

Nest Site and Microhabitat Selection by Key Largo Woodrats

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Abstract: Reductions in habitat quantity and quality have contributed to precipitous declines in the Key Largo woodrat (*Neotoma floridana smalli*) population over the last 30 years. Additional information on microhabitat and nest site selection is needed to increase quality of the remaining habitat and increase the population. In 2005–2006, we evaluated microhabitat selection by comparing structure and composition of vegetation at known woodrat locations to random locations in available areas. We evaluated nest site selection by comparing nest substrate availability and habitat characteristics around nests with random locations. We detected little support for selection of foraging areas based on structure and composition of vegetation. Key Largo woodrats selected nest sites in areas with higher abundance of artificial nest substrate and higher percentage of younger hammock. Key Largo woodrats appear to be generalists with respect to microhabitat, but display a high degree of selection for artificial nest substrate, which presumably offers greater protection from predators. Although results indicate that artificial nest substrate currently is an important habitat component for Key Largo woodrats, long term management should focus on protection of hardwood hammock to allow development of natural nest substrate.

Key words: Key Largo woodrat, microhabitat, *Neotoma floridana smalli*, nest site selection, radiotelemetry

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 65:32–37

The Key Largo woodrat (*Neotoma floridana smalli*) historically ranged throughout the hardwood hammocks of Key Largo, Florida, but currently is restricted to federal and state protected lands on the northern one-third of the island (Barbour and Humphrey 1982, McCleery et al. 2006, Winchester et al. 2009). Despite protection of remaining habitat from development, the population continued to decline and is currently at a high risk of extinction (McCleery et al. 2005). All factors contributing to the population decline are not known, but loss of habitat and degraded quality of remaining habitat has had a major influence.

Prior to protection, hardwood hammocks of north Key Largo underwent a variety of human-induced disturbances (M. S. Ross et al., Florida International University, unpublished data). Farming, fires, and abandoned urban development projects altered the extent, structure, and composition of the forested landscape resulting in patches of habitat differing in seral age. Heterogeneity in hammock age was the focus of past studies examining habitat use. Results of these studies were conflicting, with most detecting higher abundance in mature hammock (Brown 1978, Hersh 1978, Barbour and Humphrey 1982, N. C. Goodyear, unpublished report), but other studies detecting higher abundance in young hammock (McCleery et al. 2006), or equal abundance among all hammock age classes (Keith and Gaines 2002, Sasso and Gaines

2002). However, Winchester et al. (2009) concluded that delineations of hammock age used in previous studies was at too coarse of a scale to be a reliable predictor of Key Largo woodrat presence.

Evaluating microhabitat selection can provide valuable information on habitat use obscured at larger spatial scales (Castleberry et al. 2002, Mengak and Guynn 2003). When assessing habitat selection where use is disproportionate to availability, resources typically are assumed to be equally available within the area defined as available to an individual (Johnson 1980, McClean et al. 1998). However, for central place foragers (i.e., woodrats), resources farther from the central place may be less available as predation risk and energy expended increase with increasing distance from the central place (Orians and Pearson 1979, McGinley 1984). Due to increased risks at farther distances, central-place foraging theory predicts individuals will select fewer resources at greater distances from the central place (Schoener 1979). Little information is available on Key Largo woodrat foraging behavior, but individuals are known to maintain small home ranges, incorporating one or several nests that serve as day-time refugia (McCleery et al. 2006). If habitat availability and selectivity vary with distance from the nest, habitat selection models incorporating distance of foraging locations along with habitat should be more informative (Rosenberg and McKelvey 1999).

Nest sites are critical resources for Key Largo woodrats (McCleery et al. 2006; N. C. Goodyear, North Key Largo Study Committee, unpublished data). Historically, Key Largo woodrats used a variety of natural nest types, including free-standing stick nests, natural cavities in the limestone substrate, root systems of large trees, and large downed trees. Recently, nests have been associated with artificial substrate (e.g., trash piles, rock piles) from past urban development, and abandoned buildings and building materials (McCleery et al. 2006; N. C. Goodyear, North Key Largo Study Committee, unpublished data). McCleery et al. (2006) determined the majority of nests consisted of artificial substrate and occurred more frequently in younger hammock (disturbed after 1971). However, the presence of artificial substrate is a result of anthropogenic activities and typically is associated with hammock in younger seral stages. Therefore, high use of younger hammock patches may be confounded with availability of artificial substrate.

Our objective was to determine microhabitat features associated with Key Largo woodrat movements and examine the relationship between nest substrate type and hammock age. Consistent with central place foraging theory, we predicted that microhabitat selection would differ at varying distances from the nest. Also, we predicted that Key Largo woodrats would select artificial nest substrate irrespective of hammock age.

Study Area

Our study area was defined as all upland forest habitat (hardwood hammocks) occurring on Crocodile Lake National Wildlife Refuge and Dagny Johnson Key Largo State Botanical Preserve. The hardwood hammocks of this region are characterized as closed canopy forest with a limestone substrate, containing over 150 species of evergreen and semi-deciduous tree and shrub species (U.S. Fish and Wildlife Service 1999). Canopy closure creates a shaded environment on the forest floor resulting in a sparse shrub and herb layer. As a result, the understory consists primarily of seedlings and saplings of canopy and sub-canopy species (U.S. Fish and Wildlife Service 1999). Mangroves occur along both coasts creating a relatively narrow transitional zone that is comparatively open with high vine growth and numerous thorny plant species (Ross et al. 1992).

Methods

Capture and Handling

We used a combination of random and non-random sampling to capture Key Largo woodrats for radiotelemetry. Using a stratified random design and proportional allocation, we established 40 trapping grids in two strata, delineated by distance (≤ 75 or > 75 m) to artificial nest substrate (Winchester et al. 2009). Each grid con-

sisted of 9 stations and in a 3x3 array with 25 m spacing. At each station we placed two 10.2x11.4x38.1-cm, vented Sherman traps with raccoon (*Procyon lotor*)-proof door latches (Model PXL15; H. B. Sherman Traps Inc., Tallahassee, Florida). Traps were baited with peanut butter and crimped oats. We opened traps for four consecutive nights checking each trap daily within the first three hours after sunrise. Each grid was sampled three times (April–May, August–September and November–December) during 2005. We supplemented random sampling by targeting areas where woodrats were known to occur (McCleery et al. 2006, B. Muznieks, U.S. Fish and Wildlife Service, personnel communication) and areas with signs of woodrat activity (i.e., stick piling). We placed three traps at the target location for three consecutive days and checked traps daily within the first three hours after sunrise. All captured individuals were sexed, weighed, and marked with passive integrated transponder (PIT) tags and #1005 Monel ear tags (National Band and Tag Company, Newport, Kentucky).

Captured individuals weighing ≥ 180 g were selected opportunistically for radiotagging with the goal of maintaining an equal sex ratio and maximizing sample dispersion throughout the study area. Individuals were manually restrained and radiocollared with 9-g radio-transmitters (AVM Instrument Co., Colfax, California) affixed around the neck with cable ties. Radiotagged individuals were released at the capture site immediately after the radiotag was attached. All capturing and handling was conducted under Federal Fish and Wildlife Endangered Species Permit #TE0959080-1, State of Florida Fish and Wildlife Conservation Commission Special Purpose Permit #WX05089, Florida Department of Environmental Protection Research and Collection Permit #5-05-41, and University of Georgia Animal Care and Use Permit #A2005-10044-0.

Nest Site Selection

We located nests of each individual during the day, three times/month, by homing with a TRX-1000S VHF receiver (Wildlife Materials, Murphysboro, Illinois) and a folding, threeelement Yagi antenna. We recorded type of substrate used and location with a Global Positioning System (GPS; Trimble GeoXT). Nest substrate was categorized as artificial (rock piles, trash piles, abandoned buildings, or building materials) or natural (downed logs, root systems of standing or wind-blown trees). We determined the availability of artificial substrate by systematically searching the study area. We recorded the location of all rock and debris piles with a GPS. We calculated density of debris piles in each hammock age class using Hawth's Analysis Tools in ArcGIS (Environmental Systems Research Institute, Redlands, California). Telemetry data revealed radiocollared individuals moved a mean distance of 45 m from the nest. Therefore, we quantified availability of artificial nest

substrate (NEST) as the total number of rock and debris piles occurring within a 45-m radius around each nest. To evaluate selection of hammock age, we assigned a value of 1–4 to disturbed (developed or unvegetated), young (disturbed after 1971), medium (disturbed from 1940–1971), and mature (disturbed before 1940) hammock, respectively, following classifications used in previous studies (Ross et al. 1995, McCleery et al. 2006). At each nest location, we calculated the weighted average of hammock age (AGE) occurring within 45 m of the nest using Hawth's Analysis Tools in ArcGIS resulting in a value between 1 and 4. Hammock age values represent an index of the average hammock age surrounding each nest. We generated random points equal to the number of nests identified throughout the study area using ArcGIS and calculated NEST and AGE within 45 m of each random point.

Microhabitat Selection

We estimated locations of individuals using two observers taking simultaneous bearings from permanently established telemetry stations. Stations were placed within 100 m of nests occupied by radiotagged woodrats. Station coordinates were determined using a handheld GPS unit. We located individuals within the first six hours after sunset, two–five times per week, but no more than once in a 24-hr period. We used a rotating schedule, beginning with a different individual each night, to ensure data were not temporally biased. Radiotag batteries typically lasted >4 months allowing us to collect 30–45 locations/individual. We only recorded locations for those individuals judged to be active (i.e., discontinuous signal). We assumed that active individuals were foraging because woodrats are not likely to move away from the nest unless foraging due to predation risk. We calculated locations from telemetry station coordinates and azimuths using program LOCATE III (Nams 2006). We estimated telemetry error using two observers taking simultaneous bearings on test collars placed at randomly selected points within each individual's foraging range. Random location of test collars ensured that vegetation present and distances from telemetry stations were representative of actual telemetry conditions. To minimize bias from telemetry error, we removed estimated locations that were out of the range of the equipment (>500 m from telemetry station).

We examined microhabitat selection by comparing habitat characteristics in the foraging area of each radiotagged woodrat to those in the area available to each individual. To represent the foraging area of each radiotagged individual, we randomly selected five foraging locations >25 m apart. Three individuals had foraging ranges that were too small to include five locations >25 m apart. We used four locations for two individuals and three locations for the other. The area available to each individual was represented as

a circle with a radius equal to the distance from the nest, or nest centroid in the case of multiple nests, to the farthest estimated foraging location (Castleberry et al. 2001). Within the available area of each individual, we selected random locations equal to the number of randomly selected foraging locations. For each foraging and available location we measured the structure and composition of vegetation using the point-centered quarter method (Cottam and Curtis 1956). At each point, we calculated the density of understory stems (UND; 1.0–5.0 cm diameter measured at 4 cm above ground), and the mean diameter at breast height (DBH; measured at 1.4 m above stem base) of midstory (MID; 5.1–10.0 cm DBH) and overstory (OVER; >10.1 cm DBH) stems. We recorded species of each stem encountered at each point and estimated overall species richness (RICH) using program SPECRICH (Hines 1996). We measured distance from each foraging and available location to the nest or nest centroid (DIST) in ArcGIS.

Model Development and Evaluation

Artificial substrate was used frequently as nest sites by Key Largo woodrats (McCleery et al. 2006, Winchester et al. 2009) and hammock age has been examined relative to habitat selection in previous studies (Hersh 1978, Barbour and Humphrey 1982, Keith and Gaines 2002, Sasso and Gaines 2002, McCleery et al. 2006). Therefore, we developed two competing models each with a single predictor variable (NEST and AGE) to determine the effect of artificial nest substrate and hammock age on nest site selection. We developed 22 *a priori* models to examine microhabitat selection. Habitat variables included in models reflected the structure and composition of vegetation which relate to availability and diversity of food, and availability of cover. We developed models with distance from nest and distance-habitat interactions as covariates based on central-place foraging theory (Orians and Pearson 1979, Schoener 1979, Rosenberg and McKelvey 1999).

Nest site selection and microhabitat data were analyzed with logistic regression in SAS (PROC LOGISTIC; SAS Institute 1999). We compared model likelihood using Akaike's Information Criterion (AIC) and calculated Akaike weights (w_i) for each model (Burnham and Anderson 2002). We calculated Nagelkerke's R^2 for each model to evaluate the amount of variation in the response variable accounted for by the covariate. We used multi-model inference to estimate nest site selection parameters by calculating model-averaged estimates of regression coefficients and unconditional standard errors for covariates included in the confidence set of models ($\Delta AIC \leq 4$; Burnham and Anderson 2002). Variable importance for microhabitat models was determined by summing w_i for all models that included each variable (Burnham and Anderson 2002).

Results

Radiocollared individuals (20 F: 22 M) were tracked from April 2005 to February 2006. Due to predation, transmitter loss, and transmitter failure, we obtained nest site selection data from 39 individuals and obtained foraging location data on 35 individuals. The 35 individuals for which foraging location data were obtained were tracked for a mean of 13 weeks/individual, resulting in a mean of 33.0 locations/individual. Mean telemetry error determined from locations of test collars was 29.5 m (SE = 6.0).

We identified 66 unique nests. Mean number of nests used/individual was 1.9 (SE=0.2) for all individuals, with males averaging 2.3 (SE=0.2) and females averaging 1.6 (SE=0.2) nests. Artificial nest substrate was used more frequently than natural substrate and the proportion of natural substrate used increased with hammock age (Table 1). Natural nest substrate used included the root systems of standing and wind-blown trees (*n*=9), piles of dead vegetation and vines (*n*=2), and a log (*n*=1). Types of artificial nest substrate included piles of rocks and cement (*n*=25), a standing building (*n*=2), abandoned boats and cars (*n*=7), and miscellaneous debris (e.g., roofing material, truck tire, and metal debris; *n*=20). Artificial substrate was more abundant in disturbed and young hammock areas (Table 1). Areas within 45 m of nest sites had more artificial nest substrate (mean = 3.3 ± 0.4 debris piles) than random areas (mean = 0.1 ± 0.1 debris piles). Nest sites (mean age value = 2.4 ± 0.8) were surrounded by more young hammock than random sites (mean age value = 3.1 ± 1.0).

Our data supported the NEST model as the best predictor of Key Largo woodrat nest site selection (AIC=99.23; Nagelkerke's R²=0.6476). Number of rock and debris piles within a 45-m radius was positively related to nest site selection. The 95% confidence interval (CI=1.307–3.055) for the NEST parameter estimate (β = 2.181, SE=0.446) did not include zero, indicating the variable was useful for predicting nest site selection. There was insufficient evidence to consider the AGE model (AIC = 169.30; Δ AIC = 70.07) as a plausible explanation of nest site selection.

Microhabitat measured around known foraging locations was similar to microhabitat measured around random points, with the largest differences observed for DIST and UND (Table 2). There was considerable uncertainty among microhabitat models, with 14 models having a Δ AIC ≤ 4 (Table 3). We detected little support for selection of microhabitat variables alone, as models not including DIST as a main effect performed poorly (Δ AIC > 55.0). In addition, R² values were low for all models (< 0.235; Table 3). Model averaged parameter estimates were negative for OVER (β = -0.004, SE = 0.017) and DIST (β = -0.023, SE = 0.007), and positive for UND (β = 0.023, SE = 0.007), MID (β = 0.004, SE = 0.028), and RICH (β = 0.004, SE = 0.014). Sum of model weights suggested

Table 1. Number of Key Largo woodrat nests in natural and artificial substrate, proportion of natural nest substrate used, and number of artificial substrate/ha in four hammock age classes, disturbed (developed or unvegetated hammock), young (disturbed after 1971), medium (disturbed from 1940–1971), and mature hammock (disturbed before 1940). Data were collected on 39 radiotagged individuals on north Key Largo, Florida, 2005–2006.

	Disturbed (92 ha)	Young (87 ha)	Medium (327 ha)	Mature (430 ha)
Natural substrate used	2	0	6	4
Artificial substrate used	14	11	23	6
Proportion of natural substrate used	0.13	0.00	0.21	0.40
No. artificial substrate/ha	0.85	0.53	0.24	0.09

Table 2. Mean (±SE) of variables measured at foraging and random locations of 35 radiocollared Key Largo woodrats on Key Largo, Florida, 2005–2006.

Variable ^a	Used (<i>n</i> = 170)	Random (<i>n</i> = 170)
	\bar{x} (SE)	\bar{x} (SE)
UND	0.90 (0.09)	0.71 (0.07)
MID	6.72 (0.05)	6.81 (0.07)
OVER	15.50 (0.31)	15.85 (0.43)
RICH	9.17 (0.33)	9.27 (0.47)
DIST	44.58 (3.99)	78.78 (5.55)

a. UND = understory stem density (stems/ha), MID = midstory diameter at breast height (cm), OVER = overstory diameter at breast height (cm), RICH = species richness, DIST = distance from foraging or random location to nest or nests centroid (m)

Table 3. Variables, number of parameters in the model (K), Akaike's Information Criterion (AIC), difference in AIC value between the model and the model with the lowest AIC value (Δ AIC), Akaike weights (*w_i*), and Nagelkerke's R² for models evaluated to predict probability of microhabitat use of 35 radiotagged Key Largo woodrats on Key Largo, Florida, 2005–2006.

Model ^a	AIC	Δ AIC	<i>w_i</i>	R ²
DIST UND UND*DIST	415.265	0.000	0.170	0.229
DIST UND	415.478	0.213	0.153	0.222
DIST	415.617	0.352	0.143	0.215
DIST OVER UND	416.847	1.582	0.077	0.224
DIST RICH UND DIST*RICH DIST*UND	417.091	1.826	0.068	0.236
DIST OVER	417.101	1.836	0.068	0.217
DIST RICH UND	417.216	1.951	0.064	0.223
DIST RICH	417.632	2.367	0.052	0.215
DIST MID OVER	418.109	2.844	0.041	0.220
DIST RICH RICH*DIST	418.327	3.062	0.037	0.219
DIST OVER UND OVER*DIST UND*DIST	418.391	3.126	0.036	0.232
DIST MID OVER MID*DIST OVER*DIST	418.471	3.206	0.034	0.232
DIST OVER OVER*DIST	418.621	3.356	0.032	0.218
DIST RICH MID OVER	420.064	4.799	0.015	0.220
DIST RICH MID OVER RICH*DIST MID*DIST OVER*DIST	421.466	6.201	0.008	0.235
UND	470.448	55.183	0.000	0.019
UND OVER	471.967	56.702	0.000	0.021
RICH UND	471.978	56.713	0.000	0.021
OVER	474.918	59.653	0.000	0.002
RICH	475.272	60.007	0.000	0.000
RICH OVER MID	475.887	60.622	0.000	0.006
MID OVER	477.812	62.547	0.000	0.006

a. UND = understory stem density (stems/ha), MID = midstory diameter at breast height (cm), OVER = overstory diameter at breast height (cm), RICH = species richness, DIST = distance from foraging or random location to nest or nests centroid (m)

DIST ($w_i = 1.0$) was the most important variable predicting microhabitat use, followed by UND ($w_i = 0.57$), OVER ($w_i = 0.27$), RICH ($w_i = 0.24$), and MID ($w_i = 0.10$).

Discussion

Our results indicate that hammock age class alone was a poor predictor of Key Largo woodrat nest site selection. Woodrats selected nest sites in areas with high densities of artificial nest substrate regardless of hammock age. Over 80% of nests were in artificial substrate with the remainder occurring in large logs or the root systems of overstory trees. Use of artificial nest substrate was noted previously, with rock and debris piles assumed to offer greater protection from predators than freestanding stick nests (N.C. Goodyear, North Key Largo Study Committee, unpublished data). Key Largo woodrats used disturbed areas and young hammock for nest sites possibly due to the higher availability of artificial substrate in these areas. Artificial substrate is the result of grading, dredging, development, and illegal trash disposal in recently disturbed areas, and may be confounded with younger hammock. Key Largo woodrats rarely occurred in younger hammock in the absence of debris piles.

Consistent with the most recent report of Key Largo woodrat nest use (McCleery et al. 2006), we did not document freestanding stick nests in our study. Stick nests require energy to build and maintain and likely increase predation risk due to the extra excursions required for stick collecting. The lack of stick nests is not surprising given that Key Largo woodrats opportunistically select artificial substrate when available. However, the large majority of available habitat (>75%) does not contain artificial substrate.

Natural nest substrate identified in this study and previously (McCleery et al. 2006; N. C. Goodyear, North Key Largo Study Committee, unpublished data) consists of features characteristic of mature hammock (i.e., downed logs and large trees with exposed root systems). Areas of mature hammock (disturbed prior to 1940) comprise approximately 50% of the hardwood hammock, yet occupancy and nest use in mature hammock was relatively low in our study and in previous studies (McCleery et al. 2006). The hardwood hammocks of north Key Largo have undergone a variety of major disturbances from human activities over the last century, with most of the area under cultivation for fruit crops until 1935 (M. S. Ross et al., Florida International University, unpublished data). Low use of natural substrate, the absence of freestanding stick nests, and the overall low occupancy of Key Largo woodrats in areas without artificial nest substrate suggest quality natural nest substrate is lacking (Winchester et al. 2009).

Although artificial nest substrate is assumed to provide Key Largo woodrats greater protection from predators than natural sub-

strate or stick nests, few data are available on historic or current predation rates. Suitable woodrat habitat on Key Largo is bordered to the north and south by heavily urbanized areas which offer an abundance of anthropogenic food sources for mammalian predators, including raccoons and feral cats (*Felis catus*). Winchester et al. (2009) documented high use of scent stations by raccoons and feral cats and suggested that predation may be at least partially contributing to low Key Largo woodrat abundance. Further, Burmese pythons (*Python molurus bivittatus*), which have recently invaded Key Largo, may present an additional predation threat that may not be as easily deterred by artificial substrate. Further study is needed to assess differential rates of predation between individuals using artificial nest substrate with those using natural substrate.

Efficient foraging and limited long-range movement is predicted by optimal foraging theory as a means to reduce predation risk (Orians and Pearson 1979). Thus, the limited movement away from nests we observed is not surprising. However, there was little support for selection of microhabitat at different distances from the nest, as was expected based on central place foraging theory (Schoener 1979) and applied research (Rosenberg and McKelvey 1999). Our data indicate Key Largo woodrats use a variety of microhabitats independent of ground cover and canopy or midstory structure at all available distances from the nest. The hardwood hammock habitat of Key Largo contains a high diversity of plant species (M. S. Ross et al., Florida International University, unpublished data) and offers an abundance of year-round food sources due to the sub-tropical climate. As a generalist herbivore in a resource-rich environment, Key Largo woodrats may not be limited by the structure and composition of vegetation and are able to exploit a variety of microhabitats in close proximity to the nest.

Management Implications

Our results support the results of Winchester et al. (2009) that Key Largo woodrats are limited more by availability of suitable nest substrate than by quality of foraging habitat. Therefore, management actions with the goal of increasing availability of quality nest substrate are a critical component of population recovery. Frequent use of artificial substrate suggests Key Largo woodrats benefit in the short term from presence of artificial substrate. Continued protection of existing hammock habitat should increase availability of quality natural nest substrate as the structure becomes more characteristics of mature hammock (large standing and downed trees with exposed root systems). However, management of predators may be necessary to facilitate a population increase in response to increased natural nest substrate availability.

Acknowledgments

Funding, equipment, and housing were provided by the USDI Fish and Wildlife Service. Dagny Johnson Key Largo State Botanical Preserve provided access and logistical support. We thank J. Beerens, T. Bornham, E. Saunders, C. Degayner, R. Degayner, S. Klett, M. McElroy, M. Merrill, B. Muiznieks, T. Petersen, and S. Wilson for assistance with field work and project planning. M. J. Conroy and N. Nibbelink provided earlier reviews of this manuscript.

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