



Research Article

Strategic Habitat Conservation for Beach Mice: Estimating Management Scenario Efficiencies

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ABSTRACT The Perdido Key beach mouse (*Peromyscus polionotus trissyllepsis*), Choctawhatchee beach mouse (*P. p. allopshrys*), and St. Andrew beach mouse (*P. p. peninsularis*) are 3 federally endangered subspecies that inhabit coastal dunes of Alabama and Florida, USA. Conservation opportunities for these subspecies are limited and costly. Consequently, well-targeted efforts are required to achieve their downlisting criteria. To aid the development of targeted management scenarios that are designed to achieve downlisting criteria, we developed a Bayesian network model that uses habitat characteristics to predict the probability of beach mouse presence at a 30-m resolution across a portion of the Florida Panhandle. We then designed alternative management scenarios for a variety of habitat conditions for coastal dunes. Finally, we estimated how much area is needed to achieve the established downlisting criterion (i.e., habitat objective) and the amount of effort needed to achieve the habitat objective (i.e., management efficiency). The results suggest that after 7 years of post-storm recolonization, habitat objectives were met for Perdido Key (within its Florida critical habitat) and Choctawhatchee beach mice. The St. Andrew beach mouse required 5.14 km² of additional critical habitat to be protected and occupied. The St. Andrew beach mouse habitat objective might be achieved by first restoring protected critical habitat to good dune conditions and then protecting or restoring the unprotected critical habitat with the highest predicted probability of beach mouse presence. This scenario provided a 28% increase in management efficiency compared to a scenario that randomly protected or restored undeveloped unprotected critical habitat. In total, when coupled with established downlisting criteria, these quantitative and spatial decision support tools could provide insight into how much habitat is available, how much more is needed, and targeted conservation or restoration efforts that might efficiently achieve habitat objectives. © 2020 The Wildlife Society.

KEY WORDS Bayesian network, beach mice, downlisting criteria, habitat objectives, *Peromyscus polionotus*, spatially explicit, strategic habitat conservation.

Many coastlines are predominantly sandy landscapes that are shaped by physical processes (e.g., sand supply and transport by wind and waves), ecological processes (e.g., sand trapping and accretion by vegetation), and recurring large natural disturbances (e.g., flooding, storms; Defeo et al. 2009, Arkema et al. 2013, Elko et al. 2016). These processes create a dynamic landscape that naturally erodes and recovers at different spatial and temporal scales, and support diverse and often specialized and endemic wildlife assemblages (Defeo et al. 2009, Elko et al. 2016). However,

human activities increasingly and disproportionately degrade and destroy coastal landscapes. Human population density is 3 times higher in coastal areas than inland areas, and coastal erosion and flooding are expected to increase because of sea-level rise and greater frequency of intense storms (Small and Nicholls 2003, Holgate and Woodworth 2004, Feagin et al. 2005, Defeo et al. 2009, Arkema et al. 2013). These stressors negatively affect coastal wildlife, which are often threatened or endangered species, by increasing mortality and making their habitats rare or unsuitable (i.e., unable to support growth, survival, and reproduction; Defeo et al. 2009, Elko et al. 2016, Marcot et al. 2020). Consequently, linking wildlife to coastal landscape characteristics is important for coastal planners

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and natural resource managers to prioritize areas and management actions.

Beach mice are subspecies of the old field mouse (*Peromyscus polionotus*) that occur in the Atlantic and northern Gulf of Mexico coastal landscapes (U.S. Fish and Wildlife Service [USFWS] 1987). The Perdido Key beach mouse (*P. p. trissyllepsis*), Choctawhatchee beach mouse (*P. p. allophrys*), and St. Andrew beach mouse (*P. p. peninsularis*) inhabit coastal dunes in Alabama (USFWS 1987) and the Florida Panhandle, USA (Fig. 1). The Perdido Key and Choctawhatchee beach mice were listed as endangered in 1985 (USFWS 1987) and the St. Andrew beach mouse was listed as endangered in 1998 (USFWS 2010) via the United States Endangered Species Act. Human development and recreation in coastal systems may cause land use conflicts and make it economically difficult to conserve these areas because of high land prices (Shogren et al. 1999, Defeo et al. 2009). Given the limited ranges of beach mice (Fig. 1) and high desirability for coastal landscapes by humans (Defeo et al. 2009, Falcy and Danielson 2014), conservation and restoration opportunities are limited and associated with high costs. Consequently, achieving beach mice downlisting criteria will hinge on the development and implementation of management scenarios that can efficiently target areas for conservation and restoration actions.

Beach mice downlisting criteria focus on critical habitat (i.e., specific geographic areas that contain features essential for the conservation of a listed species and may require special management and protection; USFWS 2020), stating that Perdido Key, Choctawhatchee, and St. Andrew beach mice must have distinct, self-sustaining populations within their respective critical habitat (USFWS 2006a) and that a minimum percentage of each subspecies' critical habitat must be protected and occupied by that subspecies (50% for Perdido Key and Choctawhatchee beach mice, USFWS 1987; 87% for St. Andrew beach mouse, USFWS 2010). Meeting these criteria is inhibited by human development and intense storms (Falcy and Danielson 2014).

Beach mice make burrows in sand dunes (Lynn 2000, Sneckenberger 2001) and are primarily granivores that forage in the dark to minimize predation risk (Lima and Dill 1990). Their abundance is generally greatest in frontal

dunes (i.e., foredune or primary dune), with scrub dunes (i.e., secondary and tertiary dune) typically functioning as population sinks when abundance in frontal dunes is high (Swilling et al. 1998). After storm events that degrade or destroy frontal dunes, scrub dunes can function as a population source for recolonization of frontal dunes once they recover (Pries et al. 2009). Additionally, when food supply in frontal dunes is low, scrub dunes can also serve as a reserve food source (Sneckenberger 2001). Thus, development in scrub dunes reduces refugium and food availability, which may negatively affect survival. Development is associated with non-natural light at night (Eisenbeis and Hänel 2009, Gaston et al. 2012), which reduces foraging efficiency by increasing perceived predation risk (Bird et al. 2004, Wilkinson et al. 2013). Development can increase the presence of free-ranging cats (Thomas et al. 2014), which decreases beach mice survival (Frank 1996). Vehicle and foot traffic associated with development can uproot vegetation and destabilize dunes (Craig 1984, Santoro et al. 2012).

Development and storms can fragment coastal dune systems and isolate scrub dune from frontal dune. Fragmentation and isolation further reduce refugia, food, and the ability of beach mice to recolonize dunes recovering from intense storms (Pries et al. 2009, Falcy and Danielson 2014). These reductions in habitat availability may be exacerbated by an increase in the frequency of intense storms (Knutson et al. 2010, Falcy and Danielson 2014). Dune systems recover from major storms on a time scale of years to decades (Oli et al. 2001, Reed and Traylor-Holzer 2006, Falcy and Danielson 2014, Houser et al. 2015) or sooner if restoration actions are implemented (Defeo et al. 2009, Elko et al. 2016). A combination of increased development, sea-level rise, and frequency of intense storms is expected to increase extinction risk due to habitat loss and fragmentation, which may inhibit dune formation (Holgate and Woodworth 2004, Feagin et al. 2005) and prevent beach mice from finding refuge in scrub dunes during storms or recolonizing frontal dunes after storms (Falcy and Danielson 2014).

Beach mouse presence is generally expected to increase from the poorest dune conditions (e.g., scrub dune that is

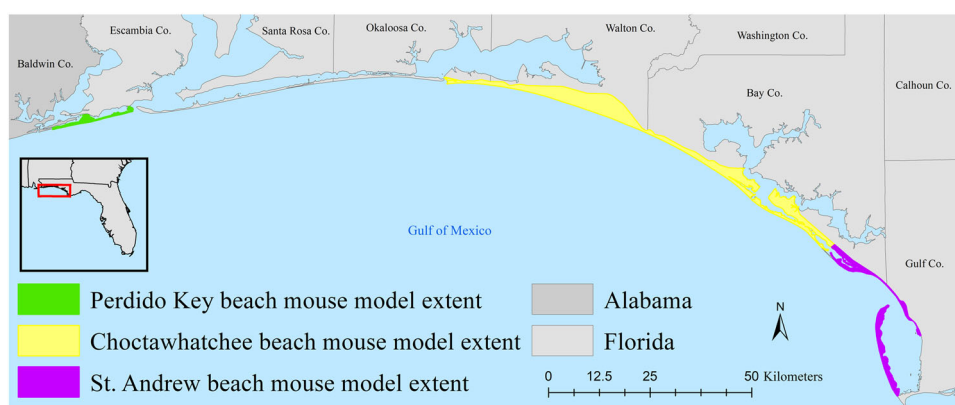


Figure 1. Study area for the Perdido Key, Choctawhatchee, and St. Andrew beach mice in Florida, USA, 2009–2014.

isolated from other dunes, near human development, light pollution and cats present) to ideal dune conditions (e.g., frontal dunes adjacent to scrub dunes, far from development, no light pollution or cats) with sufficient time since the last intense storm for maximum recolonization (USFWS 1987, 2010, Pries et al. 2009, Falcy and Danielson 2014). Consequently, management scenarios often consider actions intended to improve habitat for beach mice, including stabilizing dunes, protecting dunes from human disturbance, connecting frontal dune to scrub dune, depositing sand to restore eroded coastline, cat control measures, and light pollution control (Carlson and Godfrey 1989, Frank 1996, Sneckenberger 2001, Bird et al. 2004, Speybroeck et al. 2006).

Previous studies focused on the ability of beach mice to maintain self-sustaining populations by estimating extinction risk as a function of human development and storms (Oli et al. 2001, Falcy and Danielson 2014). But managers lack estimates on how much area is needed to achieve the subspecies downlisting criteria (i.e., habitat objectives; National Ecological Assessment Team 2006). Although critical habitat was designated for all 3 subspecies (USFWS 2006a) and protected areas are known, extinction risk and occupancy must be inferred from surveys at a limited number of field sites (Holler et al. 1989, Oli et al. 2001, Van Zant and Wooten 2003, Falcy and Danielson 2014). Moreover, the amount of effort needed to meet the habitat objectives (i.e., management efficiency) remains unknown.

Management scenarios that use predictive models of beach mouse presence to prioritize critical habitat for conservation actions may be more efficient compared to the common practice of opportunistically protecting and restoring areas (Endicott 1993, Margules and Pressey 2000). Management efficiency might also be increased by prioritizing dune restoration in protected critical habitat over protecting more critical habitat. Estimating habitat demand and the efficiency of management scenarios can help managers justify targeted conservation actions designed to mitigate stressors. Bayesian network models have been developed on a wide variety of environmental, ecological, species-specific, and management issues (McCann et al. 2006, Nyberg et al. 2006), including evaluations of tidal-marsh bird densities in the northeastern United States (Wiest et al. 2019) and salt marsh harvest mice (*Reithrodontomys raviventris*) in San Francisco Bay, coastal California, USA (Marcot et al. 2020).

Our goal was to aid strategic habitat conservation of beach mice by estimating management plan efficiencies using a spatially explicit framework. We hypothesized that the probability of beach mouse presence increases from poorest to ideal dune conditions with sufficient time since the last intense storm for maximum recolonization. We predicted that management plan efficiency would be lowest for management scenarios that randomly protect or restore critical habitat, and greatest for management scenarios that prioritize the protection or restoration of critical habitat with the highest probability of beach mice presence.

STUDY AREA

We conducted this study using data that were collected from 2009 to 2014 in portions of Florida that included or were adjacent to Perdido Key beach mouse (13.29 km²), Choctawhatchee beach mouse (225.77 km²), and St. Andrew beach mouse habitat (54 km²; Fig. 1). The climate was Humid Subtropical (i.e., warm and moderately wet spring [Mar–May], hot and wet summer [Jun–Sep], warm and dry fall [Oct–Dec] and winter [Jan–Feb]), with a mean annual high temperature of 25°C, mean annual low temperature of 15°C, and a mean annual precipitation of 155 cm. The study area included unprotected and protected (i.e., conservation estate, easements) areas, and areas that have and have not been designated as critical habitat for the 3 subspecies (Fig. 2). The topography and land use within these areas was varied, with sand dunes interspersed among natural non-dune areas (e.g., grassland, pine forest, wetland) and areas of intense human development (e.g., roads, buildings; Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory 2014). The dune system included frontal dune, scrub dune, interdune sandflats, and wet swales (Pries et al. 2009, Wilkinson et al. 2012). Frontal dunes were located immediately adjacent to the mean higher high tide line and were characterized by the presence of sea oat (*Uniola paniculata*), which traps wind-blown sands that mound, leading to dune formation (Johnson and Barbour 1990). Scrub dunes were located farther from the shoreline behind frontal dunes, often reached elevations >30 m, and supported woody vegetation such as saw palmetto (*Serenoa repens*) and sand live oak (*Quercus geminata*; Pries et al. 2009). Fauna included arthropods (e.g., *Ocyrops* spp.), reptiles (e.g., nesting loggerhead sea turtles [*Caretta caretta*]), birds (e.g., gull-billed terns [*Gelochelidon nilotica*]), and mammals (e.g., domestic cats). Habitats for all 3 subspecies were prone to disturbance by intense storms (i.e., tropical hurricanes with max. sustained winds ≥178 kph). Choctawhatchee beach mouse and St. Andrew beach mouse habitats were altered by Hurricane Opal in 1995 (National Oceanic and Atmospheric Administration 1995), Hurricane Ivan directly hit Perdido Key beach mouse habitat in 2004 (National Oceanic and Atmospheric Administration 2004), and in 2018 Hurricane Michael made landfall at the boundary of Choctawhatchee and St. Andrew beach mice ranges (National Oceanic and Atmospheric Administration 2018). Previous studies in or adjacent to our study area suggested that habitat recovered 5–10 years after a storm (Oli et al. 2001, Falcy and Danielson 2014, Houser et al. 2015).

METHODS

Below we provide a general overview of methods. A detailed description is provided in a supplemental model development file and code is provided in a supplemental model development R script (R version 3.5.2, R Foundation for Statistical Computing, Vienna, Austria) and a supplemental model application R script, which are available online in Supporting Information. The data sets and Bayesian

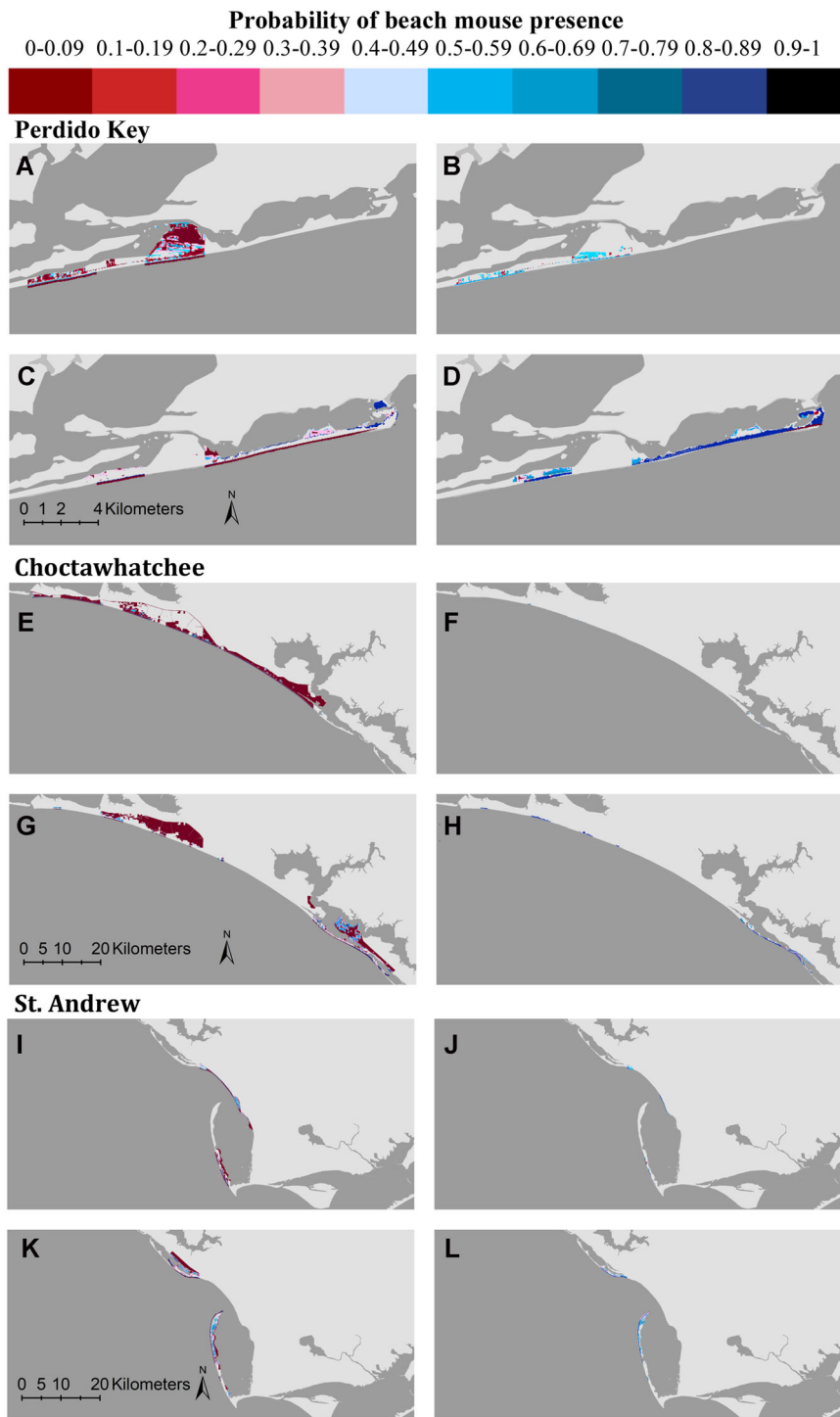


Figure 2. Expected probability of beach mouse presence for the Perdido Key, Choctawhatchee, and St. Andrew beach mice unprotected non-critical habitat (A, E, I), protected non-critical habitat (C, G, K), unprotected critical habitat (B, F, J), and protected critical habitat (D, H, L) in Florida, USA, 2011.

network model (Netica® 5.12, Norsys Software Corporation, Vancouver, Canada) are publicly available on ScienceBase (Cronin et al. 2020).

Beach Mice Detection and Non-Detection Data

We obtained monthly track tube data from 2009 (5 yrs after Hurricane Ivan) to 2014 (10 yrs after Hurricane Ivan) for Perdido Key State Park and the Gulf Islands National Seashore from the Florida Fish and Wildlife Conservation

Commission (J. A. Gore, Florida Fish and Wildlife Research Institute, unpublished data). We excluded track tube data in the Alabama portion of Perdido Key (~9% of Perdido Key Beach mouse range) because the available Alabama land cover was insufficient for our analyses. The track tube detection method used baited tubes that contained ink and paper to mark mouse tracks and was described by Loggins et al. (2010) and Greene et al. (2018). No animals were trapped or handled in this study and we

followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007, Sikes et al. 2011).

At Perdido Key State Park, 81 tubes were placed in a grid, with 100 m between tubes. At Gulf Islands National Seashore, 80 tubes were placed in groups of 5 along linear transects parallel to the shore, with 100-m spacing between tubes within a group and 500-m spacing between groups. If a track tube had signs of beach mouse use at a sample location during any month in a given year, then we classified beach mouse presence at that location in that year as detected; otherwise, we classified presence as undetected. Based on the geospatial land cover data, track tubes were located in frontal dune ($n = 81$), scrub dune ($n = 56$), natural non-dune ($n = 17$), non-road development ($n = 2$), and road development ($n = 5$) but not in water ($n = 0$).

Because the track tube survey was primarily conducted in frontal and scrub dune, we supplemented the field survey with non-dune Perdido Key locations that we randomly selected and designated them as beach mice undetected. The sample size (40 random locations at each of 4 non-dune land cover classes = 160) was a standardized value chosen to match the observed track tube sample size ($n = 161$). This prevented the model from predicting that mice were present in water and decreased the probability that mice occur in the other non-dune areas. Thus, although the model allows beach mice to be present in natural non-dune, non-road development, and road development land cover types, where the probability of presence depends on neighborhood suitability, we acknowledge that the model may underestimate presence in these land cover types because of false negatives. It might also underestimate presence because our methodology does not explicitly account for detection probability. Two beach mice experts (J. A. Gore, Florida Fish and Wildlife Research Institute; K. R. Yanchis, USFWS Ecological Services Office, personal communication), expressed that the track tube detection rates for beach mouse presence across a year are near 100% (i.e., if a population of beach mice is present and track tubes are in place throughout the year, there will be ≥ 1 detection).

Model Development

We identified habitat characteristics that may influence beach mouse presence through a review of beach mouse recovery plans, 5-year reviews, and primary literature (Table 1). We represented hypothesized relationships among habitat characteristics and beach mouse presence in the form of a draft influence diagram, which represents variables as nodes (i.e., boxes) and influences as links (i.e., arrows). Four beach mice experts participated in interactive explanation and discussion sessions where they revised the draft influence diagram (i.e., modified, added, or removed nodes and links). The experts included 1 beach mouse biologist (S. L. Sneckenberger, USFWS South Florida Ecological Service Field Office), 1 geospatial analyst (P. A. Lang, USFWS Ecological Services Office), and 2 beach mice managers (K. R. Yanchis, USFWS Ecological Services Office; B. J. Lynn, USFWS Alabama Ecological Services Field Office). This process identified 17 nodes (Fig. 3A)

that we hypothesized to either directly or indirectly influence beach mouse presence at a site (Table 1). Local suitability accounted for site-level characteristics that determine the ability of mice to burrow and acquire food, and the presence of cats. If mice are present in the surrounding neighborhood, they can disperse through non-suitable land cover types (i.e., natural non-dune, roads, non-road development). Mice do not disperse through water. Thus, an interaction between neighborhood suitability and land cover accounted for why mice can be present in non-suitable land cover types and not in water. Finally, post-storm recolonization and distance to refugia accounted for why mice can be absent from suitable sites and neighborhoods.

We translated the influence diagram into a Bayesian network model that predicts the annual probability of beach mouse presence at a 30-m resolution (Fig. 3B). We delineated subspecies model extents using the range descriptions included in each subspecies' recovery plan (USFWS 1987, 2010), from Florida's Gulf of Mexico coastline inland to the first United States or County Highway and across St. Joseph Bay into the Gulf of Mexico through Lighthouse Bayou (Fig. 1). We delineated critical habitat using USFWS's (2006a) designation of critical habitat for all 3 subspecies. We delineated protected areas using protected area databases (Conservation Biology Institute 2012, The Nature Conservancy 2015). We conducted all spatial data manipulations in ArcMap 10.5 (Esri, Redlands, CA, USA). We used geospatial inputs that were native or resampled to 30-m resolution unless otherwise specified.

The model contained nodes derived from existing geospatial data (i.e., nodes prefaced with input), nodes for which no geospatial data existed and were therefore predicted by the model, and a temporal node (i.e., post-storm recolonization; Fig. 3B). The model did not include the distance to refugium variable (Fig. 3A). Removing a node can introduce bias in the effects of other variables because the removed node's influence is uncontrolled. We chose to remove distance to refugium, however, because it is not important for the time period that we conducted our study. The effect of distance to refugium has the greatest potential to influence beach mice presence in years immediately following a flood, and its effect diminishes 5 years after a storm because frontal dunes have regenerated enough to allow for recolonization. Our study began 5 years after the last major storm and the track tube data showed that beach mice presence recovered by year 7. This suggested that removing distance to refugium is unlikely to have biased the results in years 5 and 6, and did not bias the results in year 7, which was most relevant to the downlisting criteria. The model also included 2 additional variables, critical habitat and protected status, to incorporate prior information about habitat characteristics specific to each subspecies (Fig. 3B).

Each node was discretized into unique classes and contained a table that expressed the probability of each class as either an unconditional prior probability distribution or a conditional probability distribution given the nodes that directly influence it (Marcot et al. 2006). We used a uniform unconditional prior probability distribution for post-storm

Table 1. Rationale for hypothesized relationships in the influence diagram for the Perdido Key, Choctawhatchee, and St. Andrew beach mice in Florida, USA, 2009–2014.

Response variable	Predictor variable	Rationale for hypothesized relationship
Beach mouse presence	Local suitability	Mice are more likely to use sites that are suitable for growth, survival, and reproduction (USFWS 2006 <i>b</i> , 2007, 2009, 2010, 2014).
	Neighborhood suitability	Mice are more likely to access sites that are surrounded by higher suitability sites (USFWS 2010).
	Post-storm recolonization	Mice are absent from suitable sites if they have not recolonized the landscape (Swilling et al. 1998).
	Land cover	If mice are present in the surrounding neighborhood, they might disperse through natural non-dune, roads, and non-road development, but not water.
	Distance to refugia	Mice are more likely to recolonize dunes near refugium (non-flooded areas) after a flood (Pries et al. 2009, Chen et al. 2014).
Local suitability	Burrow suitability	Mice require burrows for survival and reproduction (Lynn 2000).
	Realized food availability	Mice require food resources that are both present and accessible for survival and reproduction (USFWS 2010).
Burrow suitability	Cat presence	Cat predation decreases mice survival (Frank 1996).
	Land cover	Burrows cannot be made at natural non-dune, water, and human developed sites (Lynn 2000, Sneckenberger 2001).
	Slope	Slope determines burrow site selection in scrub dune sites but not frontal dune sites (Sneckenberger 2001).
Realized food availability	Food supply	Food resources must be present at the site if they are to be available to mice.
	Light pollution	Artificial light at night reduces the accessibility of food via increased perceived predation risk (Bird et al. 2004, Wilkinson et al. 2013).
Food supply	Land cover	Food resources are unavailable at natural non-dune, water, and developed sites (Sneckenberger 2001).
	Dune heterogeneity	Food supply is greater at sites with access to both frontal dunes, which supply food in winter and spring, and scrub dunes, which supplement food during summer and fall (Sneckenberger 2001, USFWS 2010).
Light pollution	Light guidance	Zoning guidance and ordinances restrict non-natural night light at a site or adjacent sites (USFWS 2010).
	Non-natural night light	Light fixtures increase the amount of night light at a site or adjacent sites (Longcore and Rich 2004).
Cat presence	Distance to non-road development	Cat presence is greater near non-road development (Thomas et al. 2014).
	Active cat capture	Programs that actively capture and remove cats decrease cat abundance (Oppel et al. 2014, Robley et al. 2010).
Distance to non-road development	Land cover	Sites that are classified as non-road development are located 0 m from non-road development.
Non-natural night light	Land cover	Sites with human development land cover classes are more likely to have light fixtures (Eisenbeis and Hänel 2009).
	Distance to non-road development	Sites near non-road development are more likely to receive light from light fixtures (Gaston et al. 2012).
Dune heterogeneity	Land cover	Non-dune sites cannot have dune heterogeneity.
Slope	Land cover	Dune sites are more likely to have higher slopes compared to non-dune sites.

recolonization. We modeled the unconditional prior probability table for beach mice critical habitat and the conditional probability tables (CPTs) for the remaining input nodes using geospatial data sets and Netica's incorporate case file function. The biologist completed conditional probability tables for 3 endogenous predicted nodes (burrow suitability, realized food availability, local suitability). We showed the expert the influence diagram and the CPT, which was either partially or fully completed with values that were documented from simplifying assumptions, literature-derived empirical values, and the beach mice detection and non-detection data. The expert accepted, modified, or provided probabilities given their knowledge of beach mice ecology. We used a feedback process, where we provided the expert session materials and notes after each session and conducted follow-up sessions and reviews to ensure consistency of their response (Kuhnert et al. 2010). When the expert expressed uncertainty, the interviewer instructed them to include that uncertainty in the CPT

by distributing the probabilities over >1 outcome (Marcot 2017). The light pollution CPT was deterministic, whereas the food supply and cat presence CPTs were based on simplifying assumptions and prior published data (Branch et al. 2011, Metsers et al. 2010). Finally, we modeled the beach mouse presence CPT using Netica's incorporate case file function and a case file that contained beach mouse detection, post-storm recolonization, land cover, neighborhood suitability, and local suitability classes. We then assumed that beach mice could never be present in water, could never be present in non-dune if both local and neighborhood areas were not suitable, and had a 50% probability (complete uncertainty) of being present in frontal dunes if neighborhood suitability was low and the local area was not suitable. We assumed that the model's relationships, including those learned from the Perdido Key beach mouse detection and non-detection data, did not differ among the 3 sub-species, that is, that the same causal factors influenced the 3 subspecies in the same way

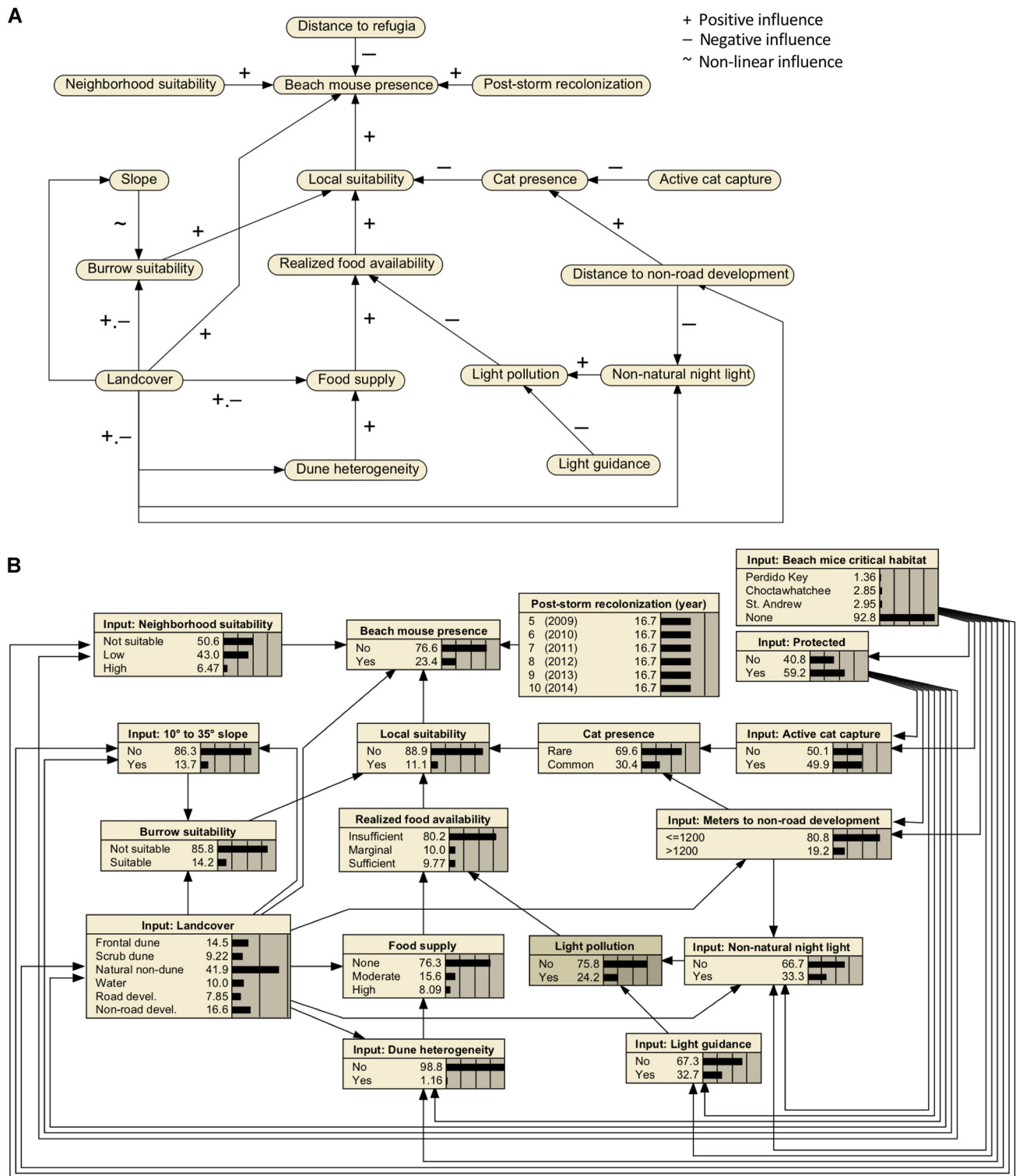


Figure 3. A) Influence diagram and B) Bayesian network model for the Perdido Key, Choctawhatchee, and St. Andrew beach mice in Florida, USA, 2009–2014.

(USFWS 2014). We then generated spatially explicit predictions for each beach mouse by feeding the geospatial inputs into the model.

Model Evaluation

We evaluated model performance using confusion matrix error rates (Marcot 2012), which compared the observed

track tube data to the model's predicted beach mouse presence (not accounting for the expert-elicited occupied threshold; see below). Independent data sets were unavailable to validate the model. In these situations, a model's veracity is established by peer review of the model at various stages of development (Marcot and Penman 2019). Therefore, all 4 experts visually inspected

the influence diagram, model behavior, and spatial outputs. Although the model behavior generally met their expectations, the review sessions resulted in the addition of the link from land cover to beach mice presence and the links among input variables (Fig. 3A). The spatial outputs were also generally consistent with their knowledge of beach mouse presence. The reviews determined that there were several locations on Perdido Key where the model's predicted beach mice presence was lower than expected because of land cover misclassifications. We did not correct the misclassification because it was located in a small area and would not change the result that the Perdido Key beach mouse habitat objective was already met.

We used sensitivity analyses to rank input variables by the degree to which they reduced uncertainty in the probability of beach mouse presence (Marcot 2012). Sensitivity results of the input variables helped identify where data collection efforts could be concentrated for factors that might be less well known or specified and could have greater influence on outcomes, particularly those factors potentially controllable by management (Marcot 2012). We conducted sensitivity analyses using Netica's sensitivity to findings function, which calculated the mutual information between beach mice presence and itself (MI_{BM}) or input variables (MI_i), and the percent reduction ($\frac{MI_i}{MI_{BM}}$), where greater mutual information and percent reduction values indicated that knowing an input variable's class more strongly reduced uncertainty about beach mice presence (Marcot et al. 2006). We conducted sensitivity analyses for either typical critical habitat (Fig. S3, available online in Supporting Information) or a typical dune critical habitat condition (Fig. S4, available online in Supporting Information). Typical critical habitat specified all combinations of critical habitat and post-storm recolonization, while all other input nodes were set to their default prior probabilities. Typical dune critical habitat also specified all combinations of critical habitat and post-storm recolonization, and additionally specified that land cover could only be frontal dune or scrub dune and neighborhood suitability could not be not suitable (i.e., frontal and scrub dunes in critical habitat do not

occur in the neighborhood suitability class not suitable; Table S9, available online in Supporting Information).

Model Application

Effects analyses.—Effects analyses quantified the effect of specifying input nodes on the probability of beach mouse presence. Consequently, the results from the effects analyses can be used to identify management actions with the potential to increase the probability of beach mouse presence. We conducted effects analyses separately for frontal and scrub dune by specifying poor, typical, good, and ideal conditions (Table 2; Fig. S5–S12, available online in Supporting Information) for all combinations of critical habitat, protected, and post-storm recolonization, and then recording the predicted probability of beach mouse presence. The poor condition set input variables at low-quality classes (e.g., no zoning guidance restricting non-natural light). The typical condition was indicative of the expected habitat quality across the landscape (i.e., input variables set at their normative prior probability distributions). The good condition set input variables that are relatively easy to influence at high-quality classes (e.g., light guidance), whereas this conduction did not adjust variables (i.e., did not enter evidence) that are relatively difficult to influence (e.g., distance to non-road development). The ideal condition set all input variables at high-quality classes. Frontal and scrub dune had many of the same specifications per condition (Table 2). We considered low neighborhood suitability to be the poor condition for frontal dune (i.e., a frontal dune in a neighborhood dominated by scrub dunes) but the good or ideal condition for scrub dune (i.e., a scrub dune in a neighborhood dominated by scrub dunes; Table 2). Conversely, we considered high neighborhood suitability to be the good or ideal condition for frontal dune (i.e., a frontal dune in a neighborhood dominated by frontal dunes) but the poor condition for scrub dune (i.e., a scrub dune in a neighborhood dominated by frontal dunes; Table 2). This reflected the relatively higher quality of frontal dune neighborhoods that extended inland toward extensive lower-quality scrub dune neighborhoods (Falcu and Danielson 2014). Additionally, we specified slope for

Table 2. Each condition's habitat characteristic specifications used in the effect analyses of the Bayesian network model for the presence of Perdido Key, Choctawhatchee, and St. Andrew beach mice in Florida, USA, 2009–2014.

Condition	Land cover	Night light	Dune heterogeneity	Slope	Neighborhood suitability	Active cat capture	Distance to NRD ^a (m)	Light guidance
Poor frontal	Frontal	Yes	No	Prior ^b	Low	No	≤1,200	No
Poor scrub	Scrub	Yes	No	No	High	No	≤1,200	No
Typical frontal	Frontal	Prior	Prior	Prior	Low, high ^c	Prior	Prior	Prior
Typical scrub	Scrub	Prior	Prior	Prior	Low, high	Prior	Prior	Prior
Good frontal	Frontal	Prior	Prior	Prior	High	Yes	Prior	Yes
Good scrub	Scrub	Prior	Prior	Yes	Low	Yes	Prior	Yes
Ideal frontal	Frontal	No	Yes	Prior	High	Yes	>1,200	Yes
Ideal scrub	Scrub	No	Yes	Yes	Low	Yes	>1,200	Yes

^a Non-road development.

^b We did not enter a class as evidence.

^c We set the probability that neighborhood suitability was not suitable to zero.

scrub dune as either no for the poor condition or yes for good and ideal conditions (Table 2). Finally, the good condition did not specify distance to non-road development, non-natural night light, and dune heterogeneity (Table 2) because managers might only be able to influence these habitat characteristics under ideal conditions (Table 2).

Habitat demand.—We predicted the probability of beach mouse presence for the entire study area from the model (Fig. 3B) using Netica's process cases function to analyze a case file for the entire study area, where each row contained values for all geospatial inputs for a single pixel in a given year. We calculated habitat objectives by first scoring (s) each pixel as occupied or unoccupied:

$$s = \begin{cases} \text{unoccupied if } y < 0.7 \\ \text{occupied if } y \geq 0.7 \end{cases}, \quad (1)$$

where y is the model-predicted probability of beach mouse presence (the dominant probability outcome), and 0.7 is an expert-elicited threshold to reflect a hypothetical manager's acceptable uncertainty of beach mouse presence (i.e., the lowest predicted probability of beach mouse presence in which the expert felt confident judging a pixel as occupied by beach mice). This threshold could be increased or decreased to reflect a manager's acceptable uncertainty of beach mouse presence. We calculated habitat objectives (H) as:

$$H = C_T \times R, \quad (2)$$

where C_T is the subspecies' total critical habitat area, and R is the subspecies' minimum percentage downlisting criteria (50% for Perdido Key beach mouse and Choctawhatchee beach mouse or 87% for St. Andrew beach mouse). The habitat demand (H_d) is the deficit or surplus area relative to the downlisting criteria, which we calculated as:

$$H_d = H - C_{PO}, \quad (3)$$

where C_{PO} is the subspecies critical habitat area that was protected and scored as occupied (i.e., Fig. 2D, H, or L with $y \geq 0.7$). A negative value of H_d denotes a surplus of area relative to the downlisting criteria, which indicates that the habitat demand is met. A positive value of H_d denotes an area deficit relative to the downlisting criteria, which indicates the habitat demand is not met. Only the St. Andrew beach mouse's habitat demand remained positive after 2010 (i.e., criteria not achieved after 7 years of post-storm recolonization), when the model's results were stable and most relevant to the downlisting criteria. These conclusions were insensitive to varying the expert's threshold from 0.8 to 0.35 (Fig. S13). Therefore, we estimated management scenario efficiencies for St. Andrew beach mouse.

Total weighted area and management scenario efficiencies.—To determine if the habitat demand for St. Andrew beach mouse might be met given the current characteristics of its critical habitat (i.e., current scenario), we estimated the total weighted area (W) from its protected critical habitat areas scored as unoccupied (i.e., Fig. 2L with $y < 0.7$) and

unprotected critical habitat areas (Fig. 2J). We chose this sample area because it is not accounted for in C_{PO} and, thus, has restoration or conservation potential to help meet the habitat demand. In this sample area, we first calculated each pixel's weighted area (km^2) value (w) as:

$$w = \begin{cases} 0.0009 \times y \text{ if } y < 0.7 \\ 0.0009 \times 1 \text{ if } y \geq 0.7 \end{cases}, \quad (4)$$

where 0.0009 is the area (km^2) of a 30-m pixel, and 0.7 is the expert-elicited occupied threshold. We then calculated the total weighted value for the sample area ($W = \sum_{i=1}^N w_i$). Many areas had a small y and, consequently, W was unable to equal or exceed the habitat demand (i.e., $W < H_d$). When this occurs, the habitat demand can never be met under the current scenario. Therefore, we implemented hypothetical management scenarios in St. Andrew beach mouse's critical habitat that restored dunes using the effect analyses' good conditions, which increased y to ≥ 0.7 , or protected dunes, and then we recalculated C_{PO} and H_d . To determine how to reach the habitat demand, we considered 4 management scenarios: scenario 1 restored dunes in protected critical habitat, scenario 2 protected dunes in unprotected critical habitat, scenario 3 restored and protected all dunes in critical habitat, and scenario 4 restored dune, natural non-habitat, and water in protected critical habitat. We then either randomly subsampled the area (representing a random, opportunistic strategy) or randomly subsampled the area from greatest y values to smaller y values (representing a targeted strategy) until W equaled or exceeded H_d and calculated the subsample size N (i.e., number of pixels) needed satisfy $W \geq H_d$. We calculated management efficiency (E) as the area of the sampled area, or:

$$E = 0.0009 \times N, \quad (5)$$

where lower values of E indicate greater efficiency in area restored or protected. Management efficiency is reported as the mean and standard deviation from the random or targeted sampling process conducted 1,000 times (N samples each).

RESULTS

The model was a good fit to the observed track tube data (2009: 22% error rate; 2010: 18% error rate; 2011, 2012, 2013, and 2014: 15% error rates). Sensitivity analyses of the beach mouse presence node for typical critical habitat (upper halves of Tables 3–5) suggested that sensitivities to input nodes generally increased from 2009 to 2011, land cover had the greatest sensitivity influence, and the percent increase of sensitivity to land cover from 2009 to 2011 was greatest for Perdido Key beach mouse and smallest for St. Andrew beach mouse. Sensitivity to the 10 input nodes was greatest for Perdido Key beach mouse and similar for the Choctawhatchee and St. Andrew beach mice (upper halves of Tables 3–5). These results did not change after 2011 (i.e., 7 years of post-storm recolonization). For typical dune critical habitat, sensitivities generally increased from 2009 to

Table 3. Sensitivities of beach mouse presence to typical condition and typical dune condition inputs for the Perdido Key beach mouse in Florida, USA, 2009–2014. Greater mutual information and percent reduction values indicate that knowing the variable's class more strongly reduces uncertainty about beach mice presence compared to variables with lower sensitivity values. A greater percent change in a variable's sensitivity from 2009 to 2011 indicates that knowing the variable's class more strongly reduces uncertainty of beach mice presence with more time since the last major storm.

Variable	Year						Change from 2009 to 2011 (%)
	2009		2010		2011–2014		
	Mutual information	% reduction	Mutual information	% reduction	Mutual information	% reduction	
Typical condition							
Land cover	0.105	10.500	0.138	14.800	0.138	14.900	42
Protected	0.006	0.552	0.020	2.100	0.021	2.240	306
Active cat capture	0.006	0.551	0.020	2.100	0.021	2.240	307
Light guidance	0.006	0.551	0.020	2.090	0.021	2.240	307
Distance to NRD ^a	0.011	1.060	0.018	1.970	0.018	1.940	83
Night light	0.007	0.692	0.015	1.570	0.016	1.680	143
Neighborhood suitability	0.003	0.335	0.003	0.299	0.003	0.340	1
Slope	0.003	0.277	0.002	0.189	0.001	0.158	−43
Dune heterogeneity	0.000	0.017	0.001	0.072	0.001	0.084	394
Total		14.54		25.19		25.82	78
Typical dune condition							
Active cat capture	0.004	0.455	0.022	2.630	0.024	2.840	524
Protected	0.005	0.456	0.022	2.630	0.024	2.840	523
Light guidance	0.004	0.455	0.022	2.620	0.024	2.830	522
Land cover	0.022	2.250	0.025	2.890	0.020	2.430	8
Distance to NRD	0.005	0.502	0.011	1.300	0.010	1.250	149
Night light	0.000	0.040	0.003	0.332	0.003	0.367	813
Neighborhood suitability	0.001	0.110	0.001	0.074	0.001	0.103	−6
Dune heterogeneity	0.000	0.002	0.000	0.004	0.000	0.007	375
Slope	0.001	0.100	0.000	0.011	0.000	0.001	−99
Total		4.37		12.49		12.67	190
Land cover change (%)		−79		−80		−84	
Total change (%)		−70		−50		−51	

^a Distance to non-road development (m).

2011 (lower halves of Tables 3–5). Compared to typical critical habitat, typical dune critical habitat sensitivities were lower: the percent decrease in sensitivities to land cover in 2011 ranged from –84% to –86% (Tables 3–5) and the percent decrease in total sensitivity to all 10 inputs ranged from –51% to –82% (Tables 3–5). These results also did not change after 2011.

The effect analyses suggested that the probability of beach mouse presence was generally greater in frontal dune compared to scrub dune under all conditions and greater in protected areas compared to unprotected areas under typical dune conditions (Fig. 4). In frontal dune, probability of beach mouse presence in 2009 was 0.55 to 0.6, and the probability of beach mouse presence responded weakly from poor to good conditions and never exceeded 0.7 (Fig. 4A–C). By 2010 and 2011, the probability of beach mouse presence in frontal dune increased from poor conditions to ideal conditions and exceeded 0.7 under good conditions in unprotected and protected areas (Fig. 4A–C). The ideal conditions provided little benefit over the good conditions (Fig. 4A–C). In scrub dune, the probability of beach mouse presence was also near complete uncertainty in 2009, and the probability of beach mouse presence decreased from poor to ideal conditions and never exceeded 0.7 (Fig. 4D–F). In 2010 and 2011, the probability of beach mouse presence in scrub dune generally increased from poor conditions to ideal conditions and exceeded 0.7 under good

conditions in unprotected and protected areas (Fig. 4D–F). These results did not change after 2011.

The habitat objectives were 2.32 km² for Perdido Key beach mouse, 4.87 km² for Choctawhatchee beach mouse, and 8.76 km² for St. Andrew beach mouse (Table 6). In 2009, after 5 years of post-storm recolonization, none of the protected critical habitat was scored as occupied (i.e., $y < 0.7$) for any subspecies (Table 6; Tables S10–S12, available online in Supporting Information). From 2009 to 2011, however, area of critical habitat that was both protected and scored as occupied increased to 53% for Perdido Key beach mouse, to 69% for Choctawhatchee beach mouse, and to 36% for St. Andrew beach mouse (Table 6). These results remained constant from 2011 to 2014 for all subspecies (Table 6). Habitat demands for Perdido Key and Choctawhatchee beach mice stabilized by 2011 at –0.16 and –1.85 km², respectively (Table 6), indicating that their habitat demand was met after 7 years of post-storm recolonization. The habitat demand for St. Andrew beach mouse stabilized by 2011 at 5.14 km² (Table 6), indicating the habitat demand was not met.

In 2011, the St. Andrew beach mouse's total weighted area ($W=3.83$) was less than the habitat demand area ($H_d=5.14$; Table 6), indicating that the habitat demand could not be met given the current scenario. Management scenarios 1, 2, and 3 caused the habitat demand to decrease from 5.14 km² to 2.89 km² (44% decrease), 1.8 km² (65%

Table 4. Sensitivities of beach mouse presence to typical condition and typical dune condition inputs for the Choctawhatchee beach mouse in Florida, USA, 2009–2014. Greater mutual information and percent reduction values indicate that knowing the variable's class more strongly reduces uncertainty about beach mice presence compared to variables with lower sensitivity values. A greater percent change in a variable's sensitivity from 2009 to 2011 indicates that knowing the variable's class more strongly reduces uncertainty of beach mice presence with more time since the last major storm.

Variable	Year						Change from 2009 to 2011 (%)
	2009		2010		2011–2014		
	Mutual information	% reduction	Mutual information	% reduction	Mutual information	% reduction	
Typical condition							
Land cover	0.082	8.190	0.100	11.300	0.098	11.300	38
Night light	0.001	0.118	0.004	0.406	0.004	0.437	270
Slope	0.002	0.177	0.003	0.320	0.003	0.336	90
Neighborhood suitability	0.004	0.366	0.003	0.288	0.003	0.321	−12
Active cat capture	0.000	0.003	0.001	0.095	0.001	0.115	3,343
Protected	0.000	0.003	0.001	0.094	0.001	0.115	3,395
Dune heterogeneity	0.000	0.010	0.001	0.084	0.001	0.115	1,055
Distance to NRD ^a	0.000	0.013	0.000	0.005	0.000	0.004	−71
Light guidance	0.000	0.000	0.000	0.000	0.000	0.001	∞
Total		8.88		12.59		12.74	44
Typical dune condition							
Land cover	0.017	1.760	0.015	2.000	0.012	1.570	−11
Night light	0.000	0.037	0.001	0.190	0.002	0.200	439
Active cat capture	0.000	0.008	0.001	0.162	0.001	0.195	2,238
Protected	0.000	0.008	0.001	0.161	0.001	0.195	2,255
Neighborhood suitability	0.000	0.002	0.001	0.093	0.000	0.056	3,069
Slope	0.000	0.000	0.000	0.011	0.000	0.016	∞
Dune heterogeneity	0.001	0.068	0.000	0.026	0.000	0.012	−82
Light guidance	0.000	0.000	0.000	0.001	0.000	0.001	∞
Distance to NRD	0.000	0.005	0.000	0.000	0.000	0.001	−78
Total		1.889		2.644		2.246	19
Land cover change (%)		−79		−82		−86	
Total change (%)		−79		−79		−82	

^a Distance to non-road development (m).

decrease), and 1.02 km² (80% decrease; Table 6). Despite the benefit of management scenarios 1–3, the total weighted area remained insufficient to meet the habitat demand (i.e., $W < H_d$; Table 6). In contrast, scenario 4 (restored dune, natural non-habitat, and water in protected critical habitat) caused the habitat demand to decrease to 1.06 km² (79% decrease) and the total weighted area (1.70 km²) was sufficient to meet the habitat demand (i.e., $W \geq H_d$; Table 6). With scenario 4, the average random management efficiency was 1.48 ± 0 (SD) and the average targeted management efficiency was 1.06 ± 0.01 km².

In St. Andrew beach mouse critical habitat, 14% of unoccupied dunes were at poor conditions for cat presence, 59% were at poor conditions for slope, and 26% were unprotected (Tables S13 and S14, available online in Supporting Information). Cat presence and slope were at poor conditions in 65% and 96% of unoccupied Perdido Key beach mouse critical habitat, and 18% and 89% of unoccupied Choctawhatchee beach mouse critical habitat (Tables S13, S14).

DISCUSSION

The St. Andrew beach mouse's 87% downlisting criterion was not met even after 7–10 years of post-storm recolonization, when only 36% of St. Andrew beach mouse critical habitat was protected and predicted to be occupied (Table 6). Only scenario 4 met the habitat objective, providing a 28%

increase in management efficiency from a random to a targeted management scenario. Scenario 4 included the restoration or conversion of water and natural non-habitat to dune. Consequently, future research could focus on determining the potential for restoring or converting these areas to dune (e.g., beach nourishment projects).

The 50% downlisting criteria for Choctawhatchee and Perdido Key beach mice (for critical habitat within Florida) were predicted to be met after 7 years of post-storm recolonization. The Perdido Key beach mouse habitat demand, however, exceeded the habitat objective by only 0.16 km² (Table 6), which indicates that the current scenario is barely sufficient. Falcy and Danielson (2014) reached a similar conclusion for the importance of preventing further habitat loss for sustaining populations of another endangered Gulf Coast beach mouse subspecies (Alabama beach mouse [*P. p. ammobates*]), where the probability of extinction over 100 years was low provided that habitat loss does not continue. We acknowledge that we lacked geospatial data sets for the Alabama portion of Perdido Key beach mouse critical habitat. The development of those inputs could provide the opportunity to revise the estimates for its habitat demand. The sensitivity analyses suggested that managers could first focus on improving land cover geospatial data sets because this will most greatly reduce uncertainty of Perdido Key beach mouse presence (top of Table 3). Because protected areas are known, additional efforts could focus on improving active cat capture

Table 5. Sensitivities of beach mouse presence to typical condition and typical dune condition inputs for the St. Andrew beach mouse in Florida, USA, 2009–2014. Greater mutual information and percent reduction values indicate that knowing the variable's class more strongly reduces uncertainty about beach mice presence compared to variables with lower sensitivity values. A greater percent change in a variable's sensitivity from 2009 to 2011 indicates that knowing the variable's class more strongly reduces uncertainty of beach mice presence with more time since the last major storm.

Variable	Year						Change from 2009 to 2011 (%)
	2009		2010		2011–2014		
	Mutual information	% reduction	Mutual information	% reduction	Mutual information	% reduction	
Typical condition							
Land cover	0.079	8.030	0.086	9.080	0.087	9.340	16
Night light	0.002	0.183	0.006	0.630	0.007	0.733	301
Dune heterogeneity	0.004	0.417	0.006	0.663	0.007	0.696	67
Slope	0.000	0.024	0.003	0.305	0.004	0.407	1,582
Neighborhood suitability	0.024	2.420	0.002	0.197	0.002	0.252	−90
Active cat capture	0.000	0.001	0.002	0.163	0.002	0.215	20,573
Protected	0.000	0.006	0.000	0.028	0.000	0.044	591
Distance to NRD ^a	0.000	0.045	0.000	0.001	0.000	0.008	−83
Light guidance	0.000	0.000	0.000	0.001	0.000	0.001	∞
Total		11.13		11.07		11.70	5
Typical dune condition							
Land cover	0.035	3.510	0.018	2.070	0.012	1.390	−60
Active cat capture	0.000	0.000	0.003	0.308	0.003	0.414	∞
Neighborhood suitability	0.013	1.260	0.001	0.128	0.003	0.336	−73
Dune heterogeneity	0.001	0.057	0.001	0.113	0.001	0.108	91
Slope	0.001	0.078	0.000	0.035	0.001	0.086	9
Protected	0.000	0.000	0.000	0.046	0.001	0.071	∞
Night light	0.000	0.004	0.000	0.053	0.001	0.067	1,675
Distance to NRD	0.000	0.042	0.000	0.000	0.000	0.007	−83
Light guidance	0.000	0.000	0.000	0.002	0.000	0.003	∞
Total		4.95		2.76		2.48	−50
Land cover change (%)		−56		−77		−85	
Total change (%)		−56		−75		−79	

^a Distance to non-road development (m).

and light guidance information, which are also relatively important in dune habitat (bottom of Table 3).

Our results further indicated that mice populations were still recolonizing after 5–7 years of post-storm recolonization. Beach mice can survive following intense storms by persisting in scrub habitat refugium until frontal dunes become habitable, which can take as long as 10 years (Pries et al. 2009, Falcy and Danielson 2014, Houser et al. 2015). At 5 years, beach mouse presence in frontal dunes was uncertain (i.e., 0.55–0.6 probability) irrespective of conditions (Fig. 4A–C). Presence in scrub dune was completely uncertain under the poor condition, and unexpectedly decreased to nearly 30% under the ideal conditions (Fig. 4D–F). The counter-intuitive decrease from poor to ideal scrub conditions might occur if scrub refugia occur under the poor condition (i.e., scrub located near developed areas that have higher probabilities of light pollution and cat presence). Beach mice may also be more likely to be present at 5 years in frontal compared to scrub dune with good or ideal conditions because they likely select frontal over scrub dune as they recolonize. This difference between frontal and scrub dune in good or ideal conditions then diminishes 5–7 years after the storm. We speculate that there may be a movement of mice from scrub to developing frontal dunes and then back into scrub as the frontal dune population increases. Although our model did not estimate beach mice population size and

did not account for distance to refugia, these results support the idea that further loss of scrub to coastal development and the isolation of frontal and scrub dunes caused by roads likely jeopardizes the sustainability of beach mice populations (Falcy and Danielson 2014).

Control of free-ranging individual and colonies of cats, which is identified as a management technique in the Perdido Key beach mouse, Choctawhatchee beach mouse, and St. Andrew beach mouse recovery plans (USFWS 1987, 2010), is more socially complex compared to implementing light guidance and managing slope. Domestic cats are efficient and abundant non-native predators that have been identified, but often are not recognized, as the cause of decline for some wildlife populations (Loss et al. 2013, McDonald et al. 2015). Cat management policies can have low public support (Lloyd and Hernandez 2012) and can be highly controversial, pitting wildlife advocates against animal-rights organizations (Loss et al. 2018). Cat management often takes the form of trap-neuter-release programs, but these programs are unlikely to reduce predation or control cat numbers anywhere there is an open boundary between human populations and ecologically sensitive areas because human populations provide a perpetual source and cats exhibit high vagility and low trapability (Gutilla and Stapp 2010). Thus, we emphasize that the model focuses on programs that actively remove free-ranging cats.

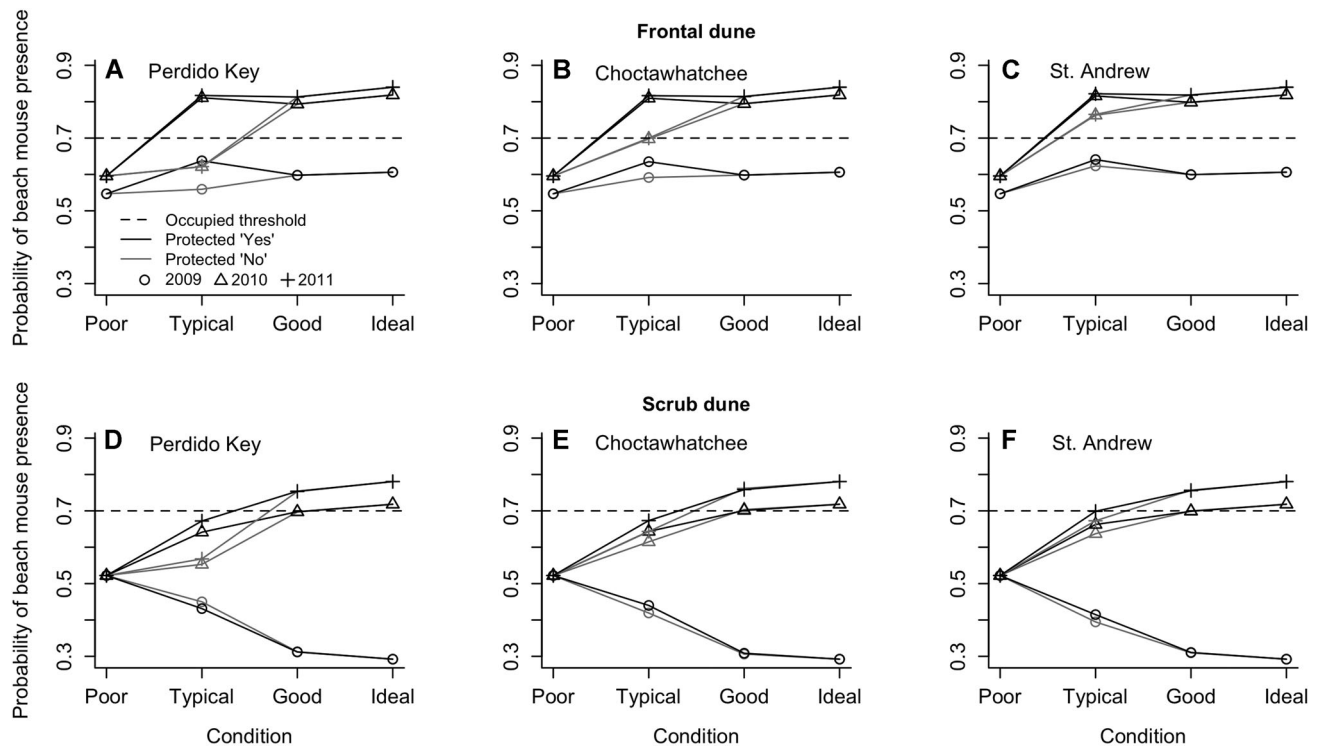


Figure 4. Effect analyses results for the Perdido Key, Choctawhatchee, and St. Andrew beach mice in Florida, USA, 2009–2011. We present the predicted probability of beach mouse presence given sites of varying conditions in areas that are protected, areas not protected, and during years 2009–2011 (5–7 years of post-storm recolonization). We considered areas with presence probabilities ≥ 0.7 to be occupied.

Human infrastructure and coastal erosion are expected to pose increasingly unprecedented threats to beach mice habitat. These stressors can make it difficult to carry out effective habitat management in dynamic landscapes. The management efficiency estimates reported here are based on the current landscape situation. They do not account for the uncertainty of habitat loss and changes in configuration that

are associated with future increases in human infrastructure, sea-level rise, frequency of intense storms, and coastal restoration activities. This uncertainty could be accounted for by developing new geospatial data sets that represent the effect of these factors on habitat characteristics. Those data sets could be used as inputs for extinction risk models that assess the ability of beach mice to maintain self-sustaining

Table 6. Habitat objective (H), habitat demand (H_d), and total weighted area (W) calculations for the Perdido Key, Choctawhatchee, and St. Andrew beach mice given the current scenario in Florida, USA, 2009–2014. The St. Andrew beach mouse also has 4 management scenarios because the total weighted area under the current scenario was never sufficient to meet its habitat demand (i.e., $W < H_d$) without additional conservation or restoration actions.

Beach mice subspecies	Scenario ^a	Year	C_T ^b (km ²)	R^c (%)	H (km ²)	C_{PO} ^d (km ²)	C_{PO} ^e (%)	H_d (km ²)	W (km ²)
Perdido Key	Current	2009	4.64	50	2.32	0	0	2.32	
		2010				2.29	49	0.03	
		2011–2014				2.48	53	–0.16	
Choctawhatchee	Current	2009	9.74	50	4.87	0	0	4.87	
		2010				6.25	64	–1.39	
		2011–2014				6.72	69	–1.85	
St. Andrew	Current	2009	10.07	87	8.76	0	0	8.76	
		2010				2.21	22	6.55	
		2011–2014				3.63	36	5.14	3.83
	1	2011–2014				5.87	58	2.89	2.35
		2				6.97	69	1.8	1.25
		3				7.75	77	1.02	0.76
		4				7.7	76	1.06	1.7

^a 1 = restored dunes in protected critical habitat; 2 = protected dunes in unprotected critical habitat; 3 = restored and protected all dunes in critical habitat; and 4 = restored dune, natural non-habitat, and water in protected critical habitat.

^b Total critical habitat.

^c Downlisting criteria.

^d Total critical habitat estimated to be protected and occupied.

^e Percentage of the total critical habitat estimated to be protected and occupied.

populations in dynamic habitat (Oli et al. 2001, Falcy and Danielson 2014) and the model presented here to estimate management efficiencies. As discussed above for the Perdido Key beach mouse, the sensitivity analyses suggest that these efforts could reduce uncertainty about beach mice presence by first focusing on land cover information (Tables 3–5). Efforts for the Choctawhatchee beach mouse could also focus on night light, slope, and neighborhood suitability (top of Table 4), with an additional emphasis on active cat capture in dunes (bottom of Table 4). Efforts for the Saint Andrew beach mouse could focus on night light, dune heterogeneity, and slope (top of Table 5), with an additional emphasis on active cat capture and neighborhood suitability in dunes (bottom of Table 5). Moreover, as management activities are continued or implemented anew, results of follow-up effectiveness monitoring could be incrementally used to further test and update the model. The very spirit of Bayesian statistical modeling is in the use of prior and new information to update not just probability projections but model structures.

The ability to assess the vulnerability of beach mouse habitat to coastal change depends on accurate measurements of dune height and position (Stockdon et al. 2009). Lidar topographic surveys, which are increasingly available, can characterize habitat at a fine spatial scale and were used to examine the effects of future storm surge on beach mouse habitat in Alabama (Chen et al. 2014). These efforts could refine dune land cover classification into primary, secondary, and tertiary dunes, which may offer alternative resources to beach mice; categorize dune slope into finer classes, which could better distinguish burrow suitability; and measure vegetation heterogeneity, which can influence beach mouse foraging (Lynn 2000, Sneckenberger 2001, Bird et al. 2004, Pries et al. 2009, Branch et al. 2011).

In addition, financial costs and benefits can determine the feasibility of implementing management scenarios. These costs are often greater in areas of high human density and for larger changes to underlying land use and land cover (e.g., scenario 4). But coastal communities are increasingly recognizing the benefits of dunes as a cost-effective method of protecting infrastructure from storm damage (Sallenger 2000, Arkema et al. 2013, National Research Council 2014). Mapping these financial costs and benefits could help identify areas of conservation conflict and opportunity (Brody et al. 2004, McCloskey et al. 2011), and could be used to conduct economic cost analyses that include explicit decision alternatives and utilities (e.g., costs, benefits). Bayesian network models provide a probabilistic framework for estimating habitat demands and management efficiencies that is also compatible with economic cost analyses because the models can be extended to include decision alternatives and utilities (i.e., Bayesian decision networks; Marcot and Penman 2019). In total, these physical and social geospatial data sets could be used in conjunction with our model to identify the location of refugia, to conduct vulnerability assessments of beach mouse presence, and to help prioritize areas for future restoration and protection of beach mouse habitat.

Finally, downlisting criteria state that beach mice must also have distinct, self-sustaining populations within their respective critical habitat (USFWS 2006a). Thus, downlisting criteria related to what defines a distinct self-sustaining population requires additional attention and could be addressed in the next 5-year reviews of these subspecies. The model could be directly incorporated into Species Status Assessments (Smith et al. 2018), a tool being used by the USFWS for listing decisions under the Endangered Species Act.

MANAGEMENT IMPLICATIONS

This study supports strategic habitat conservation for beach mice by providing decision support tools for estimating how much habitat is available and how much more is needed to achieve established downlisting criteria, and identifying specific management actions, where those actions might be taken, and over how much critical habitat they must be applied. The St. Andrew beach mice habitat objective might be achieved by first restoring protected critical habitat to good dune conditions and then protecting or restoring the unprotected critical habitat with the highest predicted probability of beach mouse presence. Because there was not enough dune area in critical habitat, this includes converting some water or natural non-habitat to dune—a potentially cost-prohibitive alternative.

For Perdido Key and Choctawhatchee beach mice, management efforts could focus on maintaining favorable dune conditions in protected critical habitat and preventing further habitat loss. Habitat loss prevention has included planting of stabilizing vegetation, creation of spoil islands to reduce coastal erosion, protections against human disturbance, and restoring habitat that is lost because of storms. In addition to minimizing habitat loss, the small surplus in habitat demand for the Perdido Key beach mouse could be increased by focusing protection efforts on unprotected critical habitat with the highest probability of beach mouse presence.

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