



Research Article

Adapting Coastal Management to Climate Change: Mitigating Our Shrinking Shorelines

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ABSTRACT Sea-level rise due to climate change is a major threat to coastal ecosystems worldwide. Current management to reduce beach erosion often focuses on protecting human structures and research on effects on wildlife is lacking. Using a combination of hierarchical models and generalized linear models, we evaluated how the gopher tortoise (*Gopherus polyphemus*) colonized constructed dunes along coastal scrub at the Merritt Island National Wildlife Refuge, central Florida, USA. Over 2 years, we surveyed tortoise populations along natural dunes and 2 constructed dunes (completed in 2012 and in 2014) and estimated tortoise density each summer and winter. Our models indicated that tortoise density along the 2014 dune was comparable to that of natural dunes (\bar{x} = 0–8 tortoises/ha), and density peaked at a mean of 21 tortoises/ha along the 2012 constructed dune. Gopher tortoises rapidly colonized constructed dunes, and dune construction may represent effective management against habitat loss for this species. © 2017 The Wildlife Society.

KEY WORDS climate change, coastal management, Florida, gopher tortoise, *Gopherus polyphemus*, land cover, sea-level rise.

Climate change is one of the greatest threats to biodiversity (Sala et al. 2000, Thomas et al. 2004). Management plans for species and land conservation will need to address potential effects of climate change to account for evolving threats to wildlife (Staudinger et al. 2013). Coastlines are particularly vulnerable as they are facing sea-level rise and a potential increase in the strength of hurricanes and tropical storms (Scavia et al. 2002, Nicholls et al. 2007, Overpeck and Weiss 2009, Zhang et al. 2013). Often, coastal management to protect against beach erosion focuses on protecting human interests, whereas the effects on wildlife are understudied (Schlacher et al. 2007, Harris et al. 2015).

Most management aimed at protecting coastlines use methods such as dune construction, sediment supplementation, and hard sea walls (Klein et al. 1998). Sea walls increase overall coastal erosion by causing a loss in beach area in front of the walls and worsening erosion along their edges (Bernatchez and Fraser 2011). If the goal is to protect coastlines and conserve natural beaches, the construction of hard wall structures may cause a loss of habitat and biodiversity; thus, construction should be discouraged in

certain areas, and considered a last resort to manage beaches (Schlacher et al. 2007, Harris et al. 2015).

One common alternative to hard-walled sea structures is beach nourishment, a soft engineering form of management to preserve natural features. Often beach nourishment involves the construction of dunes to help prevent or reduce overwash erosion where storm surges transport water and beach sediment over dune crests (Klein et al. 2001). Beach nourishment is a minor disturbance from which the ecosystem can rapidly recover (Harris et al. 2015). Constructed dunes can be part of management strategies to protect wildlife, increase coastal resilience to storms, and reduce coastal erosion (Nordstrom et al. 2000). In areas at risk from sea-level rise induced by climate change, beach nourishment or supplementation may be part of larger management plans to protect biodiversity (Schlacher et al. 2007, Nicholls and Cazenave 2010). However, research is needed to assess how native wildlife is affected by different shoreline management strategies (Schlacher et al. 2007, Spalding et al. 2014).

Climate change will not affect all wildlife equally, and it is important to identify vulnerable species to study how they respond to potential management strategies; in reptiles, climate change is one of the leading threats to biodiversity, and is expected to cause range contractions in up to 85% of turtle species (Gibbons et al. 2000, Ihlow et al. 2012). Turtles possess a unique suite of life-history traits (i.e., high adult survivorship, low hatchling and juvenile survivorship, delayed reproduction, temperature-dependent sex determination),

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which put them at increased risk to disturbance-induced declines such as climate change (Congdon et al. 1993). Tortoises (Family: Testudinidae) are likely to be severely affected by such disturbances because they usually exhibit low frequency of dispersal, long generation time, low fecundity, and low phenotypic plasticity. These traits are correlated with negative effects such as population declines and local extinctions under climate change (Staudinger et al. 2013, McCoy et al. 2014). Therefore, we evaluated the response of gopher tortoises (*Gopherus polyphemus*), a candidate species for listing under the Endangered Species Act and a threatened species in Florida, to soft engineering in the form of dune construction to mitigate the impact of sea-level rise (Berry and Aresco 2014). Gopher tortoises dig characteristic burrows that provide stable microclimates and refuge from disturbances such as wildfires or predators, and provide habitat components for ≥ 300 invertebrate and 60 vertebrate species that use tortoise burrows (Hubbard 1893, Diemer 1986, Lips 1991, Witz et al. 1991, Kinlaw and Grasmueck 2012).

Florida is a major biodiversity hotspot in North America, and because of range-wide declines of gopher tortoises over the past century, is estimated to contain most of the remaining populations of the species (James 1961, Auffenberg and Franz 1982, Noss et al. 2015). Habitat loss is one of the leading threats to the genus *Gopherus*, and will likely worsen because of sea-level rise combined with more severe storm surges that threaten developed and protected areas (Reece et al. 2013, Zhang et al. 2013). No part of Florida is >150 km from a coastline; therefore, research on potential management methods is needed (Reece et al. 2013). Translocations of gopher tortoises from areas with eroding coastlines are not a feasible solution to protect coastal tortoise populations because tortoise burrow fidelity often causes translocations to be ineffective. Tortoises rarely move >50 m from their burrows and have documented homing behaviors (Ashton and Ashton 2008, McCoy et al. 2013). Additionally, improper translocations contribute to population declines (Berry and Aresco 2014). Prior studies on coastal populations of gopher tortoises (Breininger et al. 1994b, Lau and Dodd 2015) reported that density was positively associated with ruderal and open herbaceous cover as a source of food, whereas coverage by woody vegetation was negatively associated with density. By evaluating colonization rates and local population sizes on constructed dunes, we sought to determine if gopher tortoise density along constructed dunes was similar to surrounding natural dunes, and if constructed dunes would function for a managed retreat as sea-levels rise. We investigated if coastal gopher tortoises would colonize man-made dunes as newly formed tortoise habitat. We expected gopher tortoises would rapidly colonize new dunes and that densities of tortoises would be similar to, or higher than, densities along the surrounding natural coastline because of higher availability of open, sandy habitat for burrow construction and herbaceous ground cover for forage.

STUDY AREA

The John F. Kennedy Space Center (KSC) and Merritt Island National Wildlife Refuge (MINWR), Florida, USA,

make up one of the largest protected landscapes along the Atlantic coast of Florida, covering >570 km², and are rich in biodiversity (Breininger et al. 1994a). In 1962, land was acquired by the National Aeronautics and Space Administration (NASA) for research use and as a launch site, with the majority of the land purchased by the United States Fish and Wildlife Service (USFWS) in 1963 to establish a protective buffer around the KSC, forming MINWR (Breininger et al. 1994a). Most of the land is managed by the USFWS and the United States National Park Service (NPS) for conservation, with a small interior section developed and managed by NASA. The flora and fauna assemblages of MINWR are a combination of both temperate Carolinian and tropical Caribbean species (Breininger et al. 1994a). Pine (*Pinus* spp.) flatwoods and scrub form most inland uplands ecosystems, whereas marshes cover much of the lower elevations of the barrier island (Breininger et al. 1994a). The mean daily minimum temperature is 11°C in January, with a mean daily maximum of 21°C; in July, the mean daily minimum temperature is 23°C, with a mean daily maximum of 31°C (Breininger et al. 1994a). Seasons at Merritt Island are divided between a wet, humid summer and fall when 70% of rainfall occurs, and dry winters and springs. Sea-level rise is the leading threat to KSC, and in the past decades, overwash events have contributed to eroded areas 25–60 m wide along the coastline (Rosenzweig et al. 2014). Following Hurricane Sandy in 2012, NASA proposed construction of new dunes along sections of the beach at KSC with the worst erosion to reduce overwash and to protect government infrastructure (Fig. S1, available online in Supporting Information). Construction of the first 214-m-long dune was completed in early 2012 (2012 constructed dune) and on March 2014 a second dune was finished (2014 constructed dune) extending 445 m north and 1,088 m south of the 2012 constructed dune (Rosenzweig et al. 2014). The constructed dunes were 1.77 km long, peaked at 18.3 m high and 24.4 m wide, and covered >4.3 ha. The nearby natural dunes varied greatly in height and width; however, the northern natural dune had an average height of 16 m with an asymmetric width of 5 m on the seaward side and 50 m wide on the inland side of the dune. The northern dune was dominated by a mixture of sea grapes (*Coccoloba uvifera*) and sea oats (*Uniola paniculata*). The southern natural dune was the shortest dune surveyed, with an approximate height of 9 m where it met the constructed dunes, and a low point of 1 m. The southern natural dune was roughly symmetrical with a width of 30 m, and was dominated by sea oats with several localized patches of sea grapes and one inland strand of Brazilian pepper (*Schinus terebinthifolius*). The surrounding landscape was comprised of natural coastal scrub, coastal strand, open beach, salt marsh, Brazilian pepper, and human-modified ruderal areas (2012 land cover data provided by NASA; N. R. Cancro, Kennedy Environmental and Medical Contract, personal communication).

METHODS

Prior to dune construction, KSC environmental and medical contractors captured all gopher tortoises found within the

construction footprint using bucket traps and relocated them to the adjacent coastal scrub (Enge 2001). Outside consultants led by NASA environmental researchers planted the constructed dunes with sea oats and other native herbaceous vegetation to aid colonization by wildlife and for stabilization. Long-term management efforts along the coast focused on spot removal of invasive plants and infrequent localized burns by the USFWS on an as-needed basis because of concerns about damaging nearby infrastructure. We surveyed for gopher tortoise burrows along 20 ha of the coastline within the closed-access section of KSC (Fig. S1) from June 2014 to January 2016 (Martin 2016). We selected this section of the refuge because it was a 3-km-long stretch of heterogeneous coastal landscape that was off limits to the public, and encompassed the constructed dunes and contiguous sections of the natural dunes to the north and south. Handling of gopher tortoises during this study was conducted under a USFWS permit (no. LSSC-13-00023) and approved by Towson University Institutional Animal Care and Use Committee (no. 03312014RS-01).

Population Estimation

To compare tortoise density in constructed and natural dunes, we developed a new method for estimating gopher tortoise density that explicitly incorporates variability in detection of burrows and burrow occupancy rates. We employed hierarchical models to construct theoretical distributions to simulate tortoise density based on remotely sensed land cover data. Hierarchical models use multiple component models (i.e., detection, density) to separate variation due to ecological processes and imperfect observations, factors that display different conditional probability structures (Royle and Dorazio 2008, Royle et al. 2014). This approach differs from classical multi-level modeling because each component model has an explicit biological basis (Royle et al. 2014). If tortoises used constructed dunes, then we expected the percentage of land cover that was categorized as constructed would appear as a positive covariate in models.

We used line transect distance sampling (LTDS) to estimate adult tortoise (>23 cm carapace length; Landers et al. 1982) burrow density along the 2012 constructed dune, the north and south sections of the 2014 constructed dune, and 2 800-m sections of the natural dunes immediately north and south of the construction area (Anderson et al. 2001, Nomani et al. 2008). We estimated burrow densities using hierarchical distance sampling models in the package *Unmarked* in R (R version 3.2.0, <http://www.R-project.org>, accessed 31 Aug 2013) based on our LTDS data (Royle and Dorazio 2008, Fiske and Chandler 2011). We used this method, as opposed to standard LTDS analyses established by Smith and Stober (2009) based around single point and model estimates, and tested by Castellón et al. (2015), to build higher confidence in our population estimates, while accounting for variation in burrow detection and density in a unified framework. We surveyed dune crest lines for tortoise burrows along the entire length of the constructed dunes and the 800-m sections of each natural dune. Traditionally, LTDS surveys are placed orthogonal to elevational gradients,

but we deviated from standard methodology to have long enough transects to create a high degree of confidence of finding burrows. The constructed dunes were approximately 4.8 m wide at the crest, making detection of burrows on both sides of the dune difficult. We focused survey efforts on each side of the dune independently to meet the assumption of 100% detection of burrows for line-transect surveys with a single observer at zero distance, within each transect. We performed surveys twice in summers (May–Aug) of 2014 and 2015, and once in January 2015 and January 2016 (Martin 2016). This allowed us to evaluate the excavation of new burrows over 2 years and potential seasonal changes in density. We recorded a global positioning system (GPS) coordinate for each located burrow with an entrance diameter ≥ 25 cm, using a handheld eTrex[®] 30 GPS (Garmin, Olathe, KS, USA), and imported all points into ArcMap[®] version 10.1 (ESRI, Redlands, CA, USA). We used remotely sensed data to evaluate all available land cover using ArcMap for later estimation of burrow density. Although land cover data provides less accurate information than field sampling, employing such data is quicker, requires less intensive sampling, and produces information for use in models that is easily replicable in a variety of settings.

During each of the 2 winter field seasons, we surveyed a random subset of burrows along each dune ($n = 20/\text{dune}$ or all burrows if < 20) by inserting a camera attached to a flexible conduit into the burrow to determine if the burrow was occupied by a tortoise (Buskirk and Fiedler 1986, Breininger et al. 1991, Smith et al. 2005). We randomly selected 20 burrows along each dune because of time constraints given the large number of burrows found on some dunes. In January 2016, we surveyed burrows twice to better estimate tortoise density and variability of occupancy rates following an increase in burrows along the constructed dunes. We sampled additional burrows if the selected burrow was collapsed (full blockage < 50 cm into burrow) or could not be fully scoped (because of flooding or vegetation roots). Therefore, given the 3 survey periods and 5 dunes, the potential maximum number of scoped burrows was 300, excluding replacements. We scoped burrows only in winter because this is the period of lowest activity for tortoises at our site, and it minimized the chances of falsely declaring a burrow as unoccupied. The current recommendations for gopher tortoise surveys include scoping all burrows encountered (Smith and Stober 2009, Castellón et al. 2015). If this takes > 1 day/site, tortoises may move between surveyed and unsurveyed burrows, increasing error rates in burrow occupancy estimates because of the potential to double count tortoises. This violates the assumption of a closed survey population because tortoises that move from an unsurveyed burrow to one previously surveyed and unoccupied are effectively migrating out of the survey population.

We classified surveyed burrows as empty (saw end of burrow, no tortoise present), occupied (observed tortoise), or incomplete. We classified surveyed burrows as incomplete in situations where debris inside the burrow obscured the camera view (as compared to collapsed burrows, which were visibly blocked from the outside of the burrow), or the

burrow became too small for the camera unit. Adult tortoises would not be able to fit into these narrow burrows, but we could not preclude use by smaller size classes. If we determined a selected burrow was incomplete or collapsed, we randomly selected an additional burrow to sample when possible to maintain sample sizes. We used occupied and unoccupied burrows to calculate the average tortoise burrow density for each dune. Although current recommendations focus on only modeling occupied burrows, our analysis uses an additional burrow occupancy model to estimate variability in burrow occupancy, and thus we included unoccupied burrows in our final dataset (Castellón et al. 2015). All parameters and density estimates are reported with 1 standard error.

We calculated straight-line distance from each burrow to transect using the near proximity tool in ArcMap. We calculated land cover on each transect by intersecting land cover data with 100-m buffers around the full length of each transect based on secondary foraging areas of gopher tortoises (Ashton and Ashton 2008, Berish and Medica 2014). In addition, this buffer covered most of the tortoise habitat between the ocean and the inland salt marsh (Fig. S1). We calculated percent land cover for each classification category by dividing the area of each type by the total buffer area to standardize land cover values. We kept land cover classifications (Table 1) distinct to account for potential differences even in unsuitable cover types (i.e., tortoises may move through areas associated with infrastructure but are blocked by open water). We imported distances for each burrow and percent land cover for each transect into R. We then checked percent land cover covariates for their correlation with other covariates.

We estimated burrow densities using the package Unmarked in R to test 25 *a priori* competing hierarchical models based on land cover and categorical covariates for

gopher tortoise burrow density and detectability (Table S1, available online in Supporting Information; Fiske and Chandler 2011). We chose categorical covariates based on our opinions on broad classifications that may explain variation in tortoise density. We included all burrows when calculating burrow density. This method is contrary to recommendations presented in Castellón et al. (2015) because burrow occupancy rates in coastal environments are lower than those reported by Castellón et al. (2015), and most burrows are relatively straight and easy to scope, leading to few cases of incomplete burrow status.

We tested the fit of 4 potential distributions (half-normal, hazard rate, negative exponential, uniform) for detectability as a function of distance with a null model (no covariates set) using Akaike's Information Criterion (AIC) scores to determine the best fitting distribution for later models (Akaike 1973, Burnham and Anderson 2002). We considered models to have equal likelihood if AIC scores differed by <6 because the common standard of selecting top models within 2 AIC may lead to incorrect inferences and exclusion of important parameters (Richards 2005, 2008; Grueber et al. 2011). We did not use corrected AIC scores because we created multistep models incorporating a series of sub-models; corrections, such as the alternative sample-size corrected AIC scores (AIC_c), cannot be applied to submodels based on different datasets. We used AIC_c scores for selecting the top burrow occupancy model because we modeled burrow occupancy using generalized linear models. We assessed model fit using a chi-squared goodness-of-fit test with 10,000 bootstrap samples using the package AICcmodavg in R. We calculated confidence intervals for burrow density using iterative bootstrapping of model predictions. We calculated profile confidence intervals for all parameters because this likelihood-based method does not rely on any distributional assumptions for calculating interval

Table 1. Descriptions and predicted effects of categorical and land cover covariates used in models of gopher tortoise burrow density, Merritt Island National Wildlife Refuge, central Florida, USA, 2014–2016. We based the predicted relationship between each covariate and gopher tortoise burrow density on information from published literature and our field observations.

Covariate	Description	Prediction
Type	Dune category: natural, construction, or older construction	None, control for unmeasured variation
Dune	Unique identification for each dune	None, control for unmeasured variation
Yr	Year survey occurred	Positive
Season	Annual timing of survey (summer or winter)	None, may affect detection
Orientation	Seaward or inland dune face	Increased density on inland side because of protection from storm waves
Beach	Flat, sandy beach; may provide herbaceous forage and basking sites	Positive
Barren land	Flood plain; unsuitable land cover from lack of forage and inability to construct burrows; likely difficult for tortoise to move through because of seasonal flooding	Negative
Brazilian pepper	Unsuitable land cover because of lack of available forage, but tortoises may traverse	Negative
Coastal scrub	May provide forage, basking sites, nest sites, and burrow sites	Positive
Coastal strand	Similar benefits to coastal scrub	Positive
Construction	Area made up of newly created dunes	Positive
Infrastructure	Roads and buildings; removed because of correlation with coastal strand ($r=0.723$)	
Mangrove	Unsuitable land cover and likely avoided because of daily flooding and density of mangrove roots blocking ground	Negative
Ocean	Removed because of correlation with beach ($r=0.709$)	Negative
Ruderal herbaceous	Early successional, low, herbaceous vegetation or grassy lawns; may provide forage, basking sites, nest sites, and burrow sites	Positive
Ruderal woody	Disturbed land supporting mostly tall (>1 m), woody plants; likely unsuitable, but tortoises may move through	Negative

size (Venzon and Moolgavkar 1988). We assessed burrow occupancy rates across dunes and years using generalized linear models with a binomial response variable in R to calculate average occupancy and to test the effects of dune identity over both years. We calculated confidence intervals for occupancy rates and burrow density using top models and the predict function in R.

To estimate gopher tortoise density, we constructed a theoretical distribution of burrow density along each transect by taking 10,000 random samples from a Gaussian distribution determined by the mean and standard error of burrow density from the top model. We then checked the distribution for negative numbers (e.g., parameters estimated with a low mean and high standard error), and set any negative values to zero. We generated a similar sample distribution from the burrow occupancy model using the logistic distribution. We estimated gopher tortoise density along each transect using an iterative loop in R, where we calculated potential estimates of tortoise density in each loop as the sum of n Bernoulli trials, where n was a randomly selected value from the sample burrow density distribution. Each trial had a success probability, selected at random from the burrow occupancy distribution; we ran this loop for 10,000 iterations for each transect, sampling with replacement. Because the simulated data were not normally distributed, we calculated quantiles covering 95% of the resulting distributions as final estimates of gopher tortoise density for each transect.

Our method of analysis deviates from the standard methodology for calculating tortoise density (Smith and Stober 2009) but offers several advantages. By using hierarchical models, we incorporate variation due to detectability while evaluating potential covariates in an explicit biological framework (Royle et al. 2014). Using R allows for more flexibility in model construction, gives greater control over underlying assumptions such as distributions of parameters of interest, and provides output at each step of the analysis (Mazerolle 2015). We designed the methodology to better estimate variability of burrow occupancy rates and allow surveyors to incorporate repeated surveys of burrows.

RESULTS

We removed burrows classified as incomplete (<1% of all burrows) from our dataset before modeling burrow density to address the limitations discussed by Nomani et al. (2008) regarding incorrectly calculating tortoise occupancy rates. We removed percent ocean and percent infrastructure from the land cover dataset based on high correlations ($|r| > 0.6$) with other covariates (Table 1). The top model for predicting burrow detectability was the null model fitted using a negative exponential function ($n = 448$ burrows). The top model for burrow density included percent cover for the following land cover types for each transect: beach, constructed dune, inland water, coastal strand, Brazilian pepper, ruderal herbaceous plants, coastal scrub, and an interaction between beach and constructed dune area. The top model was separated by the second-best model by a ΔAIC difference of 59.34 (Table 2).

Table 2. Hierarchical burrow density models for gopher tortoises in Merritt Island National Wildlife Refuge, central Florida, USA, 2014–2016, and difference in Akaike's Information Criterion (ΔAIC) scores. The detection component for the 3 models presented was fit to a negative exponential curve without covariates, and is not shown here. All covariates are based on percent land cover, except for 2 categorical covariates: dune (unique identification for each dune) and orientation (seaward or inland dune face). Only the top 3 models are listed here (full results including model weights in Table S1, available online in Supporting Information).

Density model	ΔAIC
Beach \times construction + inland water + coastal strand + Brazilian pepper + ruderal herbaceous + coastal scrub	0.00
Dune + orientation	59.34
Beach + construction + coastal strand + Brazilian pepper + ruderal herbaceous + coastal scrub	71.22

Observed values for burrow density did not differ from those predicted by the top model ($P = 0.253$; overdispersion [\hat{c}] = 1.08), indicating good overall model fit. Model covariates provided estimates of the relative magnitude and direction (positive or negative) of the effect for each covariate on burrow density, constrained by the minimum and maximum observed percentage of each land cover in the study area. The covariates with the largest effect on gopher tortoises were the interaction between beach and construction (−403), percent of coastal scrub (−128), percent herbaceous cover (119), percent inland water (−99), and percent construction (75). However, for interpreting effect sizes, estimates need to be considered relative to each other, and back transformed for density estimates (i.e., given a 5% increase in both coastal scrub and herbaceous cover, we would expect a change of $e^{(0.05 \times (-128) + 0.05 \times (119))}$ or 0.6 burrows/ha in the survey area; Table 3). Of the model set evaluated for burrow occupancy ($n = 221$ scoped burrows), ΔAIC_c scores for all but the null model fell within 6 of the top model (Table S2).

Predictors accounting for differences between the older constructed dune and the natural dunes were included in all competing top models, so we incorporated varying occupancy rates based on the model with the lowest AIC_c score into the estimation of gopher tortoise densities. All top models for burrow occupancy had similar estimates, so the uncertainty in model selection did not alter estimates of tortoise density.

Table 3. Covariate estimates and standard errors (SE) for the top model for gopher tortoise burrow density, Merritt Island National Wildlife Refuge, central Florida, USA, 2014–2016. Estimates reported here represent the relative effect size of each land cover type on burrow density, and the direction (positive or negative) of that effect.

Covariate	Estimate	SE
Intercept	−1.93	0.532
% beach	18.05	2.072
% construction	75.65	8.557
% inland water	−99.51	13.771
% strand	−6.30	1.272
% Brazilian pepper	−22.38	3.655
% ruderal herbaceous	119.30	15.704
% scrub	−128.30	38.268
Beach \times construction	−403.13	54.585

Final estimated gopher tortoise density was highest at the 2012 dune (11–35, \bar{x} = 21 tortoise/ha), followed by the southern natural dune (2–22, \bar{x} = 8), the 2014 dune sections (North: 0–8, \bar{x} = 3; South: 0–12, \bar{x} = 2), and the northern natural dune with the lowest density estimate (0–3, \bar{x} = 0). Our models showed that burrow occupancy was also highest along the 2012 dune (0.58, SE = 0.28) compared to the 2014 dunes (0.39, SE = 0.23) and the natural dunes (0.27, SE = 0.23), although confidence intervals overlapped for all dune types.

DISCUSSION

As we predicted, estimates of gopher tortoise density generated by our top model were significantly higher for the constructed dunes versus natural dunes at MINWR, and the overall tortoise density for constructed dunes was similar to previously reported values for natural coastal tortoise populations elsewhere (0.64–3.05 burrows/ha, Lau and Dodd [2015]; 0–30.7 individuals/ha, Breininger et al. [1994b]). We found the first burrow on the 2014 dune approximately 3 months post-construction, with a rapid increase in burrows prior to the first transect being completed in the area. All 3 categories of land cover positively associated with tortoise density (beach, construction, ruderal vegetation) were characterized by higher proportions of open area and herbaceous plants compared to the other land cover types. The negative association with other land cover may be a result of the proliferation of woody scrub and invasive plants such as saw-palmetto (*Serenoa repens*), cabbage palm (*Sabal palmetto*), sea grape, and Brazilian pepper throughout the area (Diemer 1986, Menges 2007). Our results agree with those of Breininger et al. (1994b), who reported tortoise density at KSC to be positively associated with an increase in areas that were disturbed and supported herbaceous vegetation. Lau and Dodd (2015) also reported a significant, positive relationship between herbaceous cover and coastal tortoise burrow density.

Our study is the first to focus on the effects of newly created habitat; prior studies evaluated only natural land cover types and habitat disturbed by past roadway or building construction. When looking at parameter estimates for constructed habitat, although beach and construction are both open areas positively associated with gopher tortoise density, their interaction was negative and may reflect a lack of any nearby populations that might act as sources of migrants to the study area. Tortoises do not create burrows on the open beach at KSC but have been observed foraging on vegetation along the shoreline. The beach helps support tortoises, but it lacks resident tortoises to act as potential colonizers of the constructed dunes (S.A. Martin, Towson University, unpublished data). Documenting changes in the strength of this interaction via long-term monitoring would allow for evaluation of this explanation. The strong negative association of inland water with burrow density in the surrounding area reflects the fact that water does not provide habitat for tortoises and likely acts as a barrier to movement.

Areas of coastal strand and scrub along KSC are often overgrown with high densities of woody species (chiefly sea

grapes and saw-palmetto) that reduce the availability of basking and nesting sites for tortoises. Burns to manage natural areas within KSC and increase open areas with herbaceous cover would likely increase tortoise density in strand and scrub, shifting it from the reported negative effect size into a likely positive effect on tortoise density. Brazilian pepper is also unsuitable forage for tortoises, and is currently targeted for active herbicide-spraying by the USFWS at KSC. Results from this study reinforce previous research linking open sandy areas and herbaceous cover to increasing densities of coastal gopher tortoises in Florida (Breininger et al. 1994b, Lau and Dodd 2015). However, our results are based on only 2 years of surveys, representing a small fraction of the lifespan of a tortoise. The absence of any time-based parameters in the top models is likely due to tortoise density remaining stable along the natural dunes even as individuals moved into the constructed area from outside the transects. Our study also included only 3 constructed dunes along a single coastline, and local factors may influence results. Given these limitations, our study provides evidence of the beneficial effect of dune construction for tortoises. Although individual identity could not be verified for tortoises in burrows, all previously relocated tortoises had been marked before relocation, and incidental captures were a mixture of unmarked individuals and marked individuals that had previously been relocated to the natural areas surrounding the construction footprint.

Overall, dune construction was associated with higher gopher tortoise populations at our site, with burrow density rapidly equaling and surpassing the density at natural dunes. The density along the 2012 constructed dune may be a response by gopher tortoises to a lack of open areas along other stretches of beach, indicating the potential for further habitat improvement along the natural dunes (Breininger et al. 1994b). At KSC, the lack of long-term fire management due to protection of man-made structures is responsible for the proliferation of woody vegetation; recent efforts to remove the invasive Brazilian pepper as part of coastal scrub habitat restoration are likely to improve the surrounding natural coastline for gopher tortoises. Further management to improve habitat through small controlled burns aimed at promoting the growth of herbaceous vegetation would also help improve forage without negatively affecting other species in the area (Diemer 1986, Breininger and Smith 1992, Ashton et al. 2008).

As rises in sea-level, associated with climate change, increase, the need to improve coastal resilience will become more urgent. In areas where coastal retreat is not feasible, dune construction represents a potential management option to mitigate shoreline loss and improve coastal areas for wildlife (Klein et al. 2001). In October 2016, the coastal dunes along KSC were hit by Hurricane Matthew, allowing a preliminary examination of the resilience of man-made dunes. Although the southern natural dune (the natural dune with the highest tortoise density) was completely lost to storm damage, both the 2012 and 2014 constructed dunes survived with minimal loss of area (Fig. S2). The survival of both constructed dunes following a major storm highlights

the potential for dune construction as a management tool to promote coastal resilience and create habitat for gopher tortoises in the face of eroding coastlines.

MANAGEMENT IMPLICATIONS

Gopher tortoises in our study responded positively to the construction of dunes in the coastal environment of a barrier island, and tortoise density along 2- and 4-year-old dunes was greater than or equal to tortoise densities in nearby natural dunes. In our study, peak tortoise density was 21 tortoises/ha at the older constructed dune, compared to mean densities of 8 and 0 tortoises/ha for the natural dunes at our site. In situations where coastal tortoise populations are threatened, beach nourishment through dune construction represents a potential management strategy to mitigate habitat loss and improve existing coastal habitat.

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