access to females.

Significant density-dependent effects in this study included a decrease in habitat

overlap between sexes and a reduction in habitat breadth of females with decreasing population size. Habitat breadth of males also decreased with decreasing population size, but not in April through July. If intraspecific competition is directly related to population size, these mice exhibited the greatest habitat separation and greatest habitat specialization when intersexual competition should have been minimal. When resources were most abundant, the sexes were narrow in the use of habitats. However, it is unreasonable to ignore the dramatic changes in habitat breadth of males from April to July. The consistency of the pattern over a period of months suggests a response by males to reproductive condition of females.

Our results conform most closely to the reproductive-constraints hypothesis (Morris, 1984), in which females select habitats on the basis of nest sites and pregnant females restrict their movements to foraging activities. Males, conversely, are free from these constraints and can improve their inclusive fitness by moving greater distances in an effort to gain access to more females. This is supported by the fact that males were less predictable in habitat use when females exhibited a reproductive peak (Table 1), females generally had smaller home ranges than did males (Scheibe, 1984a), their habitat breadth was small, and the nocturnal activity patterns of males varied seasonally while female patterns did not (Scheibe, 1984b). Also, recapture rate of females increased during a period of reproduction (Fig. 1b), perhaps because energetic demands of reproduction forced females to exploit trap bait as a food resource or restricted movements by the females increased their likelihood of encountering traps. Finally, in canonical discriminant space, females were less seasonally variable in use of habitat than were males (Fig. 2). These patterns suggest females are constrained in use of habitat, whereas males are not.

Patterns observed in this study are sig-

nificant beyond the context of the three hypotheses of Morris (1984) and Bowers and Smith (1979). As noted by Llewellyn and Jenkins (1987), niche metrics in *Peromyscus* are temporally dynamic, and niche differences between age classes also may exist (Van Horne, 1982). If these patterns apply to most species, community data based on only a few seasons of study may be inadequate in providing a meaningful analysis of community structure. Clearly, population structure for *P. truei* during summer is different from that during the rest of the year. Studies that survey a large number of communities sequentially (e.g., Brown and Lieberman, 1973; Scheibe, 1987) may detect trends that are a consequence of intraspecific rather than interspecific effects.

The generality of patterns concerning habitat difference between males and females should be explored. The fact that the trend has been reported in *Peromyscus* and *Microtus*, but not in heteromyid species is interesting. Do large heteromyids, because of their greater chance of iteroparity, solve the reproductive-constraints problem differently? What effects do the expanding niches of male *P. truei* have on coexisting *Dipodomys* or *P. maniculatus*? Clearly, detailed analyses of populations of small mammals may be productive in furthering our knowledge of community dynamics.

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