

# Translocation of an imperilled woodrat population: integrating spatial and habitat patterns

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## Abstract

Many species have strong habitat preferences that directly influence population viability. For successful reintroduction of threatened populations that rely on habitat structures, the correct placement of artificial structures is also important to population persistence. In this paper, we present a hierarchical approach to the problem of translocating animals that rely on permanent habitat structures, in which we first use population dynamics data to identify areas of suitable habitat, and then identify optimal configuration for habitat structures. We use data collected from a non-endangered, conspecific population of the endangered riparian woodrat (*Neotoma fuscipes riparia*) to examine the degree to which the distribution of dens in translocation sites might influence the likelihood that animals persist in their new environment. We characterize the habitats in which dens occur, analyze their spatial clustering, and compare them to temporal changes in population status for sex and age classes. We compare the potential efficacy of translocation efforts using spatial analysis versus solely habitat-based approaches and identify the optimal spatial configuration of dens that should be considered in this translocation effort. We found that patterns of habitat use were positively correlated with overstorey cover, and animal weight was positively correlated with understorey cover. Woodrats appear to select den locations on the basis of understorey cover, but also benefit from dense overstorey cover and distance to nearest tree. Our results suggest that in translocation efforts, artificial dens should be placed in clusters within a radius of 15 m, as values above and below this value showed negative correlations with body mass. Translocations should occur after reproductive events, which occur in April and August for woodrats in southern California. Our analyses provide practical guidelines in determining appropriate timing and spacing for translocation events in the context of animal condition, minimizing disease transmission, and reproduction.

## INTRODUCTION

A central challenge in conservation biology is in developing approaches for the translocation of individuals from imperilled populations into new habitats. The successful translocation of species that rely on immobile habitat structures is particularly challenging. For such species, it is necessary to determine both the location of suitable habitat and the optimal configuration of the structures within the habitat. While it is more typical in translocation efforts to emphasize habitat quality (Griffith *et al.*, 1989, Miller *et al.*, 1999), the importance of a population's spatial structure to its long-term viability (e.g., Dunning, Danielson & Pulliam, 1992; Pulliam, Dunning & Liu, 1992; Bascompte & Sole,

1998; Schultz & Crone, 2001) makes it clear that spatial patterning of habitat structures should be weighted heavily in management decisions. The choice of where to build nests, dens or other structures is a function of a number of factors, including resource requirements, social structure, risks associated with disease transmission, and available habitat (Griffith *et al.*, 1989; Bright & Morris, 1994; Miller *et al.*, 1999). These factors may cause distinct patterns in distributions that are different for age and sex classes. For example, Reichman, Whitham & Ruffner (1982) found that the geometry and spacing of burrow systems of pocket gophers differed between sexes and reproductive cohorts such that large reproductive males encountered more potential mates than other cohorts. For some animals, males tend to have larger home ranges than females, especially in polygynous species (e.g., Gaulin & FitzGerald, 1986, 1988).

Empirical evidence suggests that several factors may influence the efficacy of species translocations. First, efforts to reintroduce mammals appear to have been more successful than efforts for other taxonomic groups (Scott, Murray & Griffith, 1999). The release of animals into high-quality habitat and the use of animals from non-endangered or increasing subpopulations contribute to translocation success (Griffith *et al.*, 1989). Reintroductions are thought to be less successful in the absence of high-quality habitat or in areas outside of the historical range. For example, efforts to reintroduce the thick-billed parrot at the northern extreme of its range failed, as did efforts to reintroduce whooping cranes in Idaho outside their historical range (Scott *et al.*, 1999). Conservation strategies should also consider the spatial patterns of critical structures such as artificial reefs and bluebird nest boxes for habitat and species recovery (e.g., Newton, 1994; Pickering & Whitmarsh, 1997). When translocating animals and creating structures, it is also important to consider the risk of transmitting diseases. For example, the translocated and regionally endangered Allegheny woodrat (*Neotoma magister*) collects faeces from exotic raccoons for nest-building material and, as a result, suffers such high mortality that woodrats apparently cannot persist where raccoons are common (LoGiudice, 2000).

We present a hierarchical approach to the problem of translocating animals that rely on permanent habitat structures, in which we first use population dynamics data to identify areas of suitable habitat, and then identify optimal configuration (using Ripley's *L*-function analyses) for habitat structures within this habitat. Using data from an unimpaired population, we adopt this approach to make recommendations for the translocation of endangered riparian woodrats (*Neotoma fuscipes riparia*) in California using artificial dens. This population, a subspecies of the dusky-footed woodrat (*Neotoma fuscipes*), is limited in range to a 250 acre habitat in central California, includes fewer than 500 animals, and appears to be declining in abundance (Williams, 1993). Loss and fragmentation of habitat are the principal reasons for the decline of the riparian woodrat population. Much of this loss was the result of the construction of large dams and canals that diverted water for the irrigation of crops and permanently altered the hydrology of valley streams (Close & Williams, 1988). Currently, fire and flood pose severe threats to the only major remnant riparian community in the San Joaquin valley and the last refuge for the riparian woodrat. To reduce the potential risks associated with floods, wildfires and disease (Williams, 1993), the Endangered Species Recovery Program (ESRP) has recently proposed establishment of this subspecies in other locations. Prior to this proposed translocation effort, a number of factors should be evaluated, such as food availability, nesting sites and travelling corridors, and competition and interbreeding with other woodrats (Williams, 1993). Our study is intended to complement current research efforts being conducted by ESRP that will serve as a basis for the translocation of this subspecies.

Woodrats (genus *Neotoma*) construct complex dens composed of sticks of various sizes (Lindsdale & Tevis, 1951). They rely on these dens for shelter, protection from predators, and food storage, and the dens are often inherited between generations (Kelly, 1989). A significant amount of time and energy goes into constructing and maintaining these dens, and their spatial patterns and location in relation to construction material are important to population viability (Olsen, 1973; McGinley, 1984). For example, woodrats require habitat that provides cover and food resources, and dens are often located in or near a large core element such as a rock or a tree (McGinley, 1984). Experiments have shown that woodrats exhibit a preference for low trees with overhanging branches over other configurations (Olsen, 1973). Because woodrats have strong habitat preferences (Cameron & Rainey, 1972; Wright, 1973) and these preferences affect population viability, successful reintroduction of threatened populations, such as the endangered riparian woodrat (*N. f. riparia*), relies on the correct placement of artificial dens. Even though woodrats are prolific den builders once they become established in new habitats (Bonaccorso & Brown, 1972), artificial dens are likely to increase the probability that animals occupy new habitats in translocation efforts. Despite the importance of this information, we are not aware of previous studies of the spatial patterns of woodrat dens.

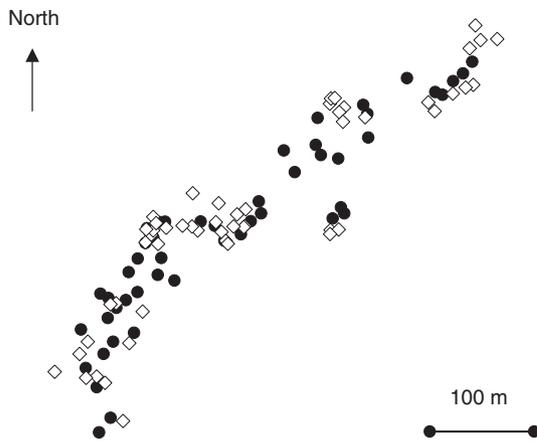
In this paper, we use data collected from a non-endangered, conspecific population of woodrats to estimate how the distribution of dens in translocation sites might influence the likelihood that animals persist in their new environment. We characterize the habitats in which dens occur, analyze their spatial clustering, and compare changes in weight over time for sex and age classes. We use our results to identify ideal conditions for establishing woodrat dens in translocation sites. We compare outcomes for translocation using spatial analysis versus solely habitat-based approaches and identify the optimal spatial configuration of dens that should be considered in translocation efforts.

## METHODS

### Description of site

Sedgwick Reserve is located in the Santa Ynez valley, 45 km northwest of Santa Barbara, California, and ranges from 335 to 720 m in elevation. Average precipitation is 38 cm/year, most of which falls between November and April. Topography includes two major drainages with flat to gentle terrain and deep alluvium over Plio-Pleistocene sediments; steep upland areas with serpentine soils overlying uplifted Franciscan melange; and side canyons associated with secondary drainages.

In this study we focused on an 8.3 ha area in which we mapped the location of 101 *Neotoma fuscipes* dens (Fig. 1). We randomly selected 49 of these dens as our focal sites for live-trapping. Primary habitat in our study site was riparian woodland including blue, live and valley oaks and western sycamore; chaparral; mixed gray pine



**Fig. 1.** Distribution of dens in study period, indicating dens where trapping was conducted (circles) and those used to calculate density estimates (diamonds)

forest; serpentine grassland with yucca and coastal sage scrub. It is important to note that, of these habitat types, oak-riparian woodland habitats are characteristic of areas occupied by *N. f. riparia*. In our study area, all habitat types had over 90% cover and had been unburned and undisturbed for over 25 years.

### Woodrat population parameters

We set Tomahawk live traps (13 × 13.5 × 41 cm) baited with oatmeal, peanut butter and fresh apple 2 nights per month at each of the focal dens over a period of 3 years. We individually marked each animal captured using ear tags, and recorded the gender, weight, age class (juvenile, subadult, adult) and reproductive status for each capture. Using these metrics, our analyses took two forms: those focused on patterns of use per den, and those focused on animals assumed to be residents for particular dens. Our analyses of patterns of use ‘per den’ were used to characterize seasonal changes in condition for sex and age classes, which will become important in determining ideal timing for translocation efforts. In particular, we tabulated the number of different animals captured and the total number of captures at each den. The total number of visitors to each den in each trapping period and the diversity of visitors (i.e., the ratio of different visitors to total captures) were used as response variables in considering the habitat and spatial attributes described below (Table 1). We also characterized differences in diversity and total captures for sex and age classes. ANOVA was used to examine the relationship between diversity (i.e., number of different animals visiting to a particular den) and frequency (i.e., total number of visits) of use of dens for sex and age classes.

In addition to analyzing overall use patterns of dens, we compared the characteristics of the resident animal in each den. Residents were defined by on two criteria: (1) the animal captured the most often at a particular den; and (2) animals captured at least three times at a particular den (the results are robust to this value as long as it is greater

than 1). Of the 49 dens where we trapped, only 19 met the requirements for having a resident animal. We used logistical regression to examine the population parameters of resident woodrats that were different from non-residents. We also compared the gender of the residents with the gender of the visitors using a  $\chi^2$  test. Finally, we used discriminant function and canonical correlation analyses to examine habitat preference and den usage patterns for different sex and age classes.

### Habitat features and animal condition

For habitat variables, we recorded: (1) the presence of all plant species within a radius of 1.5 m; (2) the percentage cover of understorey woody vegetation (<1.5 m tall); (3) the percentage cover of woody overstorey vegetation (>1.5 m tall); (4) the distance to nearest tree for the focal dens. Overstorey cover was estimated by averaging densiometer readings at each of the four cardinal directions. We replicated these measurements at 24 random locations within the study site. We interpret differences between the den sites and random samples as an indication of preference in habitat. We used Canonical Correlation Analysis to examine relationships between den characteristics and attributes of the animals captured at each den (Table 1). This analysis was also applied solely to resident animals. We also used canonical correlation analysis to examine the relationship between standardized weight of the resident animal and habitat attributes described above.

### Spatial distribution of dens and animal condition

To characterize the relative density of dens, we first used home-range estimates for male woodrats from Cranford (1977) to establish sampling areas (2289 m<sup>2</sup> or a radius of 27 m for a circular territory). For all dens where trapping was conducted, we surveyed the area within a 30 m radius of dens, mapped all den locations within this area, and estimated the density of dens. This information was used to examine the relationship between the spatial distribution of dens and patterns of use. We also evaluated the relationship between den usage patterns and population parameters. For our analysis of resident animals, we examined whether the number of dens at four different radii (5, 15, 30 and 100 m) affected the weight of the animals. We selected these radii to represent den density at four meaningful distances: (1) directly adjacent

**Table 1.** Average number of captures for each sampling event (nightly trapping), and average diversity, sex ratio, age class and weight for combined samples.

	Mean	Standard Deviation
Total captures	14.9	4.5
Diversity (number of individuals/total)	0.455	0.17
Proportion male captures	0.517	0.224
Proportion adult captures	0.86	0.14
Weight standardized by sex, age and month (g)	0.87	0.151

to a den (5 m); (2) within a core area of a territory (15 m); (3) within an average territorial radius (30 m); (4) across several adjacent territories (100 m).

To analyze the spatial pattern of dens, we used Ripley's  $L$ -function analyses to examine the degree of aggregation of dens across a range of scales,  $h$ , in which  $h$  represents a radius around a point (i.e., a den), and  $L$  is the deviation from a random distribution. Thus,  $L(h)$  is the degree of clustering of dens at radius  $h$ , and has an expected value of 0 for random distributions of points. Values of  $L(h)$  that are greater than 0 indicate clustering or underdispersion and values that are less than 0 are indicative of regular or overdispersed data (Ripley, 1979, 1981; Cressie, 1991; Bailey & Gattrell, 1995; also see Klaas, Maloney & Danielson, 2000 for a specific biological application). We used Monte Carlo simulations to construct 95% confidence intervals around a value of 0 for  $L(h)$  based on the maximum and minimum values from 1000 simulations of random distributions. We excluded peripheral areas in which no dens were located. We did this to prevent the large-scale signal that was primarily related to the presence of suitable habitat from overwhelming the fine-scale spatial pattern (Chatfield, 1984; Diggle, 1990).

## RESULTS

### Woodrat population parameters

Our analysis of changes in animal weight over time and for different age and sex categories suggests that, in general, woodrats lose weight in the dry season (Fig. 3). Based on 50 years of rainfall data from Lake Cachuma (approximately 20 km from our study site), highest rainfall occurs during January through March, and lowest rainfall occurs during June through September (Fig. 4). This suggests that the summer may be the stressful period for woodrats in southern California. Our data agree with the winter and summer body mass differences of Stallone (1979), where lower organ mass and brown fat deposits were found in *Neotoma lepida* in late summer (Davis & Hillyard, 1983).

Males were consistently heavier than females (Table 1). The relative proportion of juvenile and subadult animals was highest in April and August for this population, suggesting that there are two reproductive periods (Fig. 2). Adult females lose weight during these periods, supporting this interpretation of the data. This result corresponds with M'Closkey's (1972) work in coastal sage shrub areas in Orange County, California, where recruitment of *N. lepida* was found to be highest in April and June.

We use an ANOVA to determine whether den diversity (number of dens visited by a particular animal divided by the total captures) differed between genders or among age classes (juvenile, subadult or adult). We found no difference in den diversity (number of dens visited by a particular animal divided by the total captures) between male and female animals ( $P = 0.699$ ). However, we did detect higher den diversity for subadults compared to adults and juveniles ( $P < 0.0036$ ).

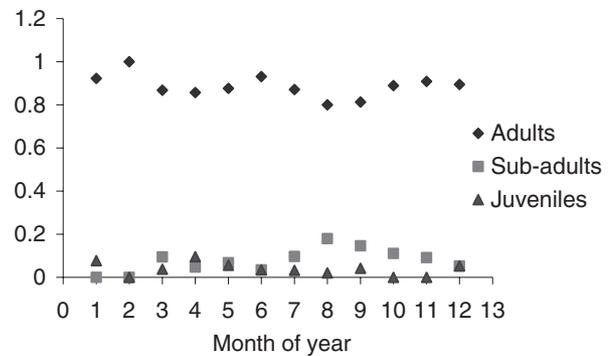


Fig. 2. Proportion of captured individuals in each age class by month

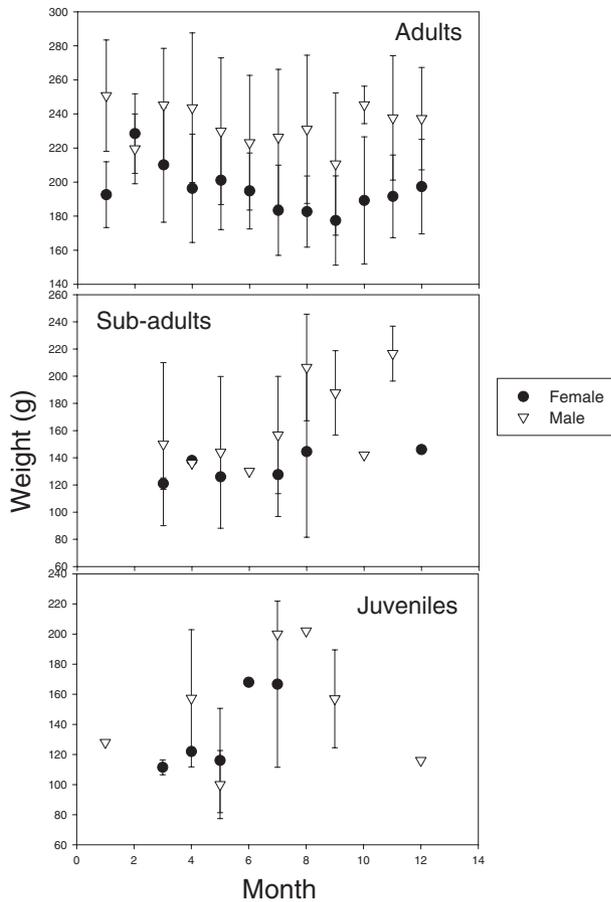
We used logistic regression to determine whether resident animals differed from non-residents with respect to the population parameters in Table 1. This analysis revealed no significant difference between resident and non-resident woodrats in terms of the proportion of males ( $P = 0.096$ ), the proportion of adults ( $P = 0.493$ ) and the standardized weight ( $P = 0.165$ ). We used discriminant function analysis to determine if male and female residents differed in their habitat preferences or the density of neighbouring dens at different distances (Table 2). We found no gender differences in habitat (Wilk's  $\lambda = 0.303$ ) or den density (Wilk's  $\lambda = 0.397$ ). We found that the gender of the resident animal did not change the proportion of males and female visitors ( $I = 0.115$ ; Fisher's exact test), although it is interesting to note that non-resident females never visited resident dens.

### Habitat features and animal condition

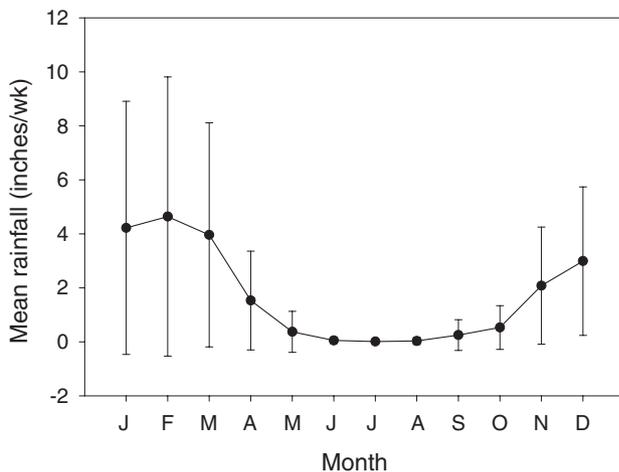
We found that a combination of three measures of habitat structure (distance to nearest tree, understorey cover and overstorey cover) precisely distinguished den versus random points using discriminant function analysis ( $r^2 = 0.55$ ; Wilk's  $\lambda < 0.001$ ). Using logistic regression, these three variables correctly classify den versus random sites 89% of the time. These results suggest that woodrats select den sites with high understorey and overstorey cover that are close to the base of trees (Table 3).

Using logistic regression, we found no overall relationship between woodrat den locations and species of the nearest tree or plant community composition. However, of the 32 overstorey plant species identified, woodrats exhibited a preference for toyon (*Heteromeles arbutifolia*) and blue oak (*Quercus douglasii*) and avoid pine (*Pinus sabiniana*) ( $P < 0.036$ ). The preferred understorey species was poison oak (*Toxicodendron diversilobum*) (present at 36% of the dens and none of the random points). Avoided species were California sage (*Artemisia californica*) ( $P < 0.023$ ), totalote (*Centaurea melitensis*) ( $P < 0.009$ ) and eriogonum (*Eriogonum fasciculatum*) ( $P < 0.003$ ).

In addition to characterizing habitat preferences, we were interested in the degree to which habitat characteristics relate to type and conditions of all individuals caught at a den. Using canonical correlation



**Fig. 3.** Seasonal changes in size distribution of woodrats for sex and age classes



**Fig. 4.** Average weekly rainfall in inches, based on 1952–99 records from Cachuma Lake (approximately 20 km from study site)

analysis, we found a significant relationship between den and animal attributes ( $r^2 = 0.67$ , Wilk’s  $\lambda = 0.003$ , Tables 1, 2). The coefficients suggest that the multivariate correlation was due primarily to a significant relationship

between percent overstorey cover and diversity of woodrat usage ( $r^2 = 0.45$ , Fig. 5(a)). This observed increase in the diversity of animal use suggests that dens established under dense tree canopy may be more likely to be used by woodrats.

The above analysis suggest that animals may exhibit a preference for habitats with high understorey and overstorey cover that are close to the base of trees for den construction. Our analyses of resident animals agree with these results. Using canonical correlation analysis, we found a strong correlation between habitat attributes and the weight of resident animals ( $r^2 = 0.64$ , Wilk’s  $\lambda = 0.0012$ ); understorey cover alone explains most of this variation ( $r^2 = 0.624$ , Fig. 5(b)). Thus, our results suggest that individuals with relatively high understorey cover near their home dens may be heavier than expected given their age, their gender and the month of the year.

**Spatial distribution of dens and animal condition**

We limited the scale of our point pattern analysis to a maximum radius of 200 m (half of the smallest dimension of our study site) to limit the influence of edge effects on detection of spatial patterns. Our point pattern analyses suggest that woodrat dens are significantly clustered at spatial scales up to radii of 200 m, and become asymptotic at 100 m (note that  $L(h)$  is always positive in Fig. 6). Further, degree of clustering increased between zero and 125 m and subsequent clustering remained relatively constant for larger scales.

In our analyses of all individuals trapped at each den, we did not find significant relationships between the spatial distribution of dens and animal attributes. This suggests that animals of different sex and age classes do not show preference for distinct aggregation distances of neighbouring dens. In addition to these overall use patterns, we examined the average number of dens visited (i.e., dens where animals were captured) by individual

**Table 2.** Den and habitat attributes for resident woodrat sites.

Den variable	Mean	Standard deviation
Number of dens within a 25 m radius	5.21	2.96
Number of dens within a 50 m radius	13.57	6.41
Number of dens within a 100 m radius	29.50	10.67
Percent woody understorey cover	53.75	28.73
Percent woody overstorey cover	61.3	24.88
Distance to nearest tree (m)	1.73	2.49

**Table 3.** Den and habitat attributes of woodrat sites relative to random points in the study site.

	Den site	Random
Percent woody understorey cover	53.75	13.6
Percent woody overstorey cover	61.3	45.3
Distance to nearest tree (m)	1.73	4.7

woodrats of different age and sex classes. We found no difference in sex categories, but found that subadult animals tended to visit more sites than juvenile and adult animals ( $P < 0.018$ ).

While the types of animals visiting a particular den were not affected by the density of neighbouring dens, we found strong relationships between the spatial distribution of neighbouring dens and the resident animal. We used canonical correlations analysis to look for a relationship between the standardized weight of the resident animal and the number of dens at different radii. We found that 49.1% of the variability in weight is explained by the density of neighbouring dens (Wilk's  $\lambda = 0.0211$ ), and the direction of this relationship varied across spatial scales. The analyses reveal a negative correlation with animal weight at the 5 m radius ( $-0.1645$ ), positive at 15 m ( $0.3954$ ), and negative at 100 m ( $-0.2277$ ).

## DISCUSSION

Because of their reliance on dens, woodrats are strong candidates for employing information about the location and spatial patterns of dens when attempting to relocate imperilled populations. Artificial dens have been successfully used for other purposes (e.g., Horne, McDonald & Reichman, 1998), suggesting that attention to details of den location may enhance the chances of success for relocation or reintroduction of threatened populations. Previous work on woodrats suggests that particular attributes of dens may significantly influence animal population parameters. In particular, dominant animals may control several dens, while homeless animals do not live long enough to build new dens (Linsdale & Tevis, 1951, 1956). Post, Reichman & Wooster (1993) found that body mass of woodrats was significantly correlated with the size of cached food. However, they did not find differences in den density for different sex and age classes of animals. Our result that both female and male animals visited males, while females never visited females, contrasts with Wallen's (1982) finding that males were unlikely to be visited and more likely to visit females. Our work suggests no difference in den usage for sex categories, but higher rates of visitation of subadults as compared to adults and juveniles.

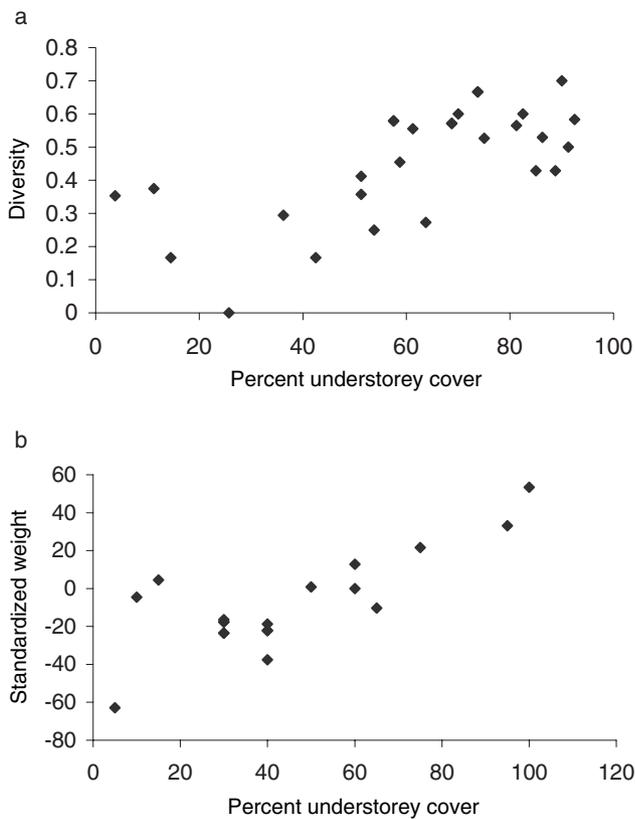
Our result that understory cover was significantly correlated with animal weight is interesting to consider in the context of earlier findings that white-throated woodrats (*Neotoma albigula*) select sites for construction of a den based on understory cover (Olsen, 1973). Our finding that understory cover is significantly correlated with animal weight probably reflects that dominant (i.e., larger) animals take over the best dens in a habitat. Previous work on habitat selection in woodrats suggests that animals prefer areas with over 90% canopy cover (Vogl, 1967). Our result that animals use patterns which are significantly correlated with overstorey cover agrees with Turowski & Watkins (1976), who reported a strong relationship between overstorey and density of dens for the white-throated woodrat. In northern California, dusky-footed woodrats occur in juniper woodland, open pine forests and

lava beds. In the Mojave Desert of California, the linkage between oak and woodrat distribution is very strong (Smith *et al.*, 2000).

Our results suggest that dusky-footed woodrats select den locations on the basis of understory cover, but also benefit from dense overstorey cover. Woodrats preferentially placed their dens in poison oak, perhaps as a deterrent to predators or because herbivores are less likely to feed on this plant, which would mean that the leafy cover would remain intact. It should be noted that the particular plant species that were avoided by woodrats tend to occur in open areas, which may influence the correlation between canopy cover and den locations. Further, woodrats did not avoid sage brush *per se*, but generally avoided chaparral habitats. The correlation between the size of the animal and the density of dens may be due to larger animals being able to out-compete other individuals for these sites. The more clustered dens may be better because they are clumped around cover or food resources. Animals may also benefit from high densities by predator swamping, as many of their predators (gray fox, bobcat, coyote, barn owl) are territorial.

One of our most interesting results was that dens with more canopy cover were visited by more individuals, or had more individuals trapped near them than those in more open sites. Denser cover may provide protection from predators and may provide more resources and shade such that there is greater intraspecific competition for dens in such areas. Therefore, when the resident has been temporarily removed by being trapped overnight, dens with favourable attributes may be taken over, resulting in more diversity of use. Conversely, if a den with less favourable attributes is not well defended, there would be few takeover attempts resulting in less diversity of use. Animals using the same area may be relatives, making the sharing of resources more acceptable. For example, female banner-tailed kangaroo rats tend to share dens with their offspring for months after weaning, but do not share with non-relatives (Jones, 1984). Alternatively, higher trap rates in high canopy cover may be attributable to higher local densities and not necessarily to takeover attempts. An important next step will be to use radio telemetry to examine these unresolved questions. In addition, future studies should employ radio telemetry to test our assumptions about distinguishing residents from visitors based on trapping data. Telemetry could also be used to test the assumption that trap success near a den indicates den use.

Our results have direct implications for identifying optimal conditions for den locations in translocation efforts for the endangered riparian woodrat. First, artificial dens should be placed in clusters at a radius of 15 m, as values above and below this showed negative correlations. At larger radii, animals may need to travel longer distances to visit other dens, and may become isolated from preferred habitats. Our finding that woodrats cluster their dens and build them under trees makes sense for both food and predator avoidance escape (woodrats being adept climbers). Second, in addition to spatial analyses used to identify optimal configuration for artificial dens, population



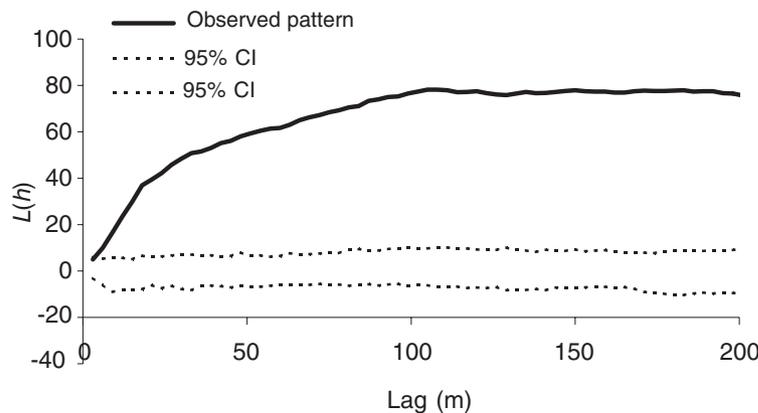
**Fig. 5.** (a) Relationship between diversity of use and overstorey cover; (b) Relationship between diversity of use and overstorey cover

monitoring is important to characterize sex- and age-specific patterns in condition and in use of dens. Third, we suggest that translocation should occur after reproductive events that occur in April and August for woodrats in southern California. Finally, because individuals occupying nearby dens may be related or may have established social relationships, the spatial distribution of translocated individuals will be critical. These results provide practical guidelines for determining appropriate timing for translocation events in the context of animal condition, minimizing disease transmission and reproduction.

In addition to these specific recommendations, we found that use of simple spatial pattern analysis can reveal important underlying structure in animal populations with permanent den or nest sites. We expect that the impacts of spatial structure are relevant for other populations, and the analysis of spatial pattern may improve conservation efforts that involve translocation or habitat improvement. For this reason, we suggest that data on spatial pattern and habitat preferences should be more frequently considered in conservation planning.

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**Fig. 6.** Results of point pattern analyses and 1000 Monte Carlo simulations, showing clustering of woodrat dens as a function of distribution (or ‘Lag’ in m) out to 200 m in radius. The y axis represents the degree of clustering where  $y > 0$  = underdispersed (clustered);  $y = 0$  = random and  $y < 0$  = overdispersed (regular). There are two dashed lines that represent the 95% confidence interval constructed around 0 using 1000 random simulations. The dark solid line is the actual pattern in the data.

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