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MICROHABITAT AND HOUSE USE BY DUSKY-FOOTED WOODRATS
(*NEOTOMA FUSCIPES*) IN NORTHWESTERN CALIFORNIA:
INSIGHT FROM TRAPPING DATA

Ted J. Slowik^{1,2}

ABSTRACT.—Capture data differed at woodrat houses associated with selected microhabitats in a chaparral-oak woodland site in the foothills of northwestern California. Mean trapping success was significantly higher at houses located under dense tree canopy (and in low scrub cover) compared with houses in high scrub cover (and under less tree canopy), as was trapping success at houses found in non-edge versus edge habitat. Woodrats trapped at houses under dense canopy also were significantly heavier than those captured in high scrub cover; however, mean body masses at edge- and non-edge houses were similar. Broadly, our results mirror existing research but indicate the need for more study of the specific microhabitat factors that influence woodrat house use in chaparral-oak habitat.

RESUMEN.—Capturos datos diferían en casas woodrat asociados a microhábitats seleccionadas en un sitio arbolado chaparral-encino en las estribaciones de la northwestern California. La media atrapando éxito fue significativamente mayor en las casas situadas bajo denso dosel de los árboles (y en la cobertura de arbustos bajos) en comparación con las casas en la cubierta matorral alto (y bajo menos copas de los árboles), como fue atrapando el éxito en las casas que se encuentran en situación de hábitat no borde versus de borde. Woodrats atrapados en las casas bajo dosel denso también fueron significativamente más pesados que los capturados en alta cobertura de matorral; sin embargo, los pesos medios en las casas de borde y no de borde fueron similares. En términos generales, nuestros resultados son similares a los de la investigación existente, pero indican la necesidad de un estudio adicional de los factores de microhábitats específicos que influyen en el uso casa woodrat en este hábitat.

Found throughout far western North America, the dusky-footed woodrat (*Neotoma fuscipes* Baird; woodrat) is a medium-sized murid rodent known for its construction of conspicuous stick-nests (houses). In California, *N. fuscipes* is a scrub and woodland specialist, keystone species, important prey animal (Vestal 1938, Horton and Wright 1944, Meserve 1974, Kelly 1990, Smith et al. 1999), and significant contributor to zoonotic disease cycles. Woodrats are reservoirs of the bacteria that cause human granulocytic ehrlichiosis, Lyme disease, plague, and tularemia in California, and along with their houses, host the arthropod vectors of these diseases (Burroughs et al. 1945, Nelson 1980, Brown and Lane 1992, Richter et al. 1996, Nicholson et al. 1999, Davis et al. 2002).

As part of a study of the control of rodent ectoparasites (Slowik et al. 2001), we collected monthly data on woodrats trapped in the foothills of the Mayacamas Mountains in Mendocino County, California, during the periods

of March–October 1998 and March–July 1999. Using approved animal-handling protocols (Slowik et al. 2001), we captured woodrats using a baited live-trap (Tomahawk Live Trap, Tomahawk, WI) placed overnight next to each of 40 houses that were deemed active based on current woodrat occupancy or activity (e.g., upkeep of house, presence of foodstuffs). Captured woodrats were aged based on their body mass, reproductive status, and fur color, and were characterized as mature (adult) or immature (juvenile and subadult). Processed animals were tagged, then immediately released at the house of capture.

The 40 houses were located in an ecosystem dominated by scrub cover primarily composed of wild lilac (*Ceanothus* spp.) and chamise (*Adenostoma fasciculatum*), or tree (canopy) cover provided by oak (*Quercus* spp.), Pacific madrone (*Arbutus menziesii*), and California buckeye (*Aesculus californica*). While mapping the study site, we used visual estimates to characterize the surrounding (5-m-diameter)

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TABLE 1. Descriptive data on *Neotoma fuscipes* trapped in a northwestern California study site, March–October 1998 and March–July 1999.

Woodrat class	Individual woodrats captured ^a	Mean number of captures overall ^b (range)	Mean number of individual nests at which woodrats captured (range)	Interyear captures ^c (% of all individuals)
Male	22	2.9 (1–8)	2.0 (1–4)	5 (9.4)
Female	31	2.0 (1–8)	1.4 (1–3)	3 (5.7)
Mature	44	2.6 (1–8)	1.6 (1–3)	6 (11.3)
Immature	9	2.3 (1–8)	1.8 (1–4)	2 (3.8)
All	53	2.5	1.7	8 (15.1)

^aEar-tagged with a unique number.

^bBased on total number of captures (132); means were rounded and include several animals that were not sexed due to health reasons or changed from “immature” to “mature” status during the study.

^cIndividuals captured in both 1998 and 1999.

microhabitat of each house as either *high-canopy/low-scrub* (HC; >60% of microhabitat area covered by trees of varying size, with minimal or no brush and understory) or *low-canopy/high-scrub* (LC; <40% of microhabitat area covered by trees, with >50% dense scrub brush/understory), and either *edge* (E; ≤10 m from a dirt road, firebreak, or open area) or *non-edge* (NE; >10 m from a dirt road, firebreak, or open area). Statistical analysis (2-tailed Fisher’s exact test) revealed similar ($P = 0.70$) numbers of HC and LC houses located in E and NE areas (i.e., canopy/scrub and edge were independent factors at the study site).

Canopy, cover, and edge characteristics influence the distribution and abundance of *Neotoma* spp. at the macro level (e.g., Markovchick-Nicholls et al. 2008, Swei et al. 2011), but their influence at the microhabitat and house level is not as well understood (Vestal 1938, Carey et al. 1991, Innes et al. 2007). Although derived from a study of ectoparasites (Slowik et al. 2001) and analyzed *a posteriori*, our trapping data nonetheless add to the overall body of woodrat research by providing insight into how these microhabitat factors may influence house selection by *N. fuscipes*.

During the entire study, 132 total woodrats were captured over 437 trap-nights, an overall trapping success of 30.2%. Trapping success ranged from a low of 16.7% (3 captures over 18 trap-nights) in March 1999, to a high of approximately 70% (19 captures over 27 trap-nights) in March 1998. Males, females, and immatures composed an average of 34.6%, 35.0%, and 30.4%, respectively, of each month’s captures; Table 1 presents individual trapping data by sex and age. Overall, males and females were trapped at a mean of 2 and 1.4 individual houses, respectively, a ratio

comparable to previous research (Linsdale and Tevis 1951, Kelly 1990; Table 1). The typically larger home ranges of males (e.g., Cranford 1977) may have accounted for the higher mean number of nests at which they were captured and their higher mean number of individual captures overall, relative to females and young in our study (Table 1). Immatures were captured less frequently than matures, as shown previously (e.g., Innes et al. 2007; Table 1).

The mean number of monthly captures peaked during the spring of 1998 (13.7; March–May) and was annually highest in 1998 (12.1). Females (41.4%) accounted for the highest mean percentage of all captures in summer months (June–August); males (35.6%) and immatures (35.5%) accounted for the highest percentages, on average, in spring. These trends in trapping success reflect the seasonality of woodrat foraging, house use, and capture frequency observed by others (e.g., Linsdale and Tevis 1951, Cranford 1977), and may also indicate sex-based differences in habitat use.

A mean of over 70% of all woodrats were recaptured each month, but recapture rates varied by season, sex, and status. All of the woodrats captured in July 1999 were recaptures from the previous month, for example, whereas only 41.7% were recaptured from March 1998 to April 1998. A mean of approximately 37% of males, 32% of females, and 30% of immature woodrats were recaptured each month during the study. Collectively, our data confirm the well-documented “trap-happiness” of *N. fuscipes* (e.g., Innes et al. 2007). Approximately 15% of all individual woodrats were captured in both 1998 and 1999, and interyear captures were highest for male and mature individuals (Table 1); however, we did not directly measure survival rates.

The mean body mass of males and females captured during the study was 225.6 g and 211.3 g, respectively. Woodrat body masses ranged from a 130-g immature to a 280-g male, and our data support previous observations that *N. fuscipes* males are typically heavier than females in California (e.g., Kelly 1990). We observed trends in woodrat mass by season that have been noted in other studies (Vestal 1938, Linsdale and Tevis 1951, Cranford 1977). These trends were likely due to month-to-month changes in temperature, vegetation, and behavior. The mean body masses of all captured woodrats were seasonally highest in spring and summer (225.1 g), lowest in the fall (212.2 g), and varied between 1998 (218.7 g) and 1999 (227.6 g). We suspect that El Niño (1998) and La Niña (1999) weather variations also may have affected body mass data during our study.

Differences in trapping data emerged when comparisons were made based on the microhabitats associated with the houses. In a comparison of mean monthly trapping success, there was a significant (Fisher's exact test: $P < 0.001$) difference between HC (32.7%; 5.2 captures over 15.9 trap-nights) and LC houses (24.7%; 4.3 captures over 17.4 trap-nights). The percentage of interyear captures also was significantly ($P = 0.005$; Fisher's exact test) higher at HC (14.9%) than at LC houses (2.1%). These higher capture percentages at HC-associated houses likely reflect ongoing occupancy, as well as the suitability of these houses and the surrounding microhabitat. Because *Quercus* spp. trees provided much of the canopy at HC houses at the study site, these data appear to support previous research that identified oaks as the preferred source of food, shelter, and house materials for *N. fuscipes* (e.g., Linsdale and Tevis 1951, Tevis 1956, Atsatt and Ingram 1983).

However, more recent studies have provided a more nuanced picture of the influence of tree canopy in general, and oaks specifically, on woodrat abundance and house density. Willy (1992), for example, found no relationship between the densities of oaks and woodrat houses in coastal California. Yet Swei et al. (2011) determined that *Quercus* spp. mortality had a negative effect on *N. fuscipes* abundance in north coastal California, despite finding that survival was not correlated with vegetational parameters, such as oak biomass.

Woodrats in the Innes et al. (2007) study occurred at higher densities in sites with greater numbers of large oaks, but not small oaks; house sites also were most likely to be located near large logs and tree stumps.

Gerber et al. (2003) concluded that dense tree canopy (overstory) was positively correlated with habitat use by *N. fuscipes riparia*, which benefitted from both canopy and tree proximity. However, these authors also found that the woodrats selected houses based on brush (understory) cover. Mat-forming shrubs were a microhabitat factor identified with houses, yet taller shrub density did not influence house locations (Innes et al. 2007). These studies' conclusions seem to contradict our study results, but they highlight the complex influences on woodrat house abundance and use. Clearly, more research is needed to determine the specific factors associated with oak, non-oak, and shrub cover that drive *N. fuscipes* behavior in various microhabitats.

Over- and understory cover ameliorates climatologic factors such as moisture and temperature, which are important to woodrat survival (Linsdale and Tevis 1956, Cranford 1977, McMurry et al. 1993, Lee and Tietje 2005). Increased cover also reduces risk of predation (e.g., Sakai and Noon 1997) and improves the quality of foraging for food and house materials by offering more diversity and abundance in flora (e.g., Horton and Wright 1944, Vogl 1967, Carraway and Verts 1991, Willy 1992). This earlier research may support our findings that monthly mean trapping success was significantly (Fisher's exact test: $P < 0.02$) higher at NE (31.5%; 6.3 captures over 20.0 trap-nights) than at E (21.3%; 2.9 captures over 13.6 trap-nights) houses, despite statistical similarity in the percentages of interyear captures at NE (6.4%) and E (8.5%) houses.

The higher percentage of captures at NE houses in this study also may support previously documented correlations of woodrat abundance with vegetative density (e.g., Sakai and Noon 1993), and house density with areas of increased cover (Linsdale and Tevis 1951, Tevis 1956, Vogl 1967, Cranford 1977, Willy 1992, Innes et al. 2007). Working within a kilometer of our study site, Padgett et al. (2009) did not capture any *N. fuscipes* in chaparral that was previously subjected to a prescribed burn.

During the study, we also recorded the number of damaged (non-intact) or inactive houses, which varied by month and year. Eighty-three percent of these houses were edge-associated despite being approximately equally distributed in HC and LC microhabitats. Edge appeared to increase the houses' exposure to damage by weather and predators: 87% of the E houses appeared to have been eroded, dug up, or dismantled. Conversely, NE houses in our study appeared to offer a level of protection that resulted in lower levels of disturbance, higher occupancy, and higher percentages of capture. Although Innes et al. (2007) found that the probability of a site containing a house increased with each degree of slope, we found that about 50% of damaged, edge-associated houses were located on sloping ground. Overall, a mean of 7.5% houses per month were unoccupied, a figure comparable to about 10% of inactive *N. fuscipes* houses reported by Vestal (1938).

Woodrats collected at HC houses were significantly (Fisher's exact test: $P = 0.045$) heavier ($\bar{x} = 224.3$ g) than those captured at LC houses ($\bar{x} = 215.8$ g); those captured at E and NE houses had mean masses of approximately 220 g. These data contrast with those of Gerber et al. (2003), who found that the body mass of *N. fuscipes riparia* was positively correlated with understory cover. Although certain classes and individuals were likely over- or undersampled, and monthly bait-feeding likely increased the mass of more frequently trapped animals, our data suggest that, as previously reported (e.g., Innes et al. 2007), larger *N. fuscipes* occupy houses that are presumably more desirable in terms of size, cache materials, location, and intactness.

Collectively, our data indicate the need for additional research to clarify how cover and microhabitat affect *N. fuscipes* foraging, house-selection behavior, body mass, and survivorship in the chaparral-oak woodland habitat. A better understanding of these behaviors and factors may also have important implications for the study of enzootic diseases in which woodrats play a role.

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