



Towards recovery of an endangered island endemic: Distributional and behavioral responses of Key Largo woodrats associated with exotic predator removal



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ABSTRACT

Exotic predators create novel ecological contexts for native species, particularly when prey exhibit predator naïve behaviors. Population recovery of island endemic species following predator eradication has been documented broadly, but studies examining mammalian prey behavioral responses to exotic predator removal are less common. The Key Largo woodrat (*Neotoma floridana smalli*) is an endangered Florida endemic species that exhibited drastic declines, signified by the loss of natural stick-nests, over the past three decades due to habitat loss and effects from exotic predators. We conducted camera trap surveys of woodrats at supplemental nests and used dynamic multistate occupancy models to evaluate changes in woodrat distribution and stick-nest building behavior over a two-year period of exotic predator (domestic cats [*Felis catus*] and Burmese pythons [*Python bivittatus*]) removal. The distribution of woodrats using supplemental nests increased from 27% to 39% in the two-year period, while the proportion of occupied supplemental nests with stick-nests increased from 37% in 2013 to 54% in 2015. The probabilities of supplemental nest use and stick-nest building behavior increased over time following a gradient away from the northern extent of Key Largo, an area associated with high cat activity and the only sites of python captures during the surveys. Woodrats that built stick-nests were more detectable than those that did not, which suggests that stick-nest building could make woodrats more susceptible to predation from novel predators when performing the behavior. We documented increasing woodrat occurrence, along with increasing stick-nest building behavior, which supports recovery and management objectives focused on exotic predator removal.

1. Introduction

The loss of global biodiversity is occurring at catastrophic rates, especially on island ecosystems and fragmented habitats (Pimm et al., 2014). Rodents, particularly island endemic species, make up 50% of recently extinct mammalian species and introduced predators are often implicated in many of the population declines (IUCN, 2016; Cortés-Calva et al., 2001; Nogales et al., 2004; Smith et al., 1993). A recent global review of exotic mammal eradications concluded that these management efforts have resulted in significant increases in the distribution and abundance of island endemic taxa (Jones et al., 2016). However, few studies have previously examined how exotic predator removal can additionally induce behavioral changes in endemic prey

species (Orrock and Fletcher Jr, 2014).

The Key Largo woodrat (*Neotoma floridana smalli*) is an endemic subspecies that inhabits the upland hammock communities of Key Largo, Florida. It is one of the most endangered rodents in the United States (USFWS, 1999). Woodrats (*Neotoma* spp.) are ecosystem engineers, known for their substantial and elaborate stick-nests, which create habitat and refugia for other species (Whitford and Steinberger, 2010). These stick-nests are usually associated with a single male or female occupant, but nests can grow substantially over time due to multi-generational use of the same nest, particularly when used by females and their offspring; hence stick-nests are associated with pup-rearing and recruitment (USFWS, 1999). Key Largo woodrats are no exception and historical surveys estimated 9–13.5 stick-nests per

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hectare (Barbour and Humphrey, 1982). However, surveyors in the mid-1990s found no evidence of woodrat stick-nests as woodrats appeared to have retreated to nesting in solution holes and gaps in root systems of large trees (Frank et al., 1997; McCleery et al., 2006). Less than 100 individuals were estimated to remain in their highly-restricted habitat in 2002 (McCleery et al., 2006); however, estimates based on trapping conducted between 2007 and 2011 revealed high uncertainty fluctuating between 78 and 696 individuals (Potts et al., 2012, 2016). The causes of woodrat population declines on Key Largo are still under debate, but nesting habitat loss from historical development and exotic predators are generally accepted as the key factors (Cove et al., 2017; Winchester et al., 2009).

Exotic predators have existed on Key Largo since homesteaders began to arrive in the late 1800s. However, it is only over the past two decades that humans have actively subsidized feral and free-ranging cats (*Felis catus*) through the maintenance of large cat colonies, particularly at the northern limit of Key Largo (Hatley, 2003). Nevertheless, there is substantial evidence that feral cats cause species extinctions on islands (Cortés-Calva et al., 2001; Nogales et al., 2004; Smith et al., 1993). The first Burmese python (*Python bivittatus*) was caught on Key Largo in April 2007 with a radio-tagged woodrat in its stomach (Greene et al., 2007), but despite large-scale efforts to survey and remove pythons only four confirmed detections had occurred between that first individual and our study (EDDMapS, accessed 14 May 2018). The large native predators of Key Largo woodrats included bobcats (*Lynx rufus*) and eastern indigo snake (*Drymarchon coria couperi*), but neither have been documented in Key Largo since at least the 1990s (Lazell, 1989; M. Cove, pers. obs.).

Key Largo woodrat recovery strategies include both habitat and predator management. The U.S. Fish and Wildlife Service (hereafter: USFWS) has built supplemental nest structures to help restore woodrat nesting habitat in forests that are undergoing natural succession (Cove et al., 2017). In 2013, the USFWS implemented an integrated pest management plan to remove exotic predators (including free-ranging cats and Burmese pythons) to restore endangered island endemics including the woodrat (USFWS, 2013). This management provided an opportunity to experimentally manipulate free-ranging cat and python populations to test the hypotheses that these exotic predators played a role in changing the distribution and behavior of woodrats. In particular, we predicted that woodrat stick-nest building behavior was influenced by the presence of exotic predators because nest building might make woodrats more conspicuous and detectable to predators. We paired camera trap data and dynamic multistate occupancy models to quantify these effects of exotic predator removal on the distributional and behavioral responses of woodrats at supplemental nest structures.

2. Methods

Between 2013 and 2015, we used camera traps and visual observations to sample woodrats at supplemental nest structures throughout Crocodile Lake National Wildlife Refuge, North Key Largo, Florida, USA (Fig. 1). Supplemental nest structures had a variety of historical forms, but the majority of contemporary structures are composed of 1.5–2 m of corrugated plastic culvert covered in coral, branches, and capped with coral boulders. They occur throughout the tropical hardwood hammocks, successional, and historically disturbed habitats of the refuge (Cove et al., 2017). At the time of the surveys, there were > 1000 supplemental nests in North Key Largo that were established by volunteers to create nest corridors to connect suspected subpopulations and restore scarified and disturbed areas. The construction of a standardized sampling grid has since been established to build nests in the remainder of the wildlife refuge and adjacent Dagny Johnson Botanical State Park with management goals aimed to establish at least one supplemental nest per every 2.37 ha of habitat, which corresponds to roughly 10 woodrat home ranges (Hersh, 1981).

Forested hammocks on Key Largo consist of a 9–12 m tall canopy

with species such as pigeon plum (*Coccoloba diversifolia*), West-Indian mahogany (*Swietenia mahagoni*), wild tamarind (*Lysiloma latisiliquum*), and understory vegetation comprising species such as wild coffee (*Psychotria nervosa*), marlberry (*Ardisia escallonioides*), and Spanish stopper (*Eugenia foetida*), which all provide food and cover for woodrats (USFWS, 1999). Total rainfall during the rainy season (May–September) over the course of our study was 169.62 cm in 2012, 100.51 cm in 2013, 64.85 cm in 2014, and 50.93 cm in 2015.

Key Largo is a linear system and previous research suggested that woodrats use supplemental nest structures along a gradient from high nest use probabilities in the south to low nest use in the north (Cove et al., 2017). We defined five strata in which the nests occur that account for this spatial variation in woodrat distribution, but also representative of the abundance of supplemental nests (Fig. 1). Within each stratum, we sampled a random selection of nest structures each with a single camera trap ($n = 58$ cameras in operation – Reconyx PC800 or PC850, RECONYX, Inc., Holmen WI, USA) for 5–6 continuous trap nights, we then moved to the next randomly selected stratum and repeated the process until all strata were sampled (1–2 months of total sampling). We set each camera with high motion sensitivity and continuous photos when activated. We tagged each supplemental nest with an individual number and recorded its location with a handheld GPS unit (GPMap 60CSx, Garmin International, Inc., Olathe, KS, USA). We carefully inspected nests at the time of camera deployment to record the presence (1) or absence (0) of sticks actively deposited and maintained by woodrats on top of the supplemental nests. Stick-nest assignment was characterized by the presence of new and maintained sticks, as well as cleared entrances into nests, which could vary between seasons. Nest inspections and camera deployments were all conducted by the same two individuals (M. Cove and A. Maurer) each year of the surveys, so we did not need to account for varying observer bias in camera placements or stick-nest assignments. We repeated this design over 3 years, thus sampling followed Pollock's robust design (Pollock, 1982), in which each year was considered a primary sampling period and individual camera trap nights within each year were considered secondary sampling occasions.

The initial year (2013) was surveyed prior to exotic predator removal, and sampling in 2014 and 2015 overlapped with ongoing exotic predator removal. To monitor the effectiveness of predator removal, we used camera trap data from a survey of free-ranging cats in North Key Largo prior to removal to examine baseline cat abundance and distribution in the refuge and surrounding public lands (Cove et al., 2018). We then used opposing cameras targeted along trails to survey cats at each of 84 sites from 2013 and 2014 and resurveyed them in 2015. The opposing cameras were situated to reduce detection bias of cat activity indices. We calculated trap detection rates as the number of cat detections per 100 camera trap nights at repeated survey locations as an index of the USFWS cat removal effort. We used Poisson regression to model the number of cat detections with three predictor variables (constant, latitude, or binary north [stratum 4 and north] versus south [stratum 3 and south]) to assess the activity of cats along the north to south gradient of woodrat supplemental nest sampling.

We used ArcGIS 10.0 (Environmental Systems Research Institute [ESRI], Inc., Redlands, CA, USA) to measure nest-specific habitat covariates that we hypothesized would affect woodrat nest use and stick-nest building behavior based on prior surveys (Cove et al., 2017). We used the five strata delineations as categorical nest covariates. Additionally, we measured the linear distance to the largest free-ranging cat colony in the area as a potential predator source covariate. We measured the distance to residential areas as well because these might also serve as source populations for free-ranging cats entering the protected areas of Key Largo. Previous research suggested a slight positive association between woodrat occupancy and distance to hammock edge (Cove et al., 2017), so we also measured the linear distance between supplemental nests and hammock edge. Finally, we measured the linear distance to the major road that runs down the center of North

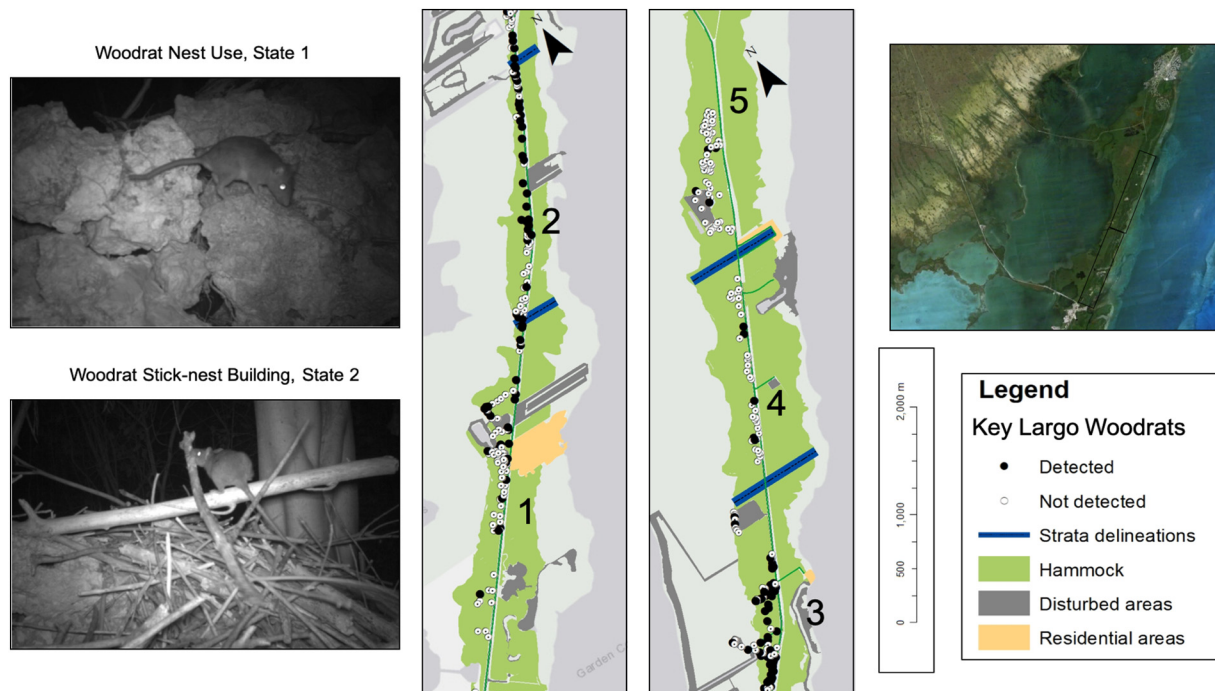


Fig. 1. Example camera trap photos of Key Largo woodrats (*Neotoma floridana smalli*) in two occupancy states, with map of woodrat detections at supplemental nests in North Key Largo (rotated 35 degrees for presentation), including the study area of Crocodile Lake National Wildlife Refuge to the west and Dagny Johnson State Botanical Park to the east of County Road 905, respectively. All 363 sampled supplemental nests occurred within the wildlife refuge during sampling between 2013 and 2015. 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, including developments to the north and south of the refuge, without any rotational change.

Key Largo to examine effects associated with the road and traffic.

We used dynamic multistate occupancy models to account for detection bias when estimating the response of woodrat nest use, stick-nest building behavior, and the effects of predator removal over time (MacKenzie et al., 2009). We use the term ‘occupancy’ to more appropriately represent ‘nest use’ since nests are not spatially independent, with multiple woodrats potentially using the same nests and individual woodrats potentially using multiple nests. We assigned photographic evidence to one of two states of woodrat occupancy. State (1) was assigned to nests with photographic evidence that woodrats were present at a supplemental nest (nest use), and state (2) was assigned to supplemental nests with photographic evidence of woodrats as well as observed stick-nest building (Fig. 1). Under this model framework, we hypothesized that changes to state (1) represented a distributional woodrat response to predator removal because nest use is an index of woodrat distribution and/or population size. We hypothesized that changes to state (2) represented a woodrat behavioral response to predator removal because stick-nest building is associated with normal woodrat behavior and potentially with reproduction and recruitment. The model structure has several parameters of interest. The first two parameters are the initial probability that a supplemental nest is occupied (ψ) and the initial probability that the woodrats are building stick-nests on the supplemental nest given that they occupy the site (R). The dynamic parameters are then probabilities of occupancy (ψ_i) and stick-nest building (R_i) in year i , conditional on the site being previously unoccupied (0), occupied (1), or occupied with stick-nest building (2) in year $i - 1$. We considered the transition from state 0 in year $i - 1$ to state 1 or state 2 in year i to represent nest colonization, whereas remaining in the same occupied state as the previous year ($i - 1$) represents nest persistence. For example, we use the notation $C\psi0(\text{year})$ to represent the probability of occupancy for each ‘year’ conditional (‘C’) on the site being unoccupied (‘0’) in the previous year’s survey. We also estimated daily detection probabilities (p) for the two states. Under this model parameterization, we fixed the probability of assigning

detected woodrats to the correct state (δ) to equal 1, because there was no uncertainty in identifying woodrats in state 2 if they were detected with camera traps and we had documented stick-nest building at the site. The number of supplemental nests with stick-nests built on them, but without photos of woodrats represents a case of a nest in state 2 reverting to state 0 (unoccupied), which we treated as an index of nest loss due to woodrat mortalities or abandonment between seasons.

The model development approach was hierarchical. We first modeled daily detection of woodrats as variable among states [M1], variable across years [M2], or as an additive model considering both covariates [M3], assuming constant occupancy and stick-nest building parameters. We then used the covariates from the top-ranking of the three detection models in all subsequent dynamic multistate occupancy models. We compared a null model with equal probabilities across occupancy and stick-nest building behavior regardless of the previous years’ state [M4] to three additional models. The next model [M5] was parameterized to differentiate between colonization (e.g., previously unoccupied) and persistence probabilities (e.g., previously occupied in state 1 or 2), but with the probability of occupancy equal to the probability of stick-nest building across time. We then modified that model to include variation between the probability of occupancy versus probability of stick-nest building behavior conditional on the previous years’ unoccupied state [M6]. We then compared a full conditional model [M7] in which all occupancy and stick-nest building parameters were estimated conditionally on previous years’ states. Finally, we used the top-ranking of those models and compared five additive models with the habitat covariates that we measured (e.g., [M8] northern to southern strata, [M9] distance from community cat colony, [M10] distance from residential areas, [M11] distance from forest edge, and [M12] distance from road) influencing both occupancy and stick-nest building. In total, we compared 12 a priori models to predict woodrat occupancy and stick-nest building behavior conditioned on previous surveys (Table 1).

We analyzed all data and implemented the models in program

Table 1

Model selection statistics for predicting Key Largo woodrat (*Neotoma floridana smalli*) use (ψ), and stick-nest building (R) at supplemental nest structures derived from multistate dynamic occupancy models applied to camera trap data from the Crocodile Lake National Wildlife Refuge, surveyed during a period of free-ranging cat (*Felis catus*) and Burmese python (*Python bivittatus*) removal, 2013–2015. Included are the AICc values, the information distance from the top ranked model (Δ AICc), Akaike weight (ω_i), number of parameters (K), and log-likelihood ($-2\log(L)$).

Model	AICc	Δ AICc	ω	K	$-2\log(L)$
[M8] $\psi(\text{FC} + \text{strata}), R(\text{FC} + \text{strata}), p(\text{state} + \text{season})$	3360.42	0	1	21	3315.71
[M9] $\psi(\text{FC} + \text{colony}), R(\text{FC} + \text{colony}), p(\text{state} + \text{season})$	3414.18	53.76	0	18	3376.19
[M11] $\psi(\text{FC} + \text{edge}), R(\text{FC} + \text{edge}), p(\text{state} + \text{season})$	3426.47	66.05	0	18	3388.48
[M12] $\psi(\text{FC} + \text{road}), R(\text{FC} + \text{road}), p(\text{state} + \text{season})$	3426.85	66.43	0	18	3388.86
[M7] $\psi(\text{FC}), R(\text{FC}), p(\text{state} + \text{season})$	3434.54	74.12	0	17	3398.77
[M10] $\psi(\text{FC} + \text{resid}), R(\text{FC} + \text{resid}), p(\text{state} + \text{season})$	3435.9	75.48	0	18	3397.91
[M5] $\psi(0) = R(0), p(\text{state} + \text{season})$	3442.58	82.16	0	7	3428.26
[M6] $\psi(0), R(0), p(\text{state} + \text{season})$	3442.66	82.24	0	10	3422.04
[M3] $\psi(\cdot), R(\cdot), p(\text{state} + \text{season})$	3485.29	124.87	0	8	3468.88
[M4] $\psi(\cdot) = R(\cdot), p(\text{state} + \text{season})$	3494.34	133.92	0	6	3482.1
[M1] $\psi(\cdot), R(\cdot), p(\text{state})$	3508.95	148.53	0	6	3496.71
[M2] $\psi(\cdot), R(\cdot), p(\text{season})$	3535.6	175.18	0	7	3521.28

Detection parameters (p) were modeled as variable by occupancy state (state), by year (season), or both (state + season). Occupancy (ψ) and stick-nest building (R) were modeled as constant (\cdot), variable dependent on colonization from the previous years' unoccupied state (0), or fully conditional on the previous years' state across years (FC), and then variable dependent on habitat covariates: strata = North-South gradient, colony = distance from free-ranging cat colony, edge = distance from habitat edge, road = distance from road, resid = distance from residential areas.

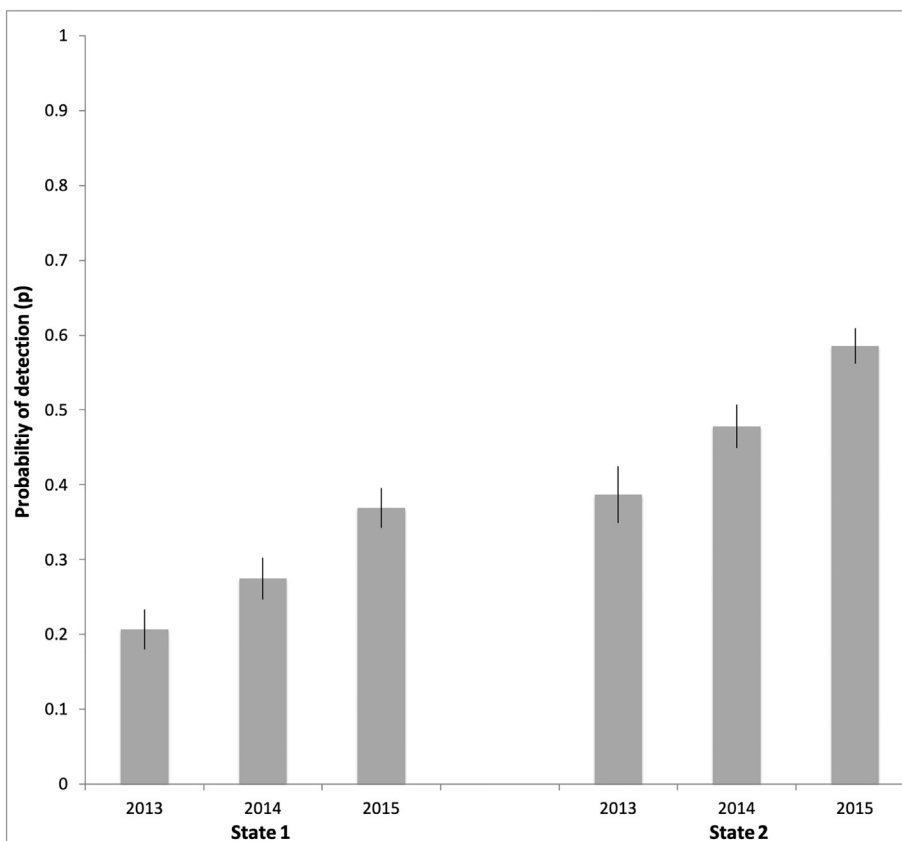


Fig. 2. Estimates (\pm SE) of the daily probability of detecting Key Largo woodrats (*Neotoma floridana smalli*) with camera traps, derived from dynamic multistate occupancy models at supplemental nest structures in Crocodile Lake National Wildlife Refuge, Florida, USA, 2013–2015. State 1 represents supplemental nest use, whereas State 2 represents stick-nest building behavior at occupied supplemental nests.

PRESENCE 11.1 (Hines, 2016). We ranked the top approximating models based on their relative Akaike Information Criterion corrected for small sample size (AICc) and Akaike weights (ω_i) to examine effects of covariates and strength of the evidence in favor of particular models (Burnham and Anderson 2002). We then used estimated occupancy and stick-nest building transition probabilities to derive estimates of overall nest occupancy (including both states ψ and R) across the three sampling periods.

3. Results

We surveyed 363 supplemental nests across three primary sampling

periods for a total survey effort of 4902 trap nights. In April–May 2013, we surveyed 284 nests and detected woodrats at 65 nests (naïve $\psi = 22.89\%$), with stick-nest building behavior at 24 nests (36.92% of occupied nests), and an additional 47 nests with sticks but no detections of woodrats (e.g., nests lost from state 2). In January–February 2014, we detected woodrats at 87 of 286 supplemental nests (naïve $\psi = 30.42\%$) with stick-nest building behavior at 48 of those nests (55.17% of occupied nests), and an additional 55 nests with sticks but no woodrat detections. In January–March 2015, we surveyed 359 nests including all but four of the previously surveyed nests. We detected woodrats at 133 nests (naïve $\psi = 37.05\%$) and observed stick-nest building at 83 of those nests (62.41% of occupied nests), with an

additional 32 nests with sticks but no woodrat detections. Over the course of our study, the USFWS removed 51 free-ranging cats from the wildlife refuge, which resulted in reduced detections of cats in our camera trap photos from 137 cat detections in 1255 trap nights (10.92 detections/100 trap nights) in 2013/2014 to 63 cat detections in 1247 trap nights (5.05 detections/100 trap nights) in 2015. The majority of cats were trapped ($n = 41$ cats) at the northern and southern edges of the refuge, yet camera trap detections of cats were positively associated with latitude across years and remained high throughout the northern extent of the protected area over the course of our surveys (Table S1). Additionally, two Burmese pythons were detected and removed from debris piles in the northern strata of the refuge over the course of our camera trap surveys.

The top dynamic multistate occupancy model received 100% of the model weight and suggested that model parameters varied across years, conditionally on the previous year's state, and varied along the north to south strata. The daily probability of detecting woodrats with camera traps varied across woodrat occupancy state and survey year. Daily detection of woodrats at occupied nests (state 1) increased annually from 0.21 (95% CI = 0.16–0.26) in 2013 to 0.37 (95% CI = 0.32–0.42) in 2015. Daily detection probabilities of woodrats with stick-nest building behavior (state 2) increased from 0.39 (95% CI = 0.32–0.46) in 2013 to 0.59 (95% CI = 0.54–0.63) in 2015 (Fig. 2).

Probabilities of initial woodrat occupancy and stick-nest building were lowest in the northern two strata on the island (Figs. 3 & 4). The probability of transitioning from an unoccupied site in 2013 to an occupied site in 2014 ranged from 0.10 (95% CI = 0.06–0.17) in the northernmost stratum 5 to 0.40 (95% CI = 0.29–0.51) in the central stratum 3. However, the probability of colonizing an unoccupied site and building a stick-nest was slightly higher than the occupancy transition for stratum 5 at 0.14 (95% CI = 0.06–0.27), compared to 0.49 (95% CI = 0.32–0.66) for stratum 3 (Fig. 4).

The probability of persistence of an occupied supplemental nest

between initial 2013 surveys and 2014 surveys increased from 0.13 (95% CI = 0.05–0.30) at the northernmost stratum to 0.47 (95% CI = 0.25–0.70) at the central stratum. These occupancy persistence probabilities further increased between 2014 and 2015 surveys with central stratum sites (0.68 [95% CI = 0.50–0.82]) and northernmost stratum sites (0.26 [95% CI = 0.13–0.46]) exhibiting the highest and lowest probabilities, respectively (Fig. 3). The probability of persistence of stick-nest building behavior at a nest remaining occupied between years ranged from 0.56 (95% CI = 0.31–0.78) in northernmost stratum sites to 0.88 (95% CI = 0.74–0.95) in central stratum sites (Fig. 4). From these transition probabilities, we derived estimates of overall nest occupancy (including both states ψ and R) that increased each year from $\psi_{2013} = 0.27$ ($\psi_{state1} = 0.17$ [95% CI = 0.12–0.22] and $R_{state2} = 0.10$ [95% CI = 0.06–0.13]), to $\psi_{2014} = 0.34$ ($\psi_{state1} = 0.18$ [95% CI = 0.12–0.23] and $R_{state2} = 0.16$ [95% CI = 0.12–0.20]), to $\psi_{2015} = 0.39$ ($\psi_{state1} = 0.18$ [95% CI = 0.14–0.23] and $R_{state2} = 0.21$ [95% CI = 0.17–0.25]).

4. Discussion

The frequency of supplemental nest occupancy increased over the course of our study, showing a positive association with exotic predator removal. Key Largo woodrat recruitment can be related to precipitation and fruit availability (McCleery et al., 2013); however, we noted a reduction in seasonal precipitation throughout our study. Furthermore, the probability of stick-nest building behavior at supplemental nests and stick-nest persistence between years was also high during the reduction of free-ranging cats and pythons. This high stick-nest persistence might explain why historical accounts draw attention to the high abundance of stick-nests (9–13.5/ha) in the early 1900s through the mid-1980s (Barbour and Humphrey, 1982). However, in the 1990s, stick-nests became rare and absent from most of the island, which corresponded to a period when a colony of free-ranging cats was

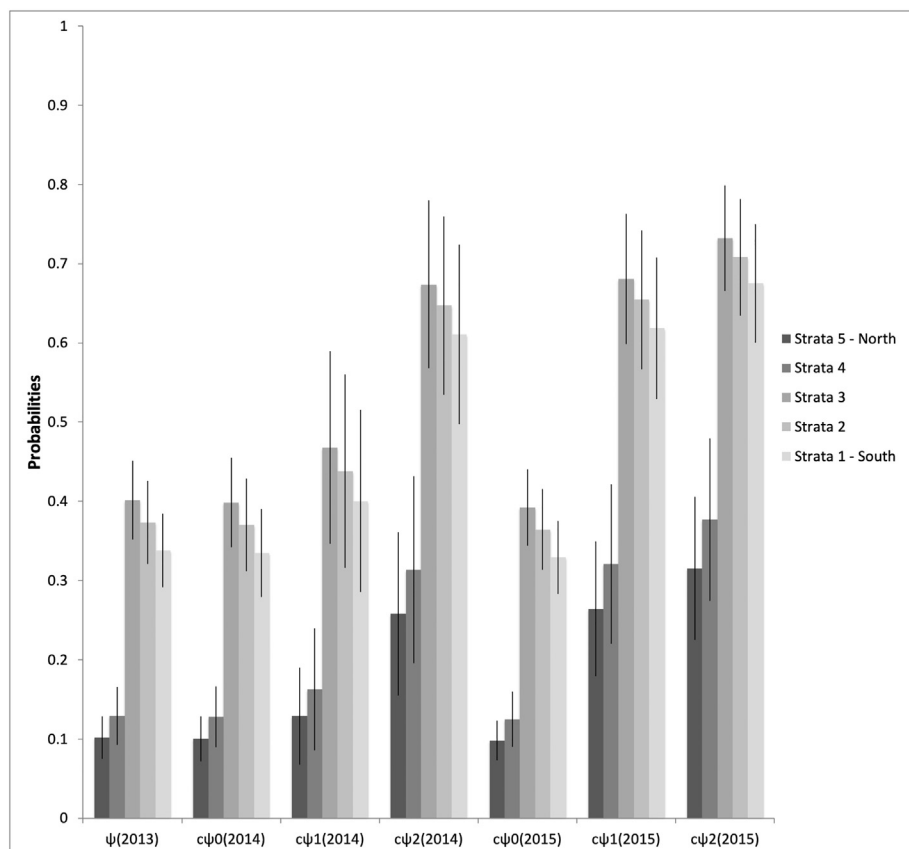


Fig. 3. Estimates (\pm SE) of the probability of Key Largo woodrats (*Neotoma floridana smalli*) use of supplemental nest structures, and dynamic parameters across five strata in Crocodile Lake National Wildlife Refuge, Florida, USA, 2013–2015. $\psi(2013)$ represents the initial probability of nest use in 2013, while $C\psi_0(\text{year})$, $C\psi_1(\text{year})$, and $C\psi_2(\text{year})$ are the conditional probabilities of transitioning to an occupied site from an unoccupied site the previous year, the probability of being occupied in year i given that it was occupied without stick-nest building the previous year, or the probability of being occupied in year i given that it was occupied with stick-nest building in the previous year, respectively. The strata 1–5 represent a south to north latitudinal gradient across the refuge.

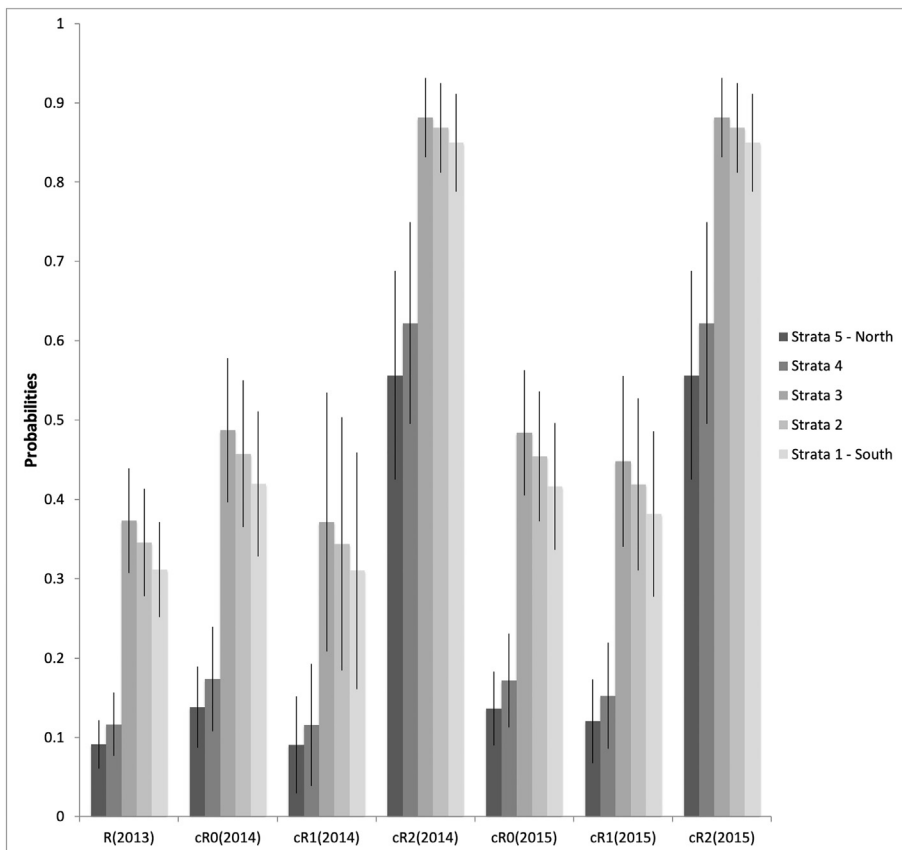


Fig. 4. Estimates (\pm SE) of the probability of Key Largo woodrats (*Neotoma floridana smalli*) building stick-nests at supplemental nest structures, and dynamic parameters across five strata in Crocodile Lake National Wildlife Refuge, Florida, USA, 2013–2015. R(2013) represents the initial probability of stick-nest building behavior at occupied sites in 2013, while CR0(year), CR1(year), and CR2(year) are the probabilities of stick-nest building at an occupied site in year i given it was unoccupied in year $i-1$, probabilities of stick-nest building at an occupied site in year i given it was occupied in year $i-1$ without a stick-nest, or probabilities of stick-nest building at an occupied site in year i given it was occupied with stick-nest building in year $i-1$, respectively. The strata 1–5 represent a south to north latitudinal gradient across the refuge.

established and over a decade prior to the first python observations in Key Largo (Greene et al., 2007; Hatley, 2003). During that period, woodrats that survived may have shifted their behavior because they used supplemental nests, debris piles, roots and solution holes instead of building stick-nests. Although woodrats were historically exposed to felid predators (e.g., bobcats and feral cats), these populations likely occurred at lower densities (e.g., 1–4.5 bobcats/10 km² – Conner et al., 1992; Ruell et al., 2009) than subsidized domestic cat populations (7.8–20.8 domestic cats/10 km² – Cove et al., 2018). Indeed exotic predators can more strongly affect prey than native predators (Salo et al., 2007), and therefore they can exert strong selective pressure when endemic prey with behavioral traits that are naïve to high predator densities experience reduced reproductive success and survival (Schlaepfer et al., 2005). In this sense, woodrat stick-nest building could be a maladaptive trait in the presence of subsidized and abundant free-ranging domestic cats because stick-nests make woodrats more detectable and vulnerable to predation when transporting cumbersome sticks > 50 m (Cove and Maurer, 2019). However, the behavior appears to be plastic because corresponding with exotic predator removal efforts, the conditional probabilities of colonizing, stick-nest building behavior, and persisting in established stick-nests on supplemental nest structures increased over time and across a gradient from areas with continued high cat camera trap detections and python observations in the north to areas of low cat detections and python observations in the south of the refuge.

Overall, the number of occupied nests increased from an estimated 27.1% to 39.2% after exotic predator removal began. It is noteworthy that woodrat daily detection probabilities also increased over time. Detection and abundance are often correlated (Royle and Nichols, 2003), so given that sampling effort remained similar over the three primary sampling periods, the increasing detections of woodrats might reflect an increase in abundance of woodrats. Woodrats were more detectable when they were performing stick-nest building behavior on

supplemental nests, a trend that increased over time. Therefore, the heightened detection probabilities of stick-nest building woodrats could further represent changing behavior with individuals becoming emboldened after exotic predator removal commenced (Orrock and Fletcher Jr, 2014; Strauß et al., 2008), but this requires further examination with concurrent tracking data on predators and prey.

The number of cats removed from the system is high considering that baseline density estimates suggested only 7–20 cats/10 km² (Cove et al., 2018), but cat trapping was camera trap-informed and targeted, which allowed for efficient cat removal early as they colonized the refuge from developed areas. Additionally, coyotes (*Canis latrans*) have recently colonized Key Largo and may exert further effects on free-ranging cat populations and distribution (Crooks and Soulé, 1999). The northern strata include areas with continued high cat detections on camera traps despite trapping efforts. Cats remain common in the northern areas of Key Largo, which hosts a large cat colony with over 60 feeding stations and 1111 cats neutered and released back into the environment over its 23-year existence (Hatley, 2003; Kreisler et al., 2019). The colony may be a source of dispersing individuals that evade capture and neutering, and it has also been suggested that the high profile nature of the colony makes it a common site of cat abandonment (Kreisler et al., 2019). The central strata exhibited the highest probability of woodrat occurrence and stick-nest building behavior across all of Key Largo despite the proximity of a waste transfer station and small subdivision, which are also potential sources of free-ranging cats that are targeted for trapping as soon as detected in the refuge. This stratum could be an historical refugium for woodrat persistence due to the long distance (> 7 km) from free-ranging cats colonizing the refuge from the residential areas to the north and south.

Only two pythons were removed between 2013 and 2015, but an additional 10+ individuals, including an adult female and a juvenile, were detected and removed from north Key Largo since 2015. Eight of these individuals were captured in the northernmost stratum and

northern residential areas, but we do not have information about the timeline of these individuals' arrival to Key Largo. Therefore, pythons may have played a role in limiting the woodrat population in those northern areas, but we would not expect the removal of only two pythons to strongly contribute to the changes in woodrat colonization and stick-nest building that were observed. However, this apparent increase in python detections and evident reproduction since the times of our surveys suggests that pythons might become an imminent threat to woodrat populations if established on the island.

Cats have been responsible for the extinctions of other nest-building rodents including several species of woodrats off the coast of Baja California (Cortés-Calva et al., 2001; Smith et al., 1993). Our results suggest that the probabilities of woodrats colonizing (distributional) and building stick-nests (behavioral) at supplemental nest sites were positively associated with the timeline of free-ranging cat removal efforts. These data support the hypothesis that woodrats are affected by exotic predators in both distribution and likely abundance, but also in behavior. We note that these results would be strengthened by including a control area (where no predator removals occur) and by studying the system for a longer time to account for natural fluctuations in the woodrat population (Krebs, 2013). Key Largo woodrats are again building stick-nests and may act as ecosystem engineers, providing refugia for other species including the endangered Key Largo cotton mouse (*Peromyscus gossypinus allapaticola* – Cove et al., 2017), various small herpetofauna, and invertebrates, while also acting as seed dispersers. Our results support recovery objectives and management plans with continued cat and python removal as a priority because exotic predator persistence could have cascading effects due to shifts in woodrat nesting behavior.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.07.032>.

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