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ABSTRACT

Ecosystem engineers play a vital role in community assembly by modifying the environment to create novel habitat features. Woodrats (*Neotoma* sp.) build and maintain intricate stick-nests that stockpile organic materials and create habitat for other small species. The Key Largo woodrat (*Neotoma floridana smalli*) is an endangered subspecies endemic to Key Largo, Florida, USA, that has undergone substantial declines due to habitat loss and predation by invasive predators. We leveraged data from a camera trap monitoring grid at supplemental woodrat nest structures to survey bird communities to evaluate the role of woodrat nest use and stick-nest building related to bird abundance using generalized linear models. We predicted that woodrat occurrence and stick-nest building would positively correlate with bird species richness and abundance due to the creation of habitat structures that support prey for birds. To test this, we analyzed the relationship that bird abundance and species richness have with several indicators of woodrat activity along with other environmental and predator variables. Bird abundance was positively associated with woodrat supplemental nest use and stick-nest building. However, these positive associations were largely negated by the presence of free-roaming cats (*Felis catus*), an invasive predator, and dampened by proximity to human development. We provide evidence that woodrats may have cascading effects on their local food webs by creating foraging grounds for birds, but this positive relationship is disrupted by the presence of an introduced predator.

1. Introduction

Ecosystem engineers are organisms that alter the ecosystems they inhabit, often creating novel habitats for other species (Jones et al., 1994, 1997). Many ecosystem engineers are large, charismatic taxa such as beavers (*Castor* sp.), American alligators (*Alligator mississippiensis*), and African elephants (*Loxodonta* sp.), but at more localized scales many small mammals also modify their environment to create habitat for other organisms (Jones et al., 1994). Karoo bush rats (*Myotomys unisulcatus*, Vermeulen and Nel, 1988) in southern Africa, greater stick-nest rats (*Leporillus conditor*) in arid Australia (Dickman, 1999), and woodrats (*Neotoma* sp.) in North America all build and maintain intricate stick-nests that stockpile organic materials and create habitat for other small species (Whitford and Steinberger, 2010). However, the impact of these nests on biodiversity is rarely studied. One study revealed that active woodrat stick-nests are associated with unique microclimates, consisting of moderate temperatures and high humidity, as well as higher concentrations of soil organic matter relative to the surrounding environment, making these nests an important refuge habitat for many species, especially arthropods (Whitford and Steinberger, 2010). Other studies show that Key Largo woodrat (*Neotoma floridana smalli*) stick-nests have unique microbial communities compared to the surrounding environment (Thoemmes and Cove, 2020) and are used by herpetofauna as potential refuge habitat (King et al., 2022). Woodrat stick-nests act as a unique microhabitat for all these species due to the decomposition of stockpiled organic material, including the feces and caches woodrats deposit within their nests (Whitford and Steinberger, 2010).

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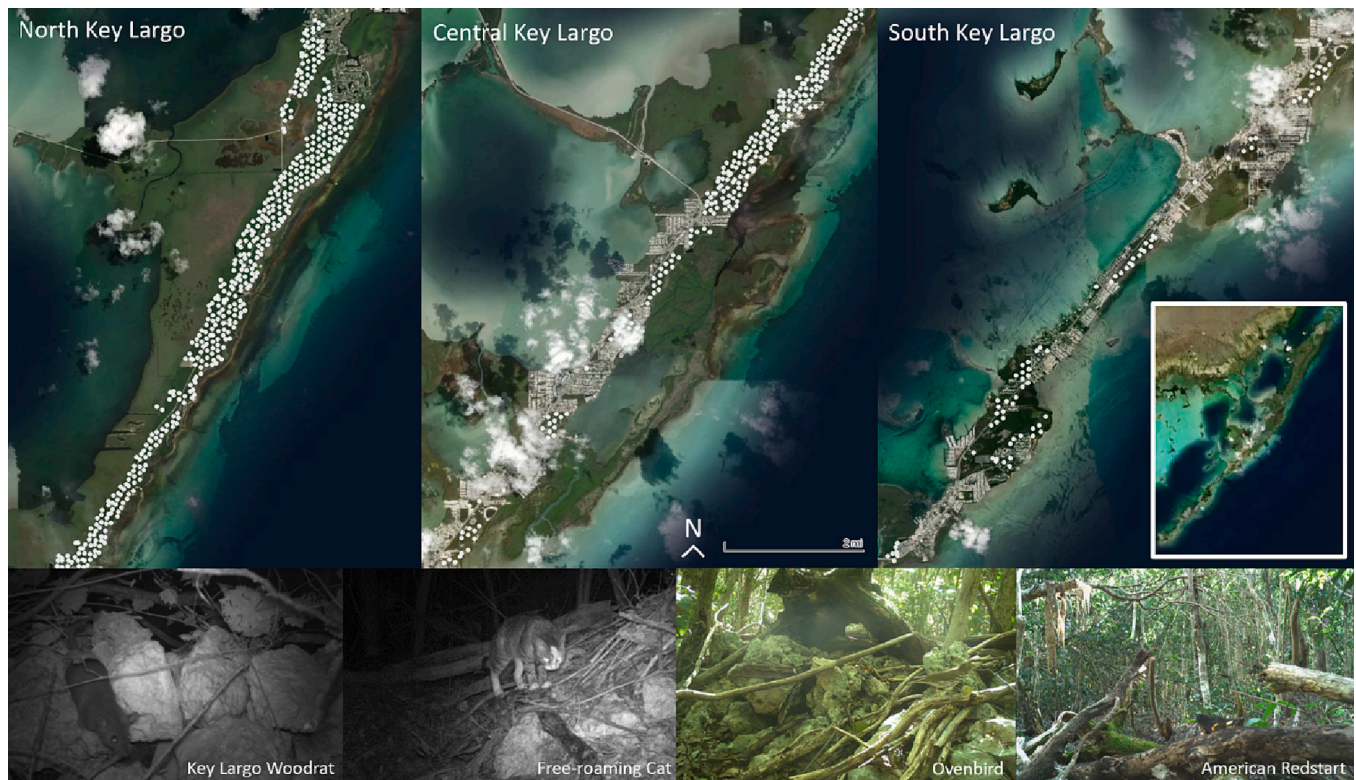*E-mail address:* ecw6931@uncw.edu (E.C. Watersmith).
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Fig. 1. Distribution of camera traps for Key Largo woodrat nest monitoring and bird surveys in North Key Largo, FL (entire study area inset), in 2018 along with example camera trap images of focal species.

The Key Largo woodrat is an insular subspecies of the Eastern woodrat (*Neotoma floridana*) endemic to Key Largo, Florida, USA. It was declared an endangered species in 1984 due to severe habitat loss (U.S. Fish and Wildlife Service, 2015). The remaining population of Key Largo woodrats declined precipitously from the 1990s through the early 2000s (McCleery et al., 2006). These declines have been attributed to habitat loss from increasing development in the Florida Keys and pressure from invasive predators, mainly free-roaming domestic cats (*Felis catus* - Cove et al., 2017). During the lowest point of their decline, woodrat stick-nests were largely absent throughout their distribution (Winchester et al., 2009). While this corresponds with the low abundance of woodrats during that time, the presence of fewer stick-nests is also due to the fear effects that free-roaming cats exert on Key Largo woodrats, making them less likely to perform stick stacking behaviors (Cove et al., 2019). The absence of stick-nests may have affected other species that used them, but no previous surveys of taxa that use woodrat nests in Key Largo exist. Since the implementation of an adaptive exotic predator management plan and the construction of supplemental nest structures in the 2010s, the distribution of woodrats throughout available habitat has expanded and the construction of stick-nests has resumed in many of the areas in which woodrats occur (Cove et al., 2019). Invasive predator management remains at the forefront of Key Largo woodrat conservation, but despite this, indoor/outdoor free-roaming cats and colony cats remain common at the urban fringes of protected areas in the Keys, with the potential to exert cascading effects on the community (Cove et al., 2018; Herrera et al., 2022a).

Since woodrat stick-nests are known to foster high arthropod diversity and abundance (Humphrey, 1992; Whitford and Steinberger, 2010), the value of these engineered structures might also benefit other species indirectly by providing a potential source of prey. Arthropods are an important food source for many insectivorous and generalist bird species (Bruns, 1960; Hirth and Marion, 1979; Kaufman, 2001). As such, an increase in both abundance and diversity of arthropods might promote high abundance and diversity of birds at nests (Bonsall and Hassell,

2007). Moreover, insectivorous bird abundance correlates with the abundance of invertebrate prey suggesting that birds could be an indicator of invertebrate populations (Martay and Pearce-Higgins, 2020). Despite this, the impacts of these nest structures as refugia for arthropods and as potential foraging grounds for birds have yet to be explored. Due to the proposed relationship between arthropods and birds, we elected to use birds as an indicator species to assess the biodiversity benefits of Key Largo woodrats and their benefits to the community and local food webs.

Other factors such as the presence of invasive predators and forest fragmentation due to human development may also influence the presence, abundance, and species richness of birds in the Florida Keys (Gates and Gysel, 1978; Yahner, 1988; Boulinier et al., 2001; Loss et al., 2013; Doherty et al., 2016). Forest patch size has been found to influence both bird species richness and changes in bird community composition over time, showing lower species richness of sensitive species and higher species turnover in small patches as compared to larger ones (Boulinier et al., 2001). Further, nest predation may increase with proximity to forest edges for forest birds (Gates and Gysel, 1978; Yahner, 1988). The presence of invasive predators, such as free-roaming cats, is also detrimental to bird communities, as they tend to over-consume these prey populations (Loss et al., 2013; Doherty et al., 2016). Therefore, we considered each of these factors individually in our analyses as multiple competing hypotheses.

We leveraged the data from a camera trap monitoring grid to survey the bird community visiting supplemental woodrat nest structures in the protected lands of Key Largo, Florida, USA. Based on the findings of previous studies, and our understanding of the interactions between Key Largo woodrats, arthropods, and birds, we predicted that bird abundance and species richness would increase when Key Largo woodrats were active at supplemental nests, particularly due to association with stick-stacking at nest sites. However, we also expected these effects would be dampened by habitat constraints due to edge effects and fragmentation associated with human development. Further, we

predicted that associations between woodrat activity with bird abundance and species richness would be constrained by free-roaming cats on the landscape due to direct predation of birds and indirectly through consumption of and fear effects on woodrats.

2. Methods

2.1. Study area and design

Remaining Key Largo woodrat habitat, tropical hardwood hammock, is largely restricted to ~1000 ha within two protected areas on the northern third of Key Largo: Crocodile Lake National Wildlife Refuge (CLNWR) and Dagny Johnson Botanical State Park (DJSP). Other small parcels of protected land containing viable Key Largo woodrat habitat exist scattered throughout the southern portion of the island, but no Key Largo woodrats have been documented in these areas for decades. CLNWR has a long history of management for woodrats, including ongoing exotic predator removal since 2013 and nest supplementation starting in 2004 (Cove et al., 2019), while DJSP more recently adopted the supplemental nest structures in 2016. Presently, over 1500 supplemental nest structures have been constructed within the two protected areas (Cove et al., 2019) with an additional 126 structures added to the parcels of habitat further south starting in 2018. Key Largo woodrats readily investigate these structures and frequently use them for nesting or cover (Cove et al., 2017).

A grid of 642 cells was overlaid with the protected habitat in northern Key Largo with an additional 126 cells in the southern study areas. One supplemental nest structure in each grid cell (~2.5 ha each) was identified as the long-term monitoring nest. This subset of supplemental nests makes up a network used to annually monitor the distribution and activity of Key Largo woodrats and other species throughout protected areas on Key Largo.

2.2. Camera trap sampling

We placed a single remote camera trap (Reconyx PC800 or PC850, RECONYX, Inc., Holmen WI, USA) at each supplemental nest structure for a period of 5–6 trap nights throughout Key Largo's conservation lands (Fig. 1). However, due to the 2018 government shutdown and some logistical constraints, some camera traps remained active for a longer period which we accounted for in our analyses (as described below). We randomly stratified the habitat and surveyed 60 nests with one camera trap per nest on any given week over the course of the sampling period. Each camera was attached to a tree within three meters of the target nest structure to document activity at the structure without requiring additional modification of the site. We set the cameras at high sensitivity to take motion triggered pictures in bursts of 10 images with no delay between subsequent motion triggers to capture images of Key Largo woodrats and other species (sensu Cove et al., 2019).

Following data collection, we uploaded all camera trap data into the Smithsonian's eMammal camera trap data repository (McShea et al., 2015) for review and management. In each independent photo sequence, we initially counted the number of visible animals and identified mammals to species where possible while marking when other groups, such as birds or reptiles, were observed. We subsequently identified birds captured to species using previously uploaded eBird (2021) images and the Birds of Florida: Field Guide, 3rd edition (Tekiela, 2020) as identification tools. We then tabulated the total number of detections and presence/absence for each species observed from each site, considering Key Largo woodrat detections and detections of stick-stacking to be indicators of woodrat activity because woodrat presence also indicates some level of internal nest activity (i.e., internal stick-stacking, deposition of feces and caches, etc.) at supplemental nest sites even if there is no external stick-stacking. Therefore, under our current study design we assumed woodrat activity represented some level of ecosystem engineering via stick-nest building whether

Table 1

Hypotheses of generalized linear models with negative binomial distribution (glm.nb) for bird abundance and species richness based on camera trap surveys for Key Largo woodrat nest monitoring and bird surveys in North Key Largo, FL, 2018.

Hypothesis	Model	Model Structure	Expected Result
No habitat covariates affect bird detections	glm.nb(.)	β_0	
Negative effect as count of free-roaming cats increases	glm.nb (cat)	$\beta_0 + \beta_1(cat)$	$\beta_1 < 0$
Negative effect associated with free-roaming cat presence	glm.nb (cat_pa)	$\beta_0 + \beta_1(cat\_pa)$	$\beta_1 < 0$
Positive effect with protected status in northern PAs	glm.nb (prot)	$\beta_0 + \beta_1(prot)$	$\beta_1 > 0$
Positive effect as distance to development increases	glm.nb (dist)	$\beta_0 + \beta_1(dist)$	$\beta_1 > 0$
Positive effect with indicators of woodrat activity	glm.nb (wr)	$\beta_0 + \beta_1(wr)$	$\beta_1 > 0$
Free-roaming cat presence, distance to development, and indicators of woodrat activity	glm.nb (global)	$\beta_0 + \beta_1(cat\_pa) + \beta_2(dist) + \beta_3(wr)$	$\beta_1 < 0, \beta_2 > 0, \beta_3 > 0$

externally visible or not. Moreover, we calculated bird species richness and abundance at each site as the number of bird species detected and the total number of individual birds of each species detected, respectively.

2.3. Statistical analyses

We tested the effect of indicators of woodrat activity on bird abundance and species richness using generalized linear models (GLMs) with a negative-binomial distribution in RStudio with R v4.0.2 using the package MASS (Venables and Ripley, 2002; R Core Team, 2020; RStudio Team, 2021). In some models, we included scaled distance to development, domestic cat presence, count of domestic cat detections, and protection status at each site as additional explanatory variables (Table 1). We assessed all model covariates for correlations ($R > 0.6$), but none met this threshold. Further, we added an offset to all models to account for the uneven sampling time across sites where camera traps were left out for longer than 5–6 trap nights. The package AICcmodavg was used to evaluate which of the a priori models carried the greatest support; models garnering >95% of the cumulative Akaike weight were considered top models for inference (Table 1; Mazerolle, 2020; RStudio Team, 2021). Finally, all figures depicting graphs were created in R using the packages ggplot2, sandwich, and msm, and our site map was created in Tableau (Jackson, 2011; Wickham, 2016; Zeileis et al., 2020; RStudio Team, 2021; Tableau Team, 2022).

3. Results

3.1. Observations

From a total effort of 5014 camera trap nights, we observed 304 bird detections of 12 different bird species (Appendix 1). Of those species, 11 are considered to exhibit some level of insectivory. Nine of the bird species detected are classified as eating primarily insects, while two species tend to supplement their diets with insects (Cornell Lab of Ornithology, 2019). We surveyed 729 sites between October 2018–April 2019 and detected Key Largo woodrats at 77 sites and stick-nest building behavior at 73 sites, for a total of 121 sites with indicators of Key Largo woodrat activity. Additionally, free-roaming cats were detected at 43 sites and birds were detected at 175 sites. Of all bird detections, 47 were from sites where Key Largo woodrats were present. In total, there were 662 woodrat detections and 108 cat detections.

Table 2

Model selection statistics for all models of bird species richness, with untransformed coefficients of covariates, based on camera trap surveys for Key Largo woodrat nest monitoring and bird surveys in North Key Largo, FL, 2018.

				Untransformed coefficients of covariates (SE)[1]				
Model	Δ_i[2]	ω_i[3]	K[4]	Intercept	Cat[5]	Distance	Protected	Woodrat
glm.nb(cat_pa)	0.00	0.29	3	−1.26 (0.09)	**−1.59 (0.75)**			
glm.nb(global)	0.16	0.27	5	−1.37 (0.11)	**−1.49 (0.75)**	0.05 (0.09)		**0.45 (0.23)**
glm.nb(cat)	0.25	0.26	3	−1.27 (0.09)	−0.91 (0.52)			
glm.nb(wr)	2.26	0.10	3	−1.42 (0.10)				**0.50 (0.23)**
glm.nb(prot)	4.11	0.04	3	−1.70 (0.27)			0.45 (0.29)	
glm.nb(.)	4.64	0.03	2	−1.31 (0.09)				
glm.nb(dist)	5.97	0.01	3	−1.31 (0.09)		0.08 (0.09)		

[1] Coefficients are in logit space and relate to standardized or categorical covariate values (cat_pa = cat presence/absence, cat = number of cat detections, wr = indicators of woodrat activity, prot = within or directly adjacent to a protected area, dist = distance from development). Significant coefficients are bolded.
[2] Δ_i, AICc difference.
[3] ω_i, Akaike weight.
[4] K, number of model parameters.
[5] Cat column represents coefficients of both glm.nb(cat_pa) and glm.nb(cat).

Table 3

Model selection statistics for all models of bird abundance, with untransformed coefficients of covariates, based on camera trap surveys for Key Largo woodrat nest monitoring and bird surveys in North Key Largo, FL, 2018.

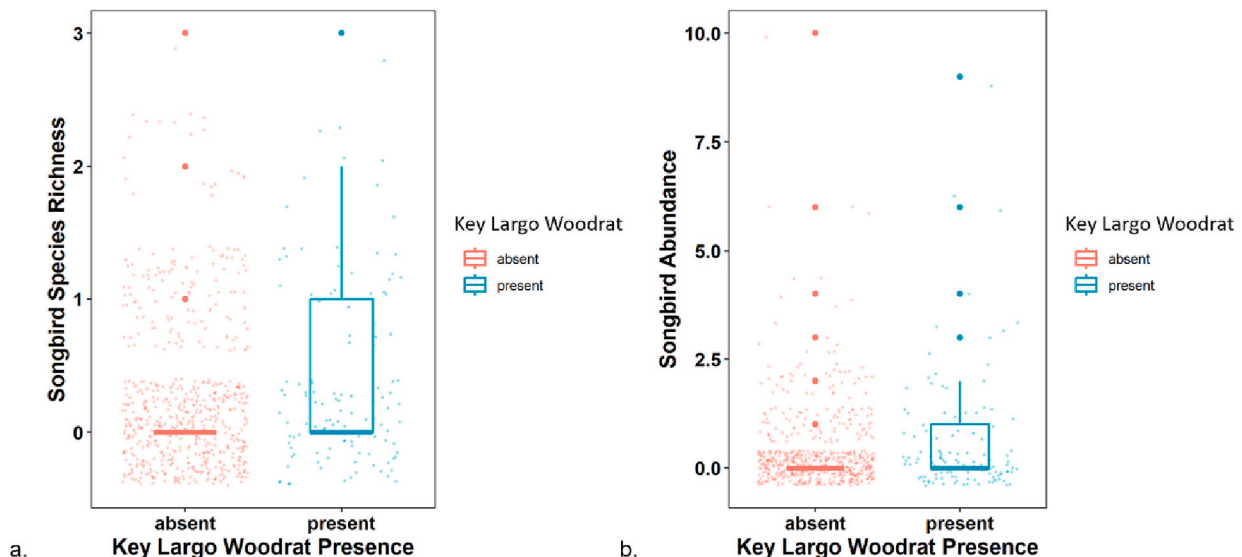|				Untransformed coefficients of covariates (SE)[1]				
Model	Δ_i[2]	ω_i[3]	K[4]	Intercept	Cat[5]	Distance	Protected	Woodrat
glm.nb(global)	0.00	0.72	5	−1.03 (0.11)	**−1.78 (0.76)**	0.13 (0.09)		**0.50 (0.23)**
glm.nb(cat_pa)	3.39	0.13	3	−0.91 (0.09)	**−1.94 (0.77)**			
glm.nb(cat)	3.93	0.10	3	−0.91 (0.09)	**−1.15 (0.55)**			
glm.nb(wr)	6.66	0.03	3	−1.09 (0.10)				0.58 (0.23)
glm.nb(prot)	8.94	0.01	3	−1.45 (0.26)			0.56 (0.28)	
glm.nb(dist)	9.02	0.01	3	−0.98 (0.09)		**0.18 (0.09)**		
glm.nb(.)	10.90	0	2	−0.96 (0.09)				

[1] Coefficients are in logit space and relate to standardized or categorical covariate values (cat_pa = cat presence/absence, cat = number of cat detections, wr = indicators of woodrat activity, prot = within or directly adjacent to a protected area, dist = distance from development). Significant coefficients are bolded.
[2] Δ_i, AICc difference.
[3] ω_i, Akaike weight.
[4] K, number of model parameters.
[5] Cat column represents coefficients of both glm.nb(cat_pa) and glm.nb(cat).

Fig. 2. Box plot including raw data points depicting the average bird species richness in the presence and absence of Key Largo woodrats (a). Box plot including raw data points depicting the average bird abundance in the presence and absence of Key Largo woodrats (b).

3.2. Analyses

The top models suggested that bird species richness and bird abundance varied with free-roaming cat presence, indicators of Key Largo woodrat activity, and distance to development (Tables 2 and 3). Our global model indicated that bird species richness increased with indicators of woodrat activity (p-value = 0.048, Fig. 2a) but decreased significantly with free-roaming cat presence (p-value = 0.047, Fig. 3a) and suggested an increasing but nonsignificant trend at nest sites farther from developed areas (p-value = 0.61, Fig. 3a). Other top models for
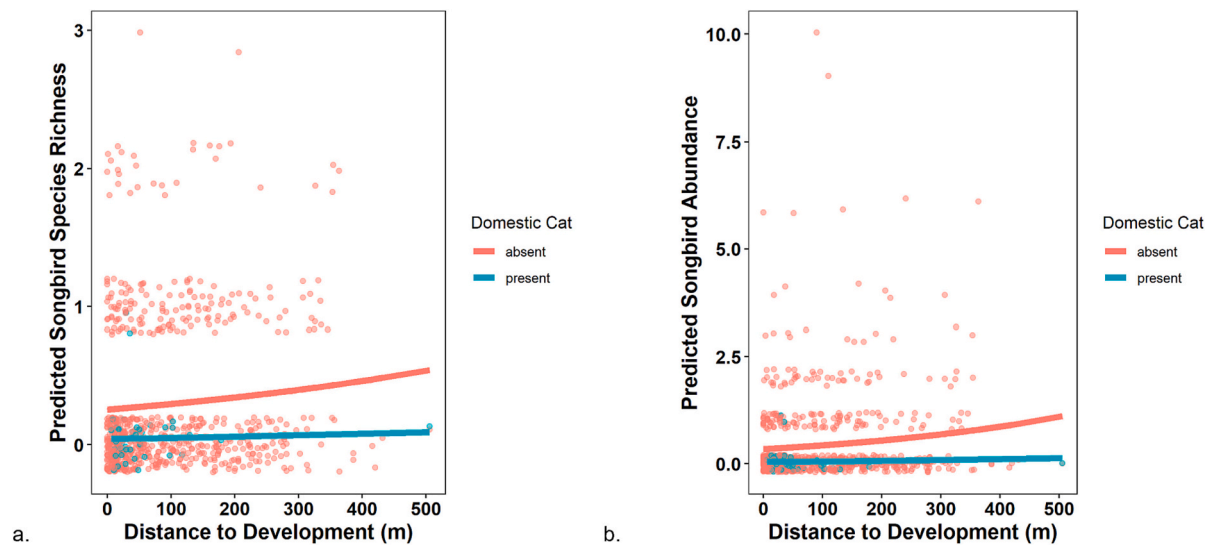
Fig. 3. a. Predicted bird species richness associated with domestic cat presence and distance to development (m). b. Predicted bird abundance (counts of all species) associated with domestic cat presence and distance to development from camera trap surveys for Key Largo woodrat nest monitoring and bird surveys in North Key Largo, FL, 2018. Points represent raw data points of bird species richness and abundance in the absence (pink) and presence (blue) of cats. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

bird species richness followed similar trends to our global model for bird species richness and included the cat presence/absence model (p-value = 0.034), the cat abundance model (p-value = 0.078), the indicators of woodrat activity model (p-value = 0.028), and the protection status model (p-value = 0.117).

Bird abundance followed a similar pattern, increasing when there were indicators of woodrat activity (*p*-value = 0.030, Fig. 2b). Further, bird abundance decreased significantly with free-roaming cat presence (p-value = 0.019, Fig. 3b), and exhibited an increasing trend as nest sites were located farther from developed areas (p-value = 0.135, Fig. 3b). Other top models which followed similar trends to our global model for bird abundance included the cat presence/absence model (p-value = 0.011) and the cat abundance model (p-value = 0.035).

4. Discussion

We provide evidence that the Key Largo woodrat may exert cascading effects on community composition of higher trophic levels by creating foraging grounds for birds through the construction and maintenance of stick-nests. Our analysis revealed that woodrat activity exhibits a positive correlation with bird species richness and abundance and that woodrat stick-nest building behaviors are also positively correlated with bird abundance. Because microhabitats and their associated food resources have been found to positively affect bird abundance and species richness, our results suggest that there is increased availability of food resources at Key Largo woodrat nests that are exploited by birds (Holmes and Robinson, 1988; Regnery et al., 2013). This supports our first hypothesis that these ecosystem engineering services are positively related to bird species richness and abundance at supplemental nest structures.

Despite the evidence of the potential effects of woodrats on organisms at lower trophic levels (Frank and Thomas, 1984; Whitford and Steinberger, 2010), there have been few studies investigating potential effects of this ecosystem engineer on organisms at higher trophic levels or how this may influence community composition. To our knowledge, there have been no prior efforts to survey Key Largo woodrat stick-nest structures for invertebrate inhabitants. While the positive relationship between indicators of Key Largo woodrat activity and bird abundance may indicate that there is indeed a high abundance of arthropods within supplemental nest structures with stick-nests built upon them, this was not directly studied. Therefore, we suggest that these nest structures be

sampled directly for invertebrates in the future to provide a better understanding of the inhabitant community composition of these nests. Since our bird detection data were relatively limited, future studies should survey bird communities over longer periods of time or during migratory seasons to better understand the impact that Key Largo woodrats exert on their community and bird food web structure. We encourage similar biodiversity surveys among the other stick-nest building rodent communities around the globe, especially in areas where invasive predators affect their distribution and abundance (e.g., stick-nest rats in Australia - Dickman, 1999).

Importantly, the negative effects of domestic cats on wildlife are well documented. Free-roaming and feral cats are a considerable source of native bird, mammal, and herpetofauna mortality (Lepczyk et al., 2004; Beckerman et al., 2007; Van Heezik et al., 2010; Loyd et al., 2013; Loss et al., 2013, 2015; Woinarski et al., 2017, 2018; Li et al., 2021). Moreover, cats have contributed in some capacity to the extinction of at least 63 species worldwide (Doherty et al., 2016). Some estimates put total bird mortality from free-roaming domestic cats at 1.3–4.0 billion and mammal mortality at 6.3–22.3 billion, just within North America (Loss et al., 2013). When introduced to island ecosystems, the impact of domestic cats tends to be more severe due to the lack of evolved predation defenses in many insular species (Medina et al., 2011). These previously described impacts of domestic cats on wildlife explain the observed negative relationship that they exhibit with birds in our study. We found cat presence to be strongly negatively associated with bird species richness and abundance at supplemental nest structures on Key Largo, giving support to our prediction that the benefits of Key Largo woodrats are constrained by the presence of this exotic predator. Furthermore, cats exert fear effects that may ultimately indirectly affect bird feeding behaviors in cases where woodrats are less likely to build stick-nests due to cat presence in the environment (Cove et al., 2019). These direct and indirect effects of introduced predators override natural commensal processes and disrupt food webs in their novel ranges, which may extend well beyond the scale of their distributions when considering migratory species stopovers.

We also identified proximity to developed areas as a covariate that was weakly negatively associated with bird species richness and abundance. This observed relationship supports our prediction that any potential effects of Key Largo woodrats on bird communities would be constrained by anthropogenic development, however this was not a strong driving factor, and it was not shown to be significant in any of our

top models. There is evidence elsewhere that small, fragmented forest patches contain fewer sensitive species (Boulinier et al., 2001), and birds close to anthropogenic development may be at higher risk of nest predation than those nesting in forest interior due to edge effects (Gates and Gysel, 1978; Yahner, 1988), but we suspect that the species represented here are less sensitive to such factors. However, the indirect effects of fragmentation and human development may manifest from the impacts of free-roaming cats associated with houses at the urban-wildland interface where they preferentially prey upon native species (Herrera et al., 2022a, 2022b).

Our results show that the activity of Key Largo woodrats, free-roaming cats, and to a lesser extent anthropogenic development serve as the best predictors of the bird communities visiting supplemental nest structures on Key Largo. The negative impact that free-roaming cats have on birds is likely compounded due to their effect on the Key Largo woodrat. Not only do free-roaming cats directly contribute to bird mortality through predation, but they can also exert indirect effects on birds by directly preying upon the Key Largo woodrat and by preventing their stick-nest building behaviors through fear (Cove et al., 2019). Further, anthropogenic development may have direct effects on the species richness and turnover of forest birds, and anthropogenic development may also indirectly affect bird communities as a source of Key Largo woodrat habitat loss (Boulinier et al., 2001). We therefore suggest that the ecosystem services and benefits that the Key Largo woodrat may offer to birds are likely negated by the presence of domestic cats, which may have cascading effects throughout the food web.

Author contribution statement

Declaration of Competing Interest

We do not declare any conflicts of interest.

Acknowledgements

Appendix 1. Appendix

All songbirds identified in this study, the number of times each species was detected and whether or not they exhibit insectivory according to the Cornell Lab of Ornithology (Cornell Lab of Ornithology, 2019).

Bird Species	Detections	Insectivore
American redstart	6	yes
Black-and-white warbler	3	yes
Black-throated blue warbler	1	yes
Carolina wren	29	yes
Common grackle	1	partial
Gray Catbird	31	yes
Hooded warbler	1	yes
Mourning dove	4	no
Northern cardinal	61	partial
Ovenbird	156	yes
Palm warbler	8	yes
Swainson's thrush	3	yes

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