

RESEARCH ARTICLE

Evaluating nest supplementation as a recovery strategy for the endangered rodents of the Florida Keys

Michael V. Cove^{1,2}, Theodore R. Simons³, Beth Gardner⁴, Andrew S. Maurer⁵, Allan F. O'Connell⁶

The Key Largo woodrat (*Neotoma floridana smalli*) and Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*) are federally endangered subspecies endemic to the tropical hardwood hammocks of Key Largo, Florida. Woodrats are considered generalists in habitat and diet, yet a steady decline in natural stick nests and capture rates over the past several decades suggests that they are limited by the availability of nesting habitat due to habitat loss and fragmentation. The more specialized Key Largo cotton mouse appears to rely on old growth hammock, a habitat type that is rare following past land clearing. In 2004, the U.S. Fish and Wildlife Service started building supplemental nest structures to restore habitat quality and connectivity for these endangered rodents, but nest use requires evaluation. We used camera traps and occupancy models to evaluate the factors influencing woodrat and cotton mouse use of the supplemental nests. We detected woodrats at 65 and cotton mice at 175 of 284 sampled nest structures, with co-occurrence at 38 nests. Woodrat nest use followed a gradient from low nest use in the north to high nest use in the south, which might relate to the proximity of free-ranging domestic cat (*Felis catus*) colonies in residential developments. Cotton mouse nest use, however, was related positively to mature hammock and related negatively to disturbed areas (e.g. scarified lands). The two species occurred independently of each other. Stick-stacking behavior was observed at supplemental nests and, although it was correlated with detection of woodrats, it was not a strong predictor of their occurrence. We suggest that nest supplementation can be an important tool for species recovery as habitat quality continues to improve with succession.

Key words: camera trap, cotton mouse, *Neotoma*, nest supplementation, occupancy, *Peromyscus*

Implications for Practice

- Supplemental nests can be used to restore habitat and facilitate connectivity of endangered nesting populations when historical development has lingering environmental effects.
- Volunteer engagement in restoration might play an important role in the future of ecology, particularly if ecological needs outstep funding availability.
- Camera traps are effective for surveying and monitoring endangered small mammals.

Introduction

The Florida Keys are home to several endemic small mammals that are threatened by habitat loss, development, predation, and a variety of other environmental factors. The Key Largo woodrat (*Neotoma floridana smalli*) and Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*) are federally protected subspecies whose ranges are limited to the last remaining tropical hardwood hammock habitat in North Key Largo. A proposed residential construction project that would have eradicated the remaining hammock habitat sparked the emergency listing of the two small mammals in 1983, eventually leading to the establishment of the Crocodile Lake National Wildlife Refuge and Dagny Johnson Botanical State Park. The two reserves protect

approximately 900 ha of the last remaining continuous hammock habitat in North Key Largo (USFWS 1999).

North Key Largo was settled and cleared for agricultural development well before the emergency listing of the two rodents. The dominant crop in the Keys in the late nineteenth and early twentieth centuries was pineapple (*Ananas comosus*), which was propagated through slash and burn agriculture and grew in the leaf mold and humus that remained after the forests were cleared. This practice required the clearing of new land every 3–4 years, which severely fragmented forest habitats

Author contributions: MVC, TRS, BG, AFO conceived and designed the research; MVC, ASM performed the experiments; MVC analyzed the data; MVC, TRS, BG, AFO contributed reagents/materials/analysis tools; MVC, TRS, BG, ASM, AFO wrote and edited the manuscript.

¹NC Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695, U.S.A.

²Address correspondence to M. V. Cove, email mvcove@ncsu.edu

³U.S. Geological Survey, NC Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695, U.S.A.

⁴School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, U.S.A.

⁵Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695, U.S.A.

⁶U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD 20707, U.S.A.

Published 2016. This article is a U.S. Government work and is in the public domain in the USA.

doi: 10.1111/rec.12418

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.12418/supinfo>

and drastically reduced natural nesting substrate (subterranean structure within humus and limestone bedrock [fossilized coral]) for the rodents. Clearing greatly reduced the number of rocky outcrops and large canopy trees, which provide further nesting structure when trees fall and cause fissures in bedrock. Fortunately, this ecologically detrimental period was short-lived because these diverse hammock communities can recover to canopy closure within 40 years after disturbance (Olmstead et al. 1983). Today the primary evidence of this disturbance is scarified limestone, windrows, abandoned buildings, vehicles, and other refuse. Nevertheless, recent genetic analyses suggest that the historic habitat fragmentation has resulted in five genetically distinct woodrat subpopulations within the already limited range (as cited by Potts et al. 2012).

The historic loss and fragmentation of habitats coincided with the introduction of exotic predators and competitors (USFWS 1999). Native predators include eastern screech owls (*Megascops asio*) and a diverse assemblage of native snakes, whereas exotic predators include free-ranging domestic cats (*Felis catus*; including feral and outdoor house cats), pythons (*Python* spp.), fire ants (*Solenopsis invicta*), and naturally invading coyotes (*Canis latrans*). Although free-ranging domestic cats have only recently been suggested as a threat to woodrats and cotton mice (Winchester et al. 2009), they were probably first introduced to the Upper Keys during the homesteading era over 100 years ago. The first python and coyote were detected more recently in 2007 and 2010, respectively, but limited sightings of either species despite significant monitoring effort suggest that they are not likely well established yet (Greene et al. 2007; C. Degayner, Friends and Volunteers of Refuges – Florida Keys, personal communication April 2012). Woodrats and cotton mice also co-occur and potentially compete with several sympatric native rodents, including hispid cotton rats (*Sigmodon hispidus*), eastern gray squirrels (*Sciurus carolinensis*), and exotic black rats (*Rattus rattus*—USFWS 1999). Removal efforts of exotic predators and pests were intermittent and mostly ad hoc prior to the establishment of an integrated pest management plan in 2013 (USFWS 2013).

Field surveys over the past three decades have documented a steady decline in Key Largo woodrat populations, with reduced abundance and in some areas a complete absence of the stick-stacking behavior and stick nests characteristic of most *Neotoma* (USFWS 1999; McCleery et al. 2006). Although population estimates vary greatly among recent surveys (McCleery et al. 2006; Winchester et al. 2009; Potts et al. 2012), all are consistently small relative to historic estimates (Barbour & Humphrey 1982). Conflicting evidence about woodrat survival and recruitment has prompted debate as to whether woodrat occurrence is limited by predation (top down, e.g. McCleery et al. 2013) or by resources and habitat preference (bottom up, e.g. Winchester et al. 2009). However, Winchester et al. (2009) characterized woodrats as habitat generalists, concluding that their occurrence was limited by the density of human-derived (Fig. 1A) or natural (e.g. rocks, uprooted trees) nesting material. Relative to generalist woodrats, Key Largo cotton mice are habitat specialists and depend on mature hammock with deep leaf litter (Barbour & Humphrey 1982). Similarly to woodrats,

statistically reliable estimates of cotton mouse abundance have been difficult to obtain, but the population trend is also declining (USFWS 1999; Greene et al. 2013).

In 2004, the U.S. Fish and Wildlife Service implemented a restoration program to increase populations of the two rodents by building supplemental nest structures. Initially, boulders and rubble piles were constructed with additional structures made of recycled jet skis that were gutted of all hazardous materials and covered in natural material (e.g. loose limestone coral, large branches, leaves, and other debris). More recently (2006–2008), a more efficient design using cinder blocks with PVC pipes, tin, and natural materials has been employed, and the current design (since 2009) uses 1–2 m segments of plastic culvert pipe cut in half longitudinally and covered in natural materials (Fig. 1B). Since the initiation of the program in 2004, volunteers have built more than 760 supplemental nest structures in the Crocodile Lake National Wildlife Refuge. Structures are distributed in both occupied and unoccupied habitats based on data from prior large-scale surveys (Winchester et al. 2009; Potts et al. 2012).

Historical data on the distribution and abundance of woodrats and cotton mice are sparse despite significant survey effort. This is most likely a consequence of the low detectability of the target species due to an apparent reduction in stick-stacking behavior by the woodrats and low capture rates due to sampling designs based on various live trapping arrays (McCleery et al. 2006; Potts et al. 2012; Greene et al. 2013). Camera traps provide a useful tool for sampling rare wildlife and can be used to generate strong inference (O’Connell et al. 2011). Thus, we analyzed camera trap data in an occupancy framework (MacKenzie et al. 2002) to evaluate woodrat and cotton mouse use of supplemental nest structures at Crocodile Lake National Wildlife Refuge. We tested multiple a priori hypotheses including nest-specific, predator, and habitat models to examine how these factors might explain the distribution of these two species and assessed their co-occurrence at supplemental nests. We also evaluated whether stick-stacking behavior provided a useful index of nest structure occupancy for woodrats.

Methods

Supplemental nest structures occur throughout much of the accessible and historically disturbed tropical hardwood hammocks of Crocodile Lake National Wildlife Refuge in northern Key Largo (Fig. 2). Hammocks are diverse forests with a 9–12 m tall canopy composed of mainly pigeon plum (*Coccoloba diversifolia*), poisonwood (*Metopium toxiferum*), west-Indian mahogany (*Swietenia mahagoni*), wild tamarind (*Lysiloma latisiliquum*), and gumbo-limbo (*Bursera simaruba*). Understory vegetation is primarily seedlings and saplings of canopy species, and also wild coffee (*Psychotria nervosa*), marlberry (*Ardisia escallonioides*), torchwood (*Amyris elemifera*), and Spanish stopper (*Eugenia foetida*), all of which provide fruit year-round (USFWS 1999). Developed areas within the refuge like the former Nike AK-3LH missile base, abandoned houses, and landfills have been restored or allowed to revert to native plant communities.

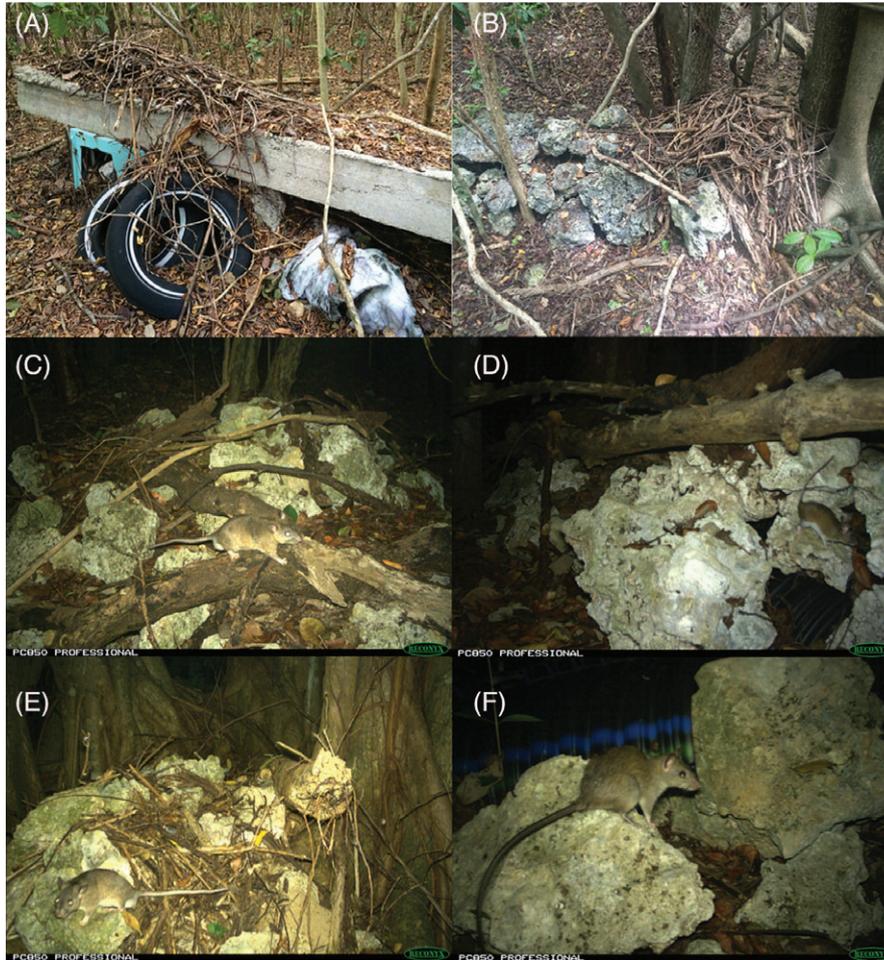


Figure 1. Photograph of a (A) woodrat nest located in typical human-derived refuse and nesting substrate (e.g. tires, oven, mattresses, and concrete); (B) supplemental woodrat nest made from a plastic culvert and natural material with woodrat stacked sticks on top; (C & D) photographs of Key Largo woodrats for comparison with Key Largo cotton mouse (D) and invasive black rat (E).

We conducted nest surveys at the onset of the rainy season with moderate mean temperatures (25.67°C , range = $22.58\text{--}28.76^{\circ}\text{C}$) and slightly above average rainfall (172.47 mm) from 5 April through 12 May 2013. We divided the area in which supplemental nests occurred into five strata (proportional to the number of nests) running from south to north to be sampled in a random order to account for sampling effects over time. Within each stratum, we sampled a random selection of 56 nest structures (60 nests in the southernmost strata) with a single camera trap (Reconyx PC800 or PC850, RECONYX, Inc., Holmen WI, U.S.A.) for 5–6 trapnights, then moved to the next randomly selected strata. We set the cameras with high motion sensitivity and continuous photos when activated, and secured them to a tree within 0.5–3 m of the nest structure. We directed camera traps at the best angle to document nest activity, which required no additional site modification. We marked each nest with a handheld GPS unit (GPSmap 60CSx, Garmin International, Inc., Olathe, KS, U.S.A.), recorded the type of nest structure (e.g. plastic culvert, rubble pile, cinderblocks, or jet ski), the distance from the camera to the nest,

presence or absence of sticks deposited by woodrats, and forest composition. We compiled daily binary detection histories for woodrats and cotton mice (1 = detected, 0 = not detected) from the camera trap survey data. We considered raw detections independent if photos were taken greater than 30 minutes apart, but we then partitioned the detection histories into daily surveys for each nest structure from 12:00 hours to 12:00 hours (one trap-night) because the rodents are nocturnal. We were able to distinguish the two species from each other and from hispid cotton rats and black rats based on morphology and size (Fig. 1C–F).

We modeled daily woodrat and cotton mouse detection (p) as either constant, variable over time, influenced by distance between the camera and the nest structure, as a function of stick-stacking behavior, or a global model that included a combination of all these covariates (five models), given a constant occupancy state across all nest structures (Table 1). We then formulated a priori occurrence models and used the best detection model based on previous model selection. Occurrence models included all biologically plausible hypotheses for predicting nest use by the rodents. We first modeled occurrence (ψ) as constant across

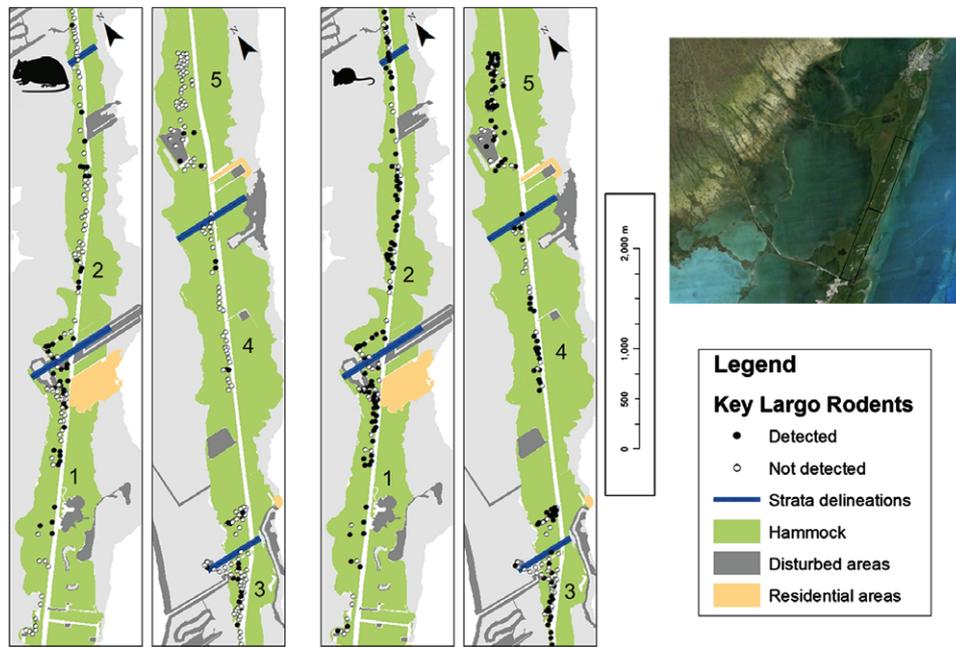


Figure 2. Map of North Key Largo (rotated 35 degrees for presentation), including the study area of Crocodile Lake National Wildlife Refuge to the west of County Road 905 and Dagny Johnson State Botanical Park to the east of County Road 905. All supplemental nests occurred within the wildlife refuge at the time of sampling. Woodrat detections are presented in the first two maps (denoted by the woodrat symbol), whereas cotton mouse detections are presented in the second two maps (denoted by the cotton mouse symbol). The five strata are numbered in order from south to north and any gaps represent areas that did not have supplemental nests at the times of the surveys. The inset shows satellite imagery of the region without any rotational change.

all nests and then as a function of covariates described further with model names designated in “quotes” to correspond with all tables. Due to the linear nature (north to south) of the habitat, we then modeled nest use as a function of a categorical covariate to account for variation across the five “strata” that would indicate a spatial gradient of nest use. Potential mammalian predators (exotic: free-ranging domestic cats, coyotes; native: opossums [*Didelphis virginiana*], and raccoons [*Procyon lotor*]) were sometimes detected at nests so we included these as a “perceived predator” binary covariate to determine if rodent nest use was related to visitation by the mesopredators.

Nest structures were not distributed randomly within the available habitat so we measured landscape covariates to determine if specific habitat covariates were associated with nest use by woodrats or cotton mice. We used ArcGIS 10.0 (Environmental Systems Research Institute [ESRI], Inc., Redlands, CA, U.S.A.) to measure the distance from each nest structure to the forest edge to assess possible “edge” effects (Woodroffe & Ginsberg 1998) such as the accessibility of nests to predators and environmental exposure. We also measured the linear distance to County Road 905 “road”, which is paved with relatively high traffic that bisects all woodrat habitat, is a potential barrier to rodent dispersal, and might be a disturbance to animals close to the edge. We identified nests built in “disturbed” areas because they likely are used differently than those occurring in hammock habitat. We also classified nests by “hammock age” (calculated based on time since most recent disturbance), which we further simplified to young (disturbed post-1971), medium (last disturbed between 1940 and 1970), and old hammocks

Table 1. Model selection statistics for predicting detection parameters (p) of Key Largo woodrats and Key Largo cotton mice at supplemental nest structures derived from occupancy models applied to camera trap data from the Crocodile Lake National Wildlife Refuge, surveyed April–May 2013. Occupancy (ψ) was held constant (.); probability of detection (p) was constant (.), varied with woodrat stick-stacking activity (sticks), varied dependent on the distance of the camera to the nest (distance), varied across sampling days (time), or varied based on all covariates (global). AIC_c is the Akaike’s information criterion corrected for small sample size, ΔAIC_c is the information distance from the top-ranked model, ω_i is the Akaike weight, K is the number of parameters, and $-2\log(\ell)$ is the -2^* log-likelihood of the model.

Species/Model	AIC_c	ΔAIC_c	ω_i	K	$-2\log(\ell)$
<i>Woodrat</i>					
$\psi(.), p(\text{global})$	728.83	0.00	0.913	9	710.17
$\psi(.), p(\text{time})$	734.56	5.73	0.052	7	720.15
$\psi(.), p(\text{sticks})$	735.90	7.07	0.027	3	729.81
$\psi(.), p(\text{distance})$	739.37	10.54	0.005	3	733.28
$\psi(.), p(.)$	739.83	11.00	0.004	2	735.79
<i>Cotton mouse</i>					
$\psi(.), p(\text{global})$	1594.37	0.00	0.561	9	1575.71
$\psi(.), p(\text{time})$	1594.86	0.49	0.439	7	1580.45
$\psi(.), p(\text{sticks})$	1625.32	30.95	0.000	3	1619.23
$\psi(.), p(.)$	1627.20	32.83	0.000	2	1623.16
$\psi(.), p(\text{distance})$	1628.92	34.55	0.000	3	1622.83

(disturbed pre-1940) to correspond with previous analyses (e.g. McCleery et al. 2006).

We overlaid the locations of woodrat captures from recent prior studies (Winchester et al. 2009; Potts et al. 2012) and

Table 2. Model selection statistics for predicting site use parameters (ψ) of Key Largo woodrats at supplemental nest structures derived from occupancy models applied to camera trap data from the Crocodile Lake National Wildlife Refuge, surveyed April–May 2013. Occupancy (ψ) was held constant (.) or varied dependent on covariates; probability of detection (p) was based on all covariates (global). AIC_c is the Akaike's information criterion corrected for small sample size, ΔAIC_c is the information distance from the top-ranked model, ω_i is the Akaike weight, K is the number of parameters, and $-2\log(\mathcal{L})$ is the $-2\log$ -likelihood of the model.

Model	AIC_c	ΔAIC_c	ω_i	K	$-2\log(\mathcal{L})$
ψ (strata)	712.13	0.00	0.994	13	684.78
ψ (edge)	722.96	10.83	0.004	10	702.15
ψ (sticks)	727.05	14.92	0.001	10	706.24
ψ (nearest nest)	728.14	16.01	0.000	10	707.33
ψ (.)	728.83	16.70	0.000	9	710.17
ψ (disturbed)	729.98	17.85	0.000	10	709.17
ψ (hammock age)	730.14	18.01	0.000	11	707.17
ψ (perceived predator)	730.39	18.26	0.000	10	709.58
ψ (gap)	730.85	18.72	0.000	10	710.04
ψ (road)	730.97	18.84	0.000	10	710.16
ψ (structure)	732.84	20.71	0.000	12	707.69

buffered them by 100 m. We designated the areas within the buffers as known populations of woodrats and identified habitat outside of the buffered areas as “gap” areas, where nests were built to try to increase connectivity between the five recognized subpopulations. To incorporate a covariate that is a measure of nest density, we measured the “nearest nest” distance as an index of nest clustering. We also included nest-specific covariates to account for differences in rodent use across the four different nest “structure” types (e.g. rubble piles, jet skis, cinder blocks, or plastic culverts). Finally, we used a binary covariate of “sticks” stacked on top of supplemental nests to assess if that covariate is a suitable predictor of woodrat nest use and hence a useful index for managers to assess woodrat distribution at supplemental nests. We included “sticks” as a covariate in cotton mouse models because the presence of sticks might influence cotton mice because the presence of sticks likely reflects a woodrat cache that cotton mice could exploit. Alternatively, woodrats might defend caches at stick nests, which could affect cotton mouse detection and nest use. We examined a total of 11 a priori hypotheses to model nest use by woodrats and cotton mice (Tables 2 & 3).

We examined the co-occurrence of woodrats and cotton mice using co-occurrence models with the alternate parameterization described by MacKenzie et al. (2004). We modeled woodrat (species B) nest use in the presence of cotton mice (i.e. species A, ψ_{BA}), and in the absence of cotton mice (ψ_{Ba}). We also modeled detection (denoted as p when only one species is present, r when both species are present) to determine if either species influenced the other or if they were independent. We tested and ranked five a priori hypotheses (Table 4).

We analyzed all data by using single-season occupancy models and two-species co-occurrence models implemented in program PRESENCE 5.1 (Hines 2012). The best approximating models were ranked based on their relative Akaike's information criterion corrected for small sample size (AIC_c). We also

Table 3. Model selection statistics for predicting site use parameters (ψ) of Key Largo cotton mice at supplemental nest structures derived from occupancy models applied to camera trap data from the Crocodile Lake National Wildlife Refuge, surveyed April–May 2013. Occupancy (ψ) was held constant (.) or varied dependent on covariates; probability of detection (p) was based on all covariates (global). AIC_c is the Akaike's information criterion corrected for small sample size, ΔAIC_c is the information distance from the top-ranked model, ω_i is the Akaike weight, K is the number of parameters, and $-2\log(\mathcal{L})$ is the $-2\log$ -likelihood of the model.

Model	AIC_c	ΔAIC_c	ω_i	K	$-2\log(\mathcal{L})$
ψ (disturbed)	1583.19	0.00	0.772	10	1562.38
ψ (hammock age)	1585.98	2.79	0.191	11	1563.01
ψ (structure)	1590.68	7.49	0.018	12	1565.53
ψ (strata)	1592.17	8.98	0.009	13	1564.82
ψ (.)	1594.37	11.18	0.003	9	1575.71
ψ (gap)	1595.14	11.95	0.002	10	1574.33
ψ (sticks)	1596.10	12.91	0.001	10	1575.29
ψ (perceived predator)	1596.16	12.97	0.001	10	1575.35
ψ (edge)	1596.46	13.27	0.001	10	1575.65
ψ (nearest nest)	1596.48	13.29	0.001	10	1575.67
ψ (road)	1596.50	13.31	0.001	10	1575.69

computed Akaike weights (ω_i) to examine effects of covariates and strength of the evidence in favor of particular models. We considered all models contained within the 90% confidence set ($\sum \omega_i > 0.90$) to have substantial support as the top-ranking models (Burnham & Anderson 2002). We computed odds ratios to compare covariate effects contained in the 90% confidence set and considered them to be strong if the 95% confidence intervals excluded zero.

Results

We surveyed 284 supplemental nest structures (approximately 40% of the total available nests) during 1,550 trapnights. We obtained 215 independent detections of woodrats at 65 of the 284 nests (naïve occupancy = 0.23) and obtained 371 detections of Key Largo cotton mice at 175 nests (naïve occupancy = 0.62). Woodrats and cotton mice co-occurred at 38 supplemental nests. We detected two other rodent species: eastern gray squirrels at eight nests and black rats at two nests. Other species detected at nests included free-ranging domestic cats ($n=2$), raccoons ($n=27$), Virginia opossums ($n=35$), and various bird species ($n=53$). We observed woodrat stick-stacking behavior at 71 nests.

The global detection model received the majority of the model support ($\omega_i > 0.90$; Table 1) for the woodrat data, suggesting that several detection covariates that we considered influence detection. Woodrats were more detectable at nests with sticks ($\beta_1 = 0.85 \pm 0.28$ SE), whereas detection was related negatively to the distance between the nest and the camera ($\beta_2 = -0.33 \pm 0.13$ SE; Table S1, Supporting Information).

Although the global detection model ranked the highest for cotton mouse detection ($\omega_i = 0.561$), the time variable model received the remainder of the support ($\omega_i = 0.439$; Table 1). Cotton mouse detection was related negatively to the presence of sticks stacked by woodrats at a nest ($\beta_1 = -0.40 \pm 0.19$ SE)

Table 4. Model selection statistics and corresponding hypotheses for supplemental nest use from multispecies models for co-occurring Key Largo cotton mice (species A) and Key Largo woodrats (species B) in Crocodile Lake National Wildlife Refuge, surveyed April–May 2013. Occupancy (ψ) for rodents was modeled as independent ($\psi_{BA} = \psi_{Ba}$, occupancy is equal regardless of cotton mouse occurrence) or varied dependent on cotton mouse occurrence; probability of detection (p when only one species is present, r when both species are present) was modeled as independent or affected by the detection of the other species as described in the hypotheses. AIC_c is the Akaike's information criterion corrected for small sample size, ΔAIC_c is the information distance from the top-ranked model, ω_i is the Akaike weight, K is the number of parameters, and $-2\log(\mathcal{L})$ is the -2 *log-likelihood of the model.

Model	Hypothesis	AIC_c	Δ	ω_i	K	$-2\log(\mathcal{L})$
$\psi_A, \psi_{BA} = \psi_{Ba}$, $p_A = r_A, p_B = r_{BA} \& r_{Ba}$	Rodent occurrence and detection are independent	2366.94	0	0.415	4	2358.94
$\psi_A, \psi_{BA}, \psi_{Ba}, p_A = r_A$, $p_B = r_{BA} \& r_{Ba}$	Rodent occurrence is not independent and detection is independent	2367.75	0.81	0.277	5	2357.75
$\psi_A, \psi_{BA} = \psi_{Ba}, p_A, r_A$, $p_B = r_{BA} \& r_{Ba}$	Rodent occurrence is independent and cotton mouse detection is affected by woodrat detection	2368.92	1.98	0.154	5	2358.92
$\psi_A, \psi_{BA}, \psi_{Ba}, p_A, r_A$, $p_B = r_{BA} \& r_{Ba}$	Rodent occurrence is not independent and cotton mouse detection is affected by woodrat detection	2369.7	2.76	0.104	6	2357.7
$\psi_A, \psi_{BA} = \psi_{Ba}, p_A, r_A$, p_B, r_{BA}, r_{Ba}	Rodent occurrence is independent and detection is affected by detection of the other species	2371.14	4.20	0.051	7	2357.14

and was positively related to distance of the camera from the nest ($\beta_1 = 0.11 \pm 0.09$ SE; Table S1).

Of the 11 a priori occurrence models, the model distinguishing between the five different strata received nearly all of the model support ($\omega_i = 0.994$; Table 2), suggesting a gradient (from north to south) in woodrat nest use among the five sampling areas. Woodrat nest use was related negatively ($\beta_1 = -2.40 \pm 0.64$ SE) to the northernmost zone (strata 5) with an apparent gradient of increasing nest use toward the southernmost strata ($\beta_0 = 0.10 \pm 0.39$ SE; Table S1).

Cotton mouse occurrence models suggested that several covariates were associated with their supplemental nest use. The top-ranking model ($\omega_i = 0.772$; Table 3) showed that cotton mice are influenced negatively by disturbance ($\beta_1 = -1.34 \pm 0.37$ SE). The hammock age model also received support ($\omega_i = 0.191$, Table 3), suggesting cotton mice use nests similarly in young- and medium-aged hammocks ($\beta_0 = 0.33 \pm 0.26$ SE and $\beta_1 = 0.30 \pm 0.32$ SE, respectively), but are more strongly associated with old growth hammocks ($\beta_2 = 1.78 \pm 0.64$ SE; Table S1).

The top-ranking co-occurrence model suggested that woodrats and cotton mice occur independently and their detection is also independent of each other ($\omega_i = 0.415$, Table 4). Cotton mice were estimated to occur at 68% (± 3 SE) of the supplemental nest structures, whereas woodrats were estimated to occur at 27% (± 3 SE) of the nests. The daily probability of detecting cotton mice was higher (0.35 ± 0.02 SE) than the probability of detecting woodrats (0.29 ± 0.03 SE).

Discussion

Although the first supplemental nest structures were built on Crocodile Lake National Wildlife Refuge nearly a decade ago, this camera trap study is the first systematic evaluation of how these structures are used by the endangered rodents on Key Largo. Supplementary nests allow woodrats and cotton mice to occur in areas with regenerating forests that are otherwise likely unsuitable for nesting because they lack fallen trees

and organic substrate required for nests. Woodrats now inhabit several areas of the refuge that were uninhabitable as recently as 30 years ago (Barbour & Humphrey 1982). Supplemental nests provide refuge from predators, which might further play a role in the colonization of disturbed areas undergoing succession. In addition, the design of the supplemental structures excludes larger species (e.g. raccoons and Virginia opossums), which presumably reduces competition for limited naturally occurring nest sites with common mesopredators.

The rodents of Key Largo are not the first species to benefit from nest supplementation (e.g. northern [*Glaucomys sabrinus*] and southern flying squirrels [*G. volans*], and red-cockaded woodpeckers [*Picoides borealis*]—Carey 2002; Franzreb 1997; Stone et al. 1996), but the current effort for woodrats is unique because it was conceived and carried out almost entirely by volunteers. Supplemental nests were placed strategically by volunteers using information on a location's distance to hammock edge, road, and proximity to other nests, in addition to deciding the type of nest structure used. These decisions were often affected by logistical constraints because accessible areas and important sites to build supplemental nests were often along abandoned roads or edge habitats. However, these factors did not strongly affect woodrat use of supplemental nests according to the lack of support for models that included them. In addition, the "gap" model did not receive any model support and this reveals that woodrats potentially are expanding into uninhabited areas where nests were placed to restore connectivity among the five sub-populations. The use of supplemental nests as corridors (effectively stepping stones) for admixture among the subpopulations warrants further examination, possibly via a conservation genetics approach. With these findings, we think that pairing volunteer conservation initiatives with carefully designed monitoring programs and the application of modern methods of data analysis can make valuable contributions to species conservation programs.

Woodrat nest use appears to vary along a north to south gradient according to the top model containing strata, with low woodrat nest use probabilities in the north transitioning

to higher probabilities in the south of the linear system. There could be multiple factors that influence this trend, such as low habitat suitability or remnant environmental toxicants from human development (e.g. Nike AK-3LH missile base and landfills); however, an alternative hypothesis could be predation pressure from exotic predators. The “perceived predator” models did not receive significant support for predicting nest use by either rodent, but we suspect that this might be an artifact of the limited detection zone when the camera is pointed directly at nests (as seen in Fig. 1C–F). The limited detection zone at nests suggests that the covariate does not appropriately reflect predation events or predation pressure when the rodents are foraging away from supplemental nests. The strata model, however, suggests a negative relationship between the present distribution of woodrats and proximity to a residential center that supports free-ranging domestic cat feeding stations and the largest known trap-neuter-release (TNR) cat colony in Florida (Hatley 2003). These feeding stations and TNR colonies are potential sources of cats dispersing into protected hammock habitat. Free-ranging domestic cats are thought to be effective Key Largo woodrat predators (Potts et al. 2012), and they have been implicated in the extinctions of several similar-sized woodrats on islands off the coast of Baja Mexico (Smith et al. 1993; Cortés-Calva et al. 2001). In their 1982 survey, Barbour and Humphrey (1982) identified the most prolific and abundant woodrat stick nests as occurring in areas that we have now identified to have the lowest woodrat occurrence probabilities in supplemental nests, supporting the hypothesis that exotic predators might affect woodrat nest use at the northern strata. This hypothesis requires further examination either via concurrent mesopredator-specific surveys and nest occupancy surveys or via additional telemetry studies of predators and prey.

We detected natural stick-stacking at supplemental nests, which is of interest because the behavior was not detected in earlier woodrat surveys (McCleery et al. 2006). Stick-stacking was positively related to woodrat detection, but it was not strongly supported as a predictor of woodrat nest use. Predation pressure has been repeatedly shown to affect prey behavior across multiple taxa (Lima & Dill 1990; Creel & Christianson 2008), which suggests that the stick-stacking behavior might decline in the presence of exotic predators because woodrats are more detectable and vulnerable while transporting large sticks. In addition, stick nests might be more conspicuous to predators and advertise prey presence, but predator visitation events were rarely detected due to the short sampling window (5–6 trapnights) at each nest. Previous studies confirmed the presence of woodrats in the absence of any evidence of natural stick nests (Barbour & Humphrey 1982; McCleery et al. 2006). Further research is required to garner additional evidence that stick-stacking behavior is negatively associated with exotic predator abundance, but it is possible that the behavior could serve as a reliable index of woodrat occurrence in the future with continued predator removal.

Key Largo cotton mice are susceptible to the same threats from exotic and native predators as woodrats, but their nest use across the refuge appears to be more dependent on habitat

age. Occurrence models suggest that cotton mice are mostly restricted to mature hammock, which corresponds with previous research (USFWS 1999; Greene et al. 2013). Current refuge restoration projects and preservation will provide additional cotton mouse habitat as the forests mature over the next several decades. Although woodrats and cotton mice have been observed to commonly co-occur and share nests (USFWS 1999), our results suggest that they nest independently of each other. This relationship likely warrants further examination because the co-occurrence of these species might be affected by other covariates that we did not consider. Cotton mouse detection was negatively related to sticks at supplemental nests, so nest size or structure material, as well as woodrat sex, age, and nesting behavior could all potentially influence their receptivity to sharing nests with cotton mice.

Our sampling effort with camera traps was modest in survey effort (trapnights) compared to past woodrat surveys conducted with live traps, yet we obtained many more detections of Key Largo woodrats than previous studies (e.g. Barbour & Humphrey 1982; McCleery et al. 2006; Winchester et al. 2009; Potts et al. 2012). Abundance estimates often require more intensive methods like capture-recapture, whereas the camera trapping protocol can effectively sample large areas to better understand patchily distributed species such as woodrats (MacKenzie et al. 2002). Low live-trapping success for woodrats (e.g. 13 unique individuals/20,000 trapnights [McCleery et al. 2006] and two unique individuals/816 trapnights in 2010 [Potts et al. 2012]) yielded abundance estimates with large confidence intervals and limited the power to reliably detect trends in population size. Camera trapping produced promising results in this study and we think it is well suited for addressing future monitoring objectives.

Nearly all the remaining upland hammock habitat on Key Largo is now under protection by the U.S. Fish and Wildlife Service and the Florida Department of Environmental Protection. Therefore opportunities to promote the conservation of endangered rodents rest primarily on providing additional nesting substrate until natural nest habitat is restored and reducing the effects of exotic predators on these protected lands. We conclude that the provision of supplemental nests has made important contributions to the recovery of Key Largo woodrats and Key Largo cotton mice as demonstrated by their expansion into previously unoccupied habitat.

Acknowledgments

This work was supported by the USFWS, the Florida Keys National Wildlife Refuge Complex, USGS Patuxent Wildlife Research Center, and NC Cooperative Fish and Wildlife Research Unit. We thank R. DeGayner and C. DeGayner for their effort building supplemental nests and sharing their knowledge of woodrats and the Keys. Thanks to J. Dixon, P. Hughes, S. Sneckenberger, A. Morkill, C. Anderson, and N. Finley for their support during their tenures in the Keys. We also thank J. Potts, R. Kays, and K. Pollock for sharing comments about supplemental nest structure surveys. All research was approved

under U.S. Fish and Wildlife Service Permit no 2013-008 and North Carolina State University Institutional Animal Care and Use Committee (IACUC) no 13-003-O. *Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.*

LITERATURE CITED

- Barbour DB, Humphrey SR (1982) Status and habitat of the Key Largo woodrat and cotton mouse (*Neotoma floridana smalli* and *Peromyscus gossypinus allapaticola*). *Journal of Mammalogy* 63:144–148
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York
- Carey AB (2002) Response of northern flying squirrels to supplementary dens. *Wildlife Society Bulletin* 30:547–556
- Cortés-Calva P, Yensen E, Alvarez-Castañeda ST (2001) *Neotoma martinensis*. *Mammalian Species* 657:1–3
- Creel S, Christianson D (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution* 23:194–201
- Franzreb KE (1997) Success of intensive management of a critically imperiled population of red-cockaded woodpeckers in South Carolina. *Journal of Field Ornithology* 68:458–470
- Greene DU, Castleberry SB, Mengak MT (2013) A methodology for long-term population monitoring of the endangered Key Largo cotton mouse. *Wildlife Society Bulletin* 37:368–374
- Greene DU, Potts JM, Duquesnel JG, Snow RW (2007) Geographic distribution: *Python molurus bivittatus* (Burmese python). *Herpetological Review* 38:355
- Hatley PJ (2003) Feral cat colonies in Florida: the fur and feathers are flying. *Journal of Land Use & Environmental Law* 18:441–465
- Hines JE (2012) Presence 5.1—software to estimate patch occupancy and related parameters. USGS-PWRC, Laurel MD. <http://www.mbr-pwrc.usgs.gov/software/presence.html> (accessed 25 Sep 2012)
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640
- MacKenzie DI, Bailey LL, Nichols JD (2004) Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73:546–555
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255
- McCleery RA, Lopez RR, Silvy NJ, Frank PA, Klett SB (2006) Population status and habitat selection of the endangered Key Largo woodrat. *American Midland Naturalist* 155:197–209
- McCleery R, Oli MK, Hostetler JA, Karmacharya B, Greene D, Winchester C, Gore J, Sneckenberger S, Castleberry SB, Mengak MT (2013) Are declines of an endangered mammal predation-driven, and can a captive-breeding and release program aid their recovery? *Journal of Zoology* 291:59–68
- O’Connell AF, Nichols JD, Karanth KU (2011) Camera traps in animal ecology: methods and analyses. Springer, Tokyo, Japan
- Olmstead I, Robertson WB Jr, Johnson J, Bass OL Jr (1983) The vegetation of Long Pine Key, Everglades National Park. Report SFRC-83/05, South Florida Research Center, Everglades National Park, Homestead, Florida
- Potts JM, Buckland ST, Thomas L, Savage A (2012) Estimating abundance of cryptic but trappable animals using trapping point transects: a case study for Key Largo woodrats. *Methods in Ecology and Evolution* 3:695–703
- Smith FA, Bestelmeyer BT, Biardi J, Strong M (1993) Anthropogenic extinction of the endemic woodrat, *Neotoma bunker* Burt. *Biodiversity Letters* 1:149–155
- Stone KD, Heidt GA, Baltosser WH, Caster PT (1996) Factors affecting nest box use by southern flying squirrels (*Glaucomys volans*) and gray squirrels (*Sciurus carolinensis*). *American Midland Naturalist* 135:9–13
- USFWS (U.S. Fish and Wildlife Service) (1999) Multi-species recovery plan for South Florida. U.S. Fish and Wildlife Service Report, USFWS, Vero Beach, Florida
- USFWS (U.S. Fish and Wildlife Service) (2013) Florida keys national wildlife refuges complex integrated predator management plan. U.S. Fish and Wildlife Service, Big Pine Key, Florida
- Winchester C, Castleberry SB, Mengak MT (2009) Evaluation of factors restricting distribution of the endangered Key Largo woodrat. *Journal of Wildlife Management* 73:374–379
- Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128

Supporting Information

The following information may be found in the online version of this article:

Table S1. Estimated covariate effects explaining variation in supplemental nest use by Key Largo woodrats and cotton mice.

Coordinating Editor: Valter Amaral

Received: 11 December, 2015; First decision: 3 February, 2016; Revised: 1 July, 2016; Accepted: 1 July, 2016