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IMPACT OF HURRICANES ON HABITAT OCCUPANCY AND SPATIAL DISTRIBUTION OF BEACH MICE

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1 Recent increases in hurricane activity along the Gulf of Mexico lend urgency to understanding storm impacts on beach mice (*Peromyscus polionotus*) that occupy dune systems along this coast in Florida and Alabama. We documented changes in occupancy patterns of the Santa Rosa beach mouse (*P. p. leucocephalus*) from Hurricane Ivan and examined predictors of habitat use before and after the hurricane. The hurricane removed 68% of frontal dune area occupied by beach mice and only 15% of scrub dune area. Occupancy of frontal dunes by beach mice dropped from 100% before to the hurricane to 60% after the hurricane. Occupancy of scrub habitat was lower than occupancy of frontal dune habitat before the hurricane (~75% occupancy) and did not change with the hurricane. Occupancy of frontal dunes after the hurricane was influenced by percent cover of woody vegetation, dune height, and distance to nearest occupied dune. Probability of occupancy of scrub habitat was positively correlated with individual dune area and amount of surrounding dune habitat before and after the hurricane. Our study supports recent efforts to define scrub dunes as Critical Habitat for beach mice and points to the importance of enhancing dune height and reducing dune isolation in coastal restoration programs.

Key words: beach mice, coastal dunes, environmental stochasticity, habitat conservation, hurricane

Identification and protection of habitat is a critical component of many conservation programs for imperiled species. For species occupying dynamic landscapes, habitat availability and quality can shift rapidly with stochastic events 2 (Carlsson and Kindvall 2001; Van Horne et al. 1997) and key features that determine spatial distribution or population density may change. Stochastic disturbances can have particularly severe impacts when coupled with human alteration of habitat (Frank 2005; Jonzen et al. 2004; Oli et al. 2001; Schrott et al. 2005). Consequently, these dynamics need to be incorporated into habitat assessments for successful long-term conservation planning. In this study, we examined hurricane impacts on habitat occupancy and spatial distribution of the Santa Rosa beach mouse (*Peromyscus polionotus leucocephalus*).

Beach mice, a complex of 7 subspecies of the oldfield mouse, occupy the coastal dunes of Alabama and Florida (Holler 1992). All populations of beach mice suffer from severe habitat loss from coastal development and habitat disturbance from hurricanes (Gore and Schaffer 1993; Swilling et al. 1998). As a result, 4 of the 5 subspecies that reside along the Gulf of Mexico are listed as threatened or endangered (Milio 1998; Potter 1985). The remaining subspecies, the Santa Rosa beach mouse, is not yet listed because its geographic range includes several federally managed lands that offer habitat protection (Gore and Schaffer 1993). However, modeling studies indicate that all subspecies of beach mice on the Gulf Coast are susceptible to extinction by hurricanes (Oli et al. 2001). Impacts of these disturbance events on the distribution of beach mice and their habitats are poorly known (Swilling et al. 1998).

Foredunes or frontal dunes located immediately adjacent to the Gulf of Mexico are believed to be primary habitat for beach mice when sparsely covered with sea oats (*Uniola paniculata*) because these areas have been documented to have the highest densities (Blair 1951; Humphrey and Barbour 1981; United States Fish and Wildlife Service 1987). Mice also occur in secondary dunes known as scrub dunes that are located farther from the shoreline and support more woody vegetation. Scrub dunes may be more important for beach mice than previously recognized because these dunes may serve as refuges following damage to frontal dunes by hurricanes (Swilling et al. 1998). However, little is known

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about what features define suitable scrub habitat for beach mice or the extent to which mice occupy scrub dunes.

North Atlantic hurricane activity, which impacts the Gulf Coast of the United States, has increased significantly since 1995 as compared to the 1970s–early 1990s (Goldenberg et al. 2001; Saunders and Lea 2008), lending urgency to understanding storm impacts on beach mice. We examined effects of Hurricane Ivan on the structure of frontal and scrub dunes, compared occupancy of dunes by Santa Rosa beach mice in these 2 habitats, and determined how these occupancy patterns changed after the hurricane. We also developed habitat models for predicting dune occupancy by Santa Rosa beach mice. Furthermore, we evaluated whether factors that influenced patterns of habitat occupancy were similar for frontal and scrub habitats, and how predictors of habitat occupancy changed with the hurricane. Understanding how prehurricane habitat conditions influence posthurricane occupancy is important for conservation planning in this stochastic environment and for defining restoration targets. In this study area, dunes form habitat patches for beach mice in a matrix of open sand and newly developing dunes. The matrix provides little habitat for foraging or burrowing. Individual dunes are not large enough to support separate populations or subpopulations of mice. Thus, dune occupancy as measured in this study reflects use of habitat patches, not assessment of occupancy at the scale of a metapopulation.

Materials and Methods

Study area and habitat mapping.—The study was conducted on Santa Rosa Island, a barrier island approximately 46 km long and 0.5 km wide, located in the Gulf of Mexico near Fort Walton Beach, Florida (30°24′N, 81°37′W; Fig. 1). The island comprises several sections of relatively intact habitat for beach mice separated by areas of high human development with no beach mouse habitat. The study area incorporated a 15-km section of the island on Eglin Air Force Base and a 10-km section on Gulf Island National Seashore, representing more than 68% of the habitat remaining for this subspecies of beach mouse after human development of the island. The eye of Hurricane Ivan passed approximately 75 km west of the western end of Gulf Islands National Seashore and 100 km west of the western end of Eglin Air Force Base on 14 September 2004. Dune habitat is similar in these 2 areas, with frontal dunes oriented parallel to the high-tide line and scrub dunes located on the bayside of the island. Both sections contain a single paved road and few man-made structures.

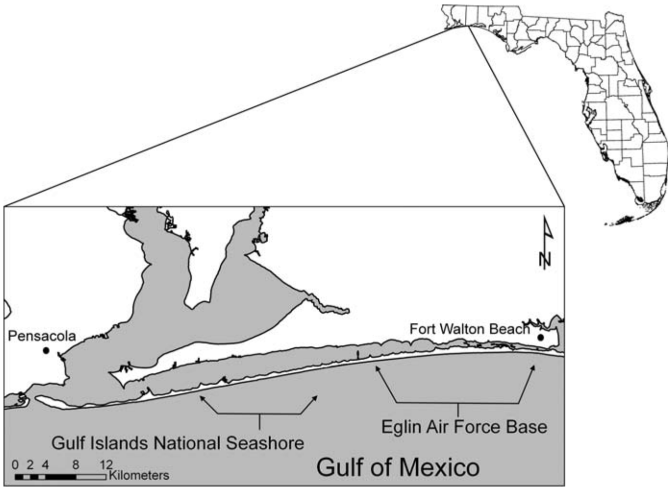

Fig. 1.—Map of Santa Rosa Island, Florida. The study areas for beach mice (*Peromyscus polionotus leucocephalus*) encompass the section of the island west of Fort Walton Beach on Eglin Air Force Base and Gulf Islands National Seashore.

Frontal dunes are dominated by herbaceous species such as sea oats, cakile (*Cakile edentula*), beach morning glory (*Ipomoea imperati*), and beach elder (*Iva geminata*). Woody species also occur on some frontal dunes. Woody species, including false rosemary (*Ceratiola ericoides*), woody goldenrod (*Chrysoma pauciflosculosa*), scrub live oak (*Quercus geminata*), and sand pine (*Pinus clausa*), dominate scrub habitat. The area between frontal and scrub dunes consists of open bare sand and gently rolling grasslands interspersed with densely vegetated wetlands. Beach mice may move across the open sand and grasslands, but wetlands probably restrict their movement (Holler 1992).

All dunes on Eglin Air Force Base were mapped in the field before and after Hurricane Ivan by recording their perimeters with a TRIMBLE GPS unit and then were differentially 3 corrected for <1-m accuracy. Dunes on Gulf Island National Seashore were mapped only after the hurricane. Dune perimeters were not visible on aerial photographs at any resolution because of the high reflectance of sand and, as a result, we were not able to augment our field data with data from aerial photographs. Global positioning system data were incorporated into geographic information system cover layers in ArcView 3.2 (Environmental Systems Research Institute 1996).

Dune occupancy.—We surveyed for presence of beach mice in all frontal ($n = 15$) and all scrub ($n = 61$) dunes equal to or larger than 0.25 ha on Eglin Air Force Base before Hurricane Ivan (June–September 2004). The same scrub dunes and all frontal dunes that remained after the hurricane ($n = 11$) also were surveyed after the hurricane (October 2004–December 2004). All frontal dunes ($n = 15$) on Gulf Islands National Seashore also were surveyed for beach mice after Hurricane Ivan (December 2004–February 2005). The smallest dunes surveyed were slightly larger than mean home-range size (0.19 ha ± 0.05) for philopatric (nondispersing) Alabama 4 beach mice (*P. p. ammobates*—Swilling and Wooten 2002), which have been studied more intensively than Santa Rosa beach mice. Presence of beach mice in each dune was determined with tracking tubes that registered footprints of mice that entered the tubes. Tracking with tubes can be conducted during weather not suitable for trapping and is less labor intensive than livetrapping and, therefore, particularly useful for large-scale surveys of distribution (Glennon et al. 2002; Mabee 1998).

Tracking tubes were constructed with polyvinyl chloride pipe (33 cm long × 5 cm diameter) and elevated 5–7 cm above the ground to prevent access by ghost crabs (*Ocypode quadrata*). Dowels placed at both ends of the tubes allowed mice, but not crabs, to enter. Each tube was baited in the middle with rolled oats. A paper liner was inserted into the bottom of each tube and felt inkpads were placed at each end. The inkpads were coated with a 2:1 mineral oil and carbon powder solution (Mabee 1998). Hispid cotton rats (*Sigmodon hispidus*) leave footprints that are substantially larger than those of Santa Rosa beach mice. The only other small rodent documented on the island, the house mouse (*Mus musculus*), occurs only in areas with human development (Gore and Schaffer 1993), which we did not sample.

Tracking tubes were placed at 15-m intervals along transects that began and ended at the dune edge and ran parallel to the long axis of the dune. We placed transects on the crest and landward side of dunes to reduce the amount of sea spray and blowing sand entering the tubes. Dunes < 0.5 ha received 8 tubes, dunes > 0.5 ha and < 2.0 ha received 16 tubes, and dunes > 2.0 ha received 32 tubes. The starting point at the dune edge for the 1st transect was selected randomly and, when >1 transect was needed, parallel transects were established 15 m apart. During each tracking session, tracking tubes remained in a dune for 5 nights. Tubes were checked and rebaited if necessary after each night. Mice were recorded as present on a dune if tracks were documented in tubes at any time during the 5-night survey. Presence–absence was recorded for the entire session rather than on a nightly basis because activity levels of beach mice vary among nights and may influence detectability. Preliminary fieldwork indicated that sampling for 5 days resulted in a high probability of detecting mice if they were present. The number of tube-nights (i.e., number of tubes × number of nights) before the hurricane was as follows on Eglin Air Force Base: frontal dunes, 840, and scrub dunes, 5,320. After the hurricane, the number of tube-nights was: Eglin Air Force Base—frontal dunes, 480, and scrub dunes, 4,880; Gulf Islands National Seashore—frontal dunes, 600. This represents our primary sample on all dunes. Additional secondary samples were obtained on a subset of these dunes to calculate detectability (see below). Tracking methods were approved by the Animal Ethics Committee of the University of Florida and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Gannon et al. 2007).

Probability of detection during presence–absence surveys often is <1, resulting in underestimation of occupancy and biased parameter estimates for habitat models (Gu and Swihart 2004; Kéry 2004). Therefore, we used statistical approaches for analysis of site occupancy that build on traditional capture–recapture methods and used repeated censuses to calculate detection probability (p) and to estimate the proportion of sites that are occupied (Ψ) after accounting for detectability (MacKenzie et al. 2002). To estimate detection probability within each habitat type, we resampled a random subset of scrub dunes ($n = 30$) on Eglin Air Force Base with tracking tubes 3 times after initial prestorm surveys. The same 30 dunes were used in all repeated surveys of scrub dunes before the storm. We also resurveyed another random subset of scrub dunes ($n = 30$) and all frontal dunes on Eglin Air Force Base 3 times after initial poststorm surveys. Frontal dunes were not resurveyed prior to the storm because all dunes were occupied in the 1st survey.

Each repeat survey was conducted over 5 nights following the sampling protocol described above, resulting in an additional 6,000 tube-nights for scrub dunes before the hurricane, 5,080 tube-nights for scrub dunes after the hurricane, and 1,440 tube-nights for frontal dunes after the hurricane. These 3 secondary surveys occurred over 15 sequential days (3 times × 5 days each) and began immediately after the primary survey effort for a particular dune. This resulted in 4 detection events over the course of 20 days for each dune with repeat surveys. Mean persistence time for Alabama beach mice within a home range is >90 days (Swilling and Wooten 2002). No data are available on Santa Rosa beach mice but based on information from this related subspecies we assumed that populations were closed over the sampling period. Secondary surveys were combined with the primary surveys completed on both Eglin and Gulf Islands National Seashore for occupancy modeling. Each 5-night survey was recorded as a binary encounter history (i.e., 0 for no tracks and 1 for tracks) and estimates of p and Ψ were calculated using PRESENCE software (MacKenzie et al. 2002). The following variables were included as covariates in modeling detectability: moon phase, total rainfall over the 5 days, and number of tubes in each dune. Detectability was not related to any of these variables and, therefore, these variables were not included in the final models.

Predictor variables for habitat models: vegetation cover and landscape structure.—Predictor variables for our habitat models included vegetation cover, characteristics of the dunes, and structure of the landscape surrounding the dunes. Sea oats and other herbaceous species are important food sources for beach mice (Moyers 1996). Woody vegetation stabilizes dunes during storms and is a key factor in dune formation and persistence (Stallins and Parker 2003; Wiedemann and Pickart 2004). Also, woody vegetation provides food and cover for foraging. For example, field studies of the Alabama beach mouse have documented extensive use of scrub oaks by mice during foraging (Sneckenberger 2001) and acorns as an important food item (Swilling et al. 1998). Dune height and area influence availability of nest sites, foraging area for mice, and impact of storm surge on dunes (Lynn 2000; Pries et al. 2008). The distance between dunes and amount of dune habitat in an area influence the availability of foraging habitat to mice and, potentially, predation risk while foraging.

We measured vegetation cover before and after Hurricane Ivan on all scrub dunes surveyed for mice. Measurements of vegetation cover were not completed on frontal dunes before the hurricane. Therefore, these variables were included in habitat models only posthurricane. Vegetation cover was

Table 1.—Means and standard errors for structural and vegetation variables measured for modeling occupancy of frontal and scrub habitat by Santa Rosa beach mice (*Peromyscus polionotus leucocephalus*) on Eglin Air Force Base (EAFB) and Gulf Islands National Seashore (GINS) on Santa Rosa Island, Forida. Variables were assessed before and after Hurricane Ivan made landfall on 18 September 2005. Differences between means before and after Ivan were compared for dunes on EAFB using paired *t*-tests adjusted with Bonferroni's correction for multiple tests. * $P < 0.05$.

	Frontal dunes $\bar{X}$ (± *SE*)			Scrub dunes $\bar{X}$ (± *SE*)	
Variable	EAFB before hurricane (n = 15)	EAFB after hurricane (n = 11)	GINS after hurricane (n = 15)	EAFB before hurricane (n = 61)	EAFB after hurricane (n = 61)
Dune area (ha)	0.59 (0.09)	0.26 (0.06)*	0.15 (0.03)	1.82 (0.38)	1.55 (0.37)*
Dune height (m)	4.01 (0.33)	3.13 (0.35)*	3.24 (0.20)	4.64 (0.3)	3.32 (0.17)*
Dune habitat within 200 m (ha)	0.29 (0.09)	0.22 (0.08)	0.24 (0.05)	2.21 (0.28)	1.71 (0.19)*
Dune habitat within 1 km (ha)	8.45 (1.48)	8.67 (1.44)	1.94 (0.29)	12.73 (1.19)	11.29 (1.03)*
Distance to nearest occupied dune (m)	219.2 (54.7)	161.9 (25.9)[a]	126.2 (39.4)	176.1 (38.3)	174.2 (37.6)
% woody cover	—	6.5 (1.4)	3.3 (2.1)	19.6 (1.6)	19.9 (1.6)
% herbaceous cover	—	24.5 (2.9)	19.2 (2.3)	14.1 (1.4)	7.4 (0.8)*
East–west coordinate (UTM; m)	52,2959 (1,337)	524,208 (879)	506,117 (1,709)	524519 (653)	524,519 (653)

[a] Distance to nearest occupied dune dropped after the hurricane because the 4 dunes that were destroyed were very isolated (mean distance to nearest occupied dune for those dunes = 459.5 m). Prehurricane mean for distance to nearest occupied dune for the 11 dunes that survived Ivan = 131.7 m. 6

quantified using the line-intercept method (Bonham 1989) along three 50-m transects placed 20 m apart and perpendicular to the long axis of each dune (i.e., at each site sampled for beach mice). We recorded linear distances (cm) of sea oats, other herbaceous vegetation, woody vegetation, and open sand along each transect and divided these values by total transect length to obtain percent cover for each cover class. We averaged data for the 3 transects to obtain standard vegetation measures for each dune (mean cover ± *SE*) that can be compared easily with data from future habitat studies for this species. Arcsine transformations were performed on data before analysis.

We recorded dune height (m) by measuring height every 15 m along the long axis of each dune using a telescoping pole and then averaged all values for each dune. We calculated dune area and amount of dune habitat surrounding each dune in ArcView 3.2 using the geographic information system database created from field mapping of dunes. We also used this database to calculate distance to the nearest occupied dune as an index of dune isolation by measuring straight-line distance from the closest edge of the focal dune to the closest edge of the nearest occupied dune in ArcView 3.2. We used the BUFFER function in ArcView 3.2 to estimate total area of dune habitat surrounding each dune at the foraging (200-m) and dispersal (1-km) scales of beach mice (Bird 2002; Swilling and Wooten 2002). The east–west coordinate (Universal Transverse Mercator [UTM]) at the center of each dune was included in habitat models to examine how spatial location relative to the eye of Hurricane Ivan influenced dune occupancy by mice. We compared structural and vegetation variables measured before and after Hurricane Ivan with *t*-tests
5 adjusted with Bonferroni's correction for multiple tests.

Occupancy models.—We created and ranked a series of models with PRESENCE to identify variables that influenced distribution of beach mice in frontal dune and scrub habitats. Frontal dunes and scrub dunes were modeled separately because key habitat variables differed greatly between dune types (e.g., dune area; Table 1), resulting in a confounding of dune type and habitat factors that we wished to analyze. All frontal dunes were occupied before Hurricane Ivan, so no model was created for this period. We developed 40 candidate models for frontal dunes on Eglin Air Force Base and Gulf Islands National Seashore after Hurricane Ivan. To reduce risk of an overparameterized model with the smaller sample size for frontal dunes as compared to scrub dunes, we restricted the total number of variables in a model to 3. The first 8 base models included a combination of patch-level features (e.g., dune area, percent cover woody vegetation, percent cover herbaceous vegetation, and dune height). An additional 32 models were created by including distance to nearest occupied dune, 200-m habitat buffer, 1-km habitat buffer, or east–west coordinate to base models.

Fifty-six candidate models were evaluated for scrub dunes using a combination of variables measured before Hurricane Ivan and similar models were created with posthurricane data. We focused on habitat factors influencing occupancy pre- and posthurricane rather than examining habitat variables related to extinction and colonization with a multiseason model because low turnover resulted in few extinction and colonization events for modeling. The first 8 base models were the same as in frontal habitat (i.e., patch-level features). An additional 24 models were created by adding distance to nearest occupied dune, the 200-m habitat buffer, or 1-km habitat buffer to the original base models. Finally, we created another 24 models by including the east–west coordinate to form the ''base model + landscape context'' models.

We also modeled posthurricane occupancy of frontal and scrub dunes on Eglin Air Force Base with prehurricane conditions to assess the role of prehurricane conditions on posthurricane occupancy. Models were created using the same procedure as described above except vegetation cover was omitted for frontal dunes because these data were not measured before the hurricane. Before constructing all habitat models, correlations among variables were examined and generally found to be low (Appendices I and II). Correlated variables ($|r| > 0.60$) were not included in the same model (Welch and MacMahon 2005) except in 4 cases. In 4 models incorporating landscape structure, a regression was conducted with the 2 correlated variables and residuals were included in the model as an independent measure of 1 of the variables (Cooper and Walters 2002). These variable sets included dune habitat within 1 km and east–west coordinate, and dune habitat within 200 m and distance to nearest occupied dune (Appendices I and II).

We used an Akaike information criterion corrected for small sample bias (AIC_c) to rank models. We present AIC differences ($\Delta AIC_c = AIC_{ci} - $ minimum AIC_c), so that the best model has $\Delta AICc = 0$ (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ are considered competitive models. We also include Akaike weight (w_i), which indicates relative likelihood that model i is the best model. The relative importance of each habitat variable (w_{sum}) was obtained by summing w_i for all models that contained this variable (Burnham and Anderson 2002). We performed model averaging to obtain parameter estimates and unconditional standard errors for each habitat variable of interest to reduce the bias of estimating parameter effects from a single model (Burnham and Anderson 2002). When the confidence interval around a model-averaged parameter estimate is >0, probability of occupancy increases as the variable increases, and a value < 0 indicates that an increase in the variable decreases the probability of occupancy (Buskirk 2005; Mazerolle et al. 2005). Estimated probability of detection (p) and overall occupancy rate (Ψ) also were obtained using this approach.

RESULTS

Hurricane impacts on beach mouse habitat.—Hurricane Ivan significantly reduced mean area of both types of dunes (Table 1), but frontal dunes lost a much greater proportion of area. Storm damage resulted in a loss of 68.2% of the total area of frontal dunes on our study site at Eglin Air Force Base, including the complete destruction of 4 dunes. No scrub dunes were destroyed entirely but the total area of scrub dunes was reduced by 14.8%. Dune height also was reduced significantly for both dune types (Table 1). The amount of habitat within 200 m and 1 km of a dune was reduced significantly for scrub dunes but not frontal dunes. However, frontal dunes already had little habitat within 200 m before the hurricane (Table 1). Herbaceous cover on scrub dunes was reduced with the hurricane, but woody cover did not change.

Dune occupancy.—Beach mice occurred in 100% of the frontal dunes on Eglin Air Force Base before the hurricane. Occupancy of frontal dunes that remained after the hurricane was much lower (model-averaged occupancy ± unconditional *SE*, 59.7% ± 5.1%). Data from Gulf Islands National Seashore and Eglin Air Force Base were included in these posthurricane models to increase sample sizes for habitat modeling after loss of frontal dunes on Eglin Air Force Base (Table 1). Field estimates of occupancy (i.e., uncorrected for detectability) of frontal dunes after the hurricane were 58% for Eglin Air Force Base and 47% for Gulf Islands National Seashore. Occupancy of scrub dunes before and after the hurricane did not differ (model-averaged occupancy ± unconditional *SE*, 75.1% ± 5.5% and 78.6% ± 4.9%, respectively). Detection probability of mice was high throughout the study at all sites (frontal dunes—prehurricane, 100%, and posthurricane, 89.8% ± 5.5% *SE*; scrub dunes—prehurricane, 88.6% ± 5.6%, and posthurricane, 90.1% ± 3.1%).

Habitat models.—A combination of patch-level and landscape-level features ranked high in models of occupancy of frontal and scrub dunes before and after the hurricane (Table 2). The strongest model for occupancy of frontal dunes after Hurricane Ivan based on posthurricane conditions included percent woody vegetation cover and distance to nearest occupied dune (Table 2). The likelihood of occupancy increased with increasing cover of woody vegetation and this variable was the top ranked variable in models of occupancy (Table 3). The negative parameter estimate for distance to the nearest occupied dune indicated an inverse relationship between this variable and probability of occupancy after the hurricane, but this relationship was not statistically significant. When posthurricane occupancy of frontal dunes on Eglin Air Force Base was modeled with variables related to the structural and landscape context of dunes before the hurricane, dune height and distance to the nearest occupied dune were the most important predictors of occupancy. The likelihood of occupancy of frontal dunes by beach mice after the hurricane increased significantly with a greater dune height and a lower distance to the nearest occupied dune before the hurricane.

The best model for scrub dunes before the hurricane included dune area, percent woody vegetation cover, and amount of dune habitat within 200 m (Table 2). No other models were competitive. After the hurricane, the same model was the strongest; however, the Akaike weight was lower and several additional models were competitive. All competitive models contained some combination of the variables in the best model; however, dune height and herbaceous cover also were included in several models. Ranking of the variables based on the sum of their Akaike weights revealed that amount of dune habitat within 200 m of scrub dunes was the most important variable in explaining probability of occupancy of scrub dunes by mice before and after the hurricane, followed by dune area (Table 3). Probability of beach mice occupying a scrub dune increased as amount of habitat surrounding the dune within 200 m and dune area increased. Top models of posthurricane occupancy in scrub dunes using prehurricane conditions retained the same suite of predictor variables (Table 2).

TABLE 2.—Akaike information criterion (AIC)–based selection of site occupancy models for Santa Rosa beach mice (*Peromyscus polionotus leucocephalus*) in frontal and scrub dune habitat before and after Hurricane Ivan on Santa Rosa Island, Florida. K = number of explanatory variables plus 2, $\Delta AIC_c = AIC_{ci} - \text{minimum } AIC_{ci}$, w_i = Akaike weight. Models with $\Delta AIC_c \leq 2$ are presented.

Habitat and conditions	Period of occupancy	Model	K	ΔAIC_c	w_i
Frontal posthurricane	Posthurricane	% woody cover, distance to nearest occupied dune	4	0.00	0.58
Frontal prehurricane[a]	Posthurricane	Dune height, distance to nearest occupied dune	4	0.00	0.73
Scrub prehurricane	Prehurricane	Dune area, habitat within 200 m, % woody cover	5	0.00	0.42
Scrub posthurricane	Posthurricane	Dune area, habitat within 200 m, % woody cover	5	0.00	0.18
		Dune area, habitat within 200 m	4	0.25	0.16
		Dune height, % woody cover, habitat within 200 m	5	0.50	0.14
		% woody cover, habitat within 200 m	4	0.94	0.12
		% herbaceous cover, habitat within 200 m	4	1.63	0.08
		Dune height, habitat within 200 m	4	1.69	0.08
		Dune area, % herbaceous cover, habitat within 200 m	5	1.98	0.07
Scrub prehurricane	Posthurricane	Dune area, habitat within 200 m, % woody cover	5	0.00	0.26
		Dune habitat within 200 m	3	0.70	0.18
		% woody cover, dune habitat within 200 m	4	1.53	0.12
		Dune area, dune habitat within 200 m	4	1.60	0.12
		Dune height, dune habitat within 200 m, % woody cover	5	1.91	0.10
		Dune area, % herbaceous cover, dune habitat within 200 m	5	1.91	0.10

[a] This model was developed with data on the structure and landscape context of dunes and does not include vegetation variables that are in other models.

DISCUSSION

Because optimal habitat for beach mice along the Gulf of Mexico generally was believed to consist of tall frontal dunes covered by sea oats and other herbaceous species (Holler 1992), until recently, conservation efforts have focused on this habitat (United States Fish and Wildlife Service 1987) and scrub dunes have not been protected. Our study indicates that multiple habitat types are important for beach mice under

TABLE 3.—Relative importance (w_{sum}), model-averaged parameter estimates, and unconditional standard errors for variables identified in top habitat models for occupancy of dunes by Santa Rosa beach mice (*Peromyscus polionotus leucocephalus*) on Santa Rosa Island, Florida. w_{sum} was estimated by summing Akaike weights (w_is) of all models with a variable of interest. * = confidence intervals do not contain 0 and indicate that variable significantly influences occupancy.

Habitat	w_{sum}	Parameter estimate	SE	90% CI
Frontal posthurricane habitat				
Posthurricane occupancy				
% woody cover*	0.969	16.355	9.854	0.146–32.564
Distance to nearest occupied dune (m)	0.769	−2.627	1.851	−5.672–0.418
Frontal prehurricane habitat				
Posthurricane occupancy				
Dune height (m)*	0.730	0.485	0.151	0.237–0.733
Distance to nearest occupied dune (m)*	0.828	−0.015	0.008	−0.028– −0.002
Scrub prehurricane habitat				
Prehurricane occupancy				
Dune area (ha)*	0.679	0.709	0.418	0.022–1.396
% woody cover	0.642	1.717	1.221	−0.292–3.726
Dune habitat within 200 m (ha)*	0.888	0.719	0.351	0.142–1.296
Scrub posthurricane habitat				
Posthurricane occupancy				
Dune area (ha)*	0.536	0.548	0.319	0.023–1.073
Dune height (m)	0.257	0.081	0.106	−0.093–0.255
% woody cover	0.498	1.024	0.943	−0.527–2.575
% herbaceous cover	0.197	−0.106	0.714	−1.281–1.069
Dune habitat within 200 m (ha)*	0.864	1.089	0.574	0.145–2.033
Scrub prehurricane habitat				
Posthurricane occupancy				
Dune area (ha)*	0.524	0.516	0.298	0.026–1.006
% woody cover	0.498	1.218	1.048	−0.506–2.942
Dune habitat within 200 m (ha)*	0.936	1.022	0.461	0.264–1.780

changing environmental conditions and supports recent efforts to redefine Critical Habitat for beach mice under the Endangered Species Act to include scrub dunes (United States Fish and Wildlife Service 2006).

Frontal dunes near the high-tide line are subjected to major impacts during hurricanes and their regeneration is hindered by high frequency of storms. Before Hurricane Opal (1995), frontal dunes ran almost continuously along the length of Santa Rosa Island in areas without intensive human development (Stone et al. 2004). Hurricane Opal fragmented this habitat and storm surge from Hurricane Ivan removed close to 70% of the remaining frontal dunes in our study area. In contrast, no scrub dunes, which are located on the bay side of the island, were lost completely in Hurricane Ivan. Reduction in area of scrub dunes occurred along dune edges from passing storm surge. However, scrub dunes are likely to suffer more erosion during future hurricanes as buffering capacity provided by frontal dunes is lost (Pries et al. 2008).

The lower occupancy of scrub habitat by beach mice as compared to frontal habitat that we observed before Hurricane Ivan is consistent with documentation of lower density in scrub habitat from other studies (Swilling et al. 1998) and may indicate that scrub habitat is lower quality (e.g., has lower resource availability or higher predation) than frontal dunes under prehurricane conditions. However, scrub dunes provide more stable habitat for beach mice than frontal dunes when hurricanes occur. In addition, scrub dunes may serve as refugia if mice can move from frontal dunes to scrub during hurricanes and can serve as a source for recolonization of frontal dunes following hurricanes.

We documented a substantial reduction of occupancy of frontal dunes by beach mice following Hurricane Ivan. Because of the rapid and extensive loss of frontal habitat, we suspect that this change in occupancy reflects, at least partially, a reduction in population size. This pattern also could result from movement of mice from frontal to scrub dunes, although occupancy did not increase in scrub dunes following the hurricane. During Hurricane Opal, Alabama beach mice were observed to move from frontal areas to neighboring transition dunes that received less impact than frontal dunes (Swilling et al. 1998). Our ongoing research with marked mice indicates that Santa Rosa beach mice exhibit little movement between frontal and scrub dunes in the absence of a hurricane (e.g., <5% exchange of individuals between these habitats per year). Frontal and scrub dunes on Santa Rosa Island often are separated by swales that are subject to extensive flooding with hurricanes and may reduce the possibility of successful movement between frontal and scrub dunes during hurricanes. Long-term population data spanning hurricane events are needed to determine the degree to which changes in the distribution of beach mice result from changes in population size versus habitat use.

Because prehurricane and posthurricane surveys were conducted in different months (June–September and October–February, respectively), changes in occupancy also possibly could reflect seasonal changes in population size unrelated to the hurricane. Population data from other studies indicate that this is unlikely. Trapping studies for Santa Rosa and Alabama beach mice have documented little change in population sizes throughout the year or lower population sizes in summer and early autumn than other times of year (Blair 1951; Rave and Holler 1992; Swilling et al. 1998). Thus, if occupancy patterns followed seasonal changes in population size, we would expect to observe no difference in occupancy or the reverse of the pattern that we observed.

Predictors of site occupancy for beach mice in frontal habitat after the hurricane were tied closely to proximity to other occupied dunes and local habitat features. Distance between dunes was important, whether modeled with pre- or posthurricane habitat conditions. Beach mice occupying frontal dunes before Hurricane Opal experienced fairly continuous habitat and broadly distributed resources. Frontal dunes fragmented by Hurricane Opal and subsequent storms are too small to support separate populations of beach mice. Open sand and early stages of regenerating dunes provide little food between frontal dune fragments. Close proximity of frontal dunes likely facilitates movement among dunes during foraging and decreases the risk, or perceived risk, of predation associated with moving across open sandy areas between dunes (Bird et al. 2004).

Dune height before the hurricane was a significant predictor of occupancy of frontal dunes after the hurricane. This relationship likely reflects the role of dune height in preventing overwash by storm surge and maintaining dune stability in storms (Pries et al. 2008). Dune height was significantly lower after the hurricane and not an important predictor of occupancy by beach mice. These results indicate a need for considering physical structure of dunes in beach restoration programs aimed at enhancing persistence of beach mouse populations, a point that would have been missed with analyses focused only on current factors influencing distribution of mice.

Although early work on beach mice emphasized herbaceous cover (Holler 1992), woody vegetation was more important in models of dune occupancy in our study area. Frontal dunes with greater cover of woody vegetation after the hurricane had a higher probability of posthurricane occupancy. Cover of woody vegetation was generally low throughout our study area (<10% for frontal dunes and <20% for scrub dunes), and our results may differ from areas with high shrub cover. However, if we had been able to incorporate measures of vegetation on frontal dunes before the hurricane, we suspect that woody cover befoer the hurricane also would be important in predicting posthurricane occupancy because of the role of woody vegetation in maintaining dune stability during storms (Stallins and Parker 2003). The structure of woody plants also enhances dune development (Stallins and Parker 2003) and provides cover, which strongly influences foraging by beach mice (Bird 2002). Woody plants also produce fruit and seeds eaten by mice (Moyers 1996; Sneckenberger 2001). Dune restoration after hurricanes historically has focused on reestablishment of sea oats, which produce a lattice of rhizomes that accumulate sand and are an important food plant for beach mice. Our research supports the need for including woody species in restoration efforts.

Predictors of occupancy in scrub habitat were related to habitat amount (i.e., dune area and amount of surrounding habitat) before and after the hurricane and, as expected from the small change in occupancy, the best habitat models were similar for the 2 periods. Woody vegetation also appeared to influence occupancy of scrub dunes by beach mice, but this relationship was not as clear as in frontal dunes. The importance of amount of habitat for occupancy of scrub dunes could reflect low habitat quality in these dunes with large amounts of habitat required to maintain populations. Alabama beach mice travel further distances to forage in scrub habitat than in frontal habitat during the winter and spring, suggesting that resources may be scarcer in scrub during this period, but the pattern is reversed for autumn (Sneckenberger 2001). Field data on resource use, foraging activity, and population dynamics of Santa Rosa beach mice in scrub and frontal dunes are lacking and would significantly enhance our understanding of habitat quality for these mice.

Although a dynamic hurricane-dune regeneration cycle is critical for maintenance of barrier islands along the coast of the Gulf of Mexico, regeneration of dunes following hurricanes is relatively slow compared to the rapid removal of dunes by hurricanes (Pries et al. 2008). Human development alters dune regeneration and can serve as a barrier to recolonization of regenerating habitat following local extirpation. The continued growth of human populations along the coast, combined with hurricane impacts on remaining habitat, constitutes a growing challenge for conservation of beach mouse populations and their habitat. The role of stochasticity and uncertainty in management outcomes has been explored extensively with respect to impacts on population size and persistence of species of conservation concern (Beissinger and Westphal 1998; Burgman et al. 2005; Wiegand et al. 2004). Results from our study underscore the importance of incorporating environmental stochasticity into habitat planning for beach mice and other species that live in habitats with high levels of disturbance. Habitat availability for species in dynamic landscapes can change quickly and additional habitats may become critically important, and thus in need of protection, either as refugia or as sources of colonization after stochastic events (Biedermann 2004; Carlsson and Kindvall 2001).

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Appendix I

Correlations for habitat and landscape variables measured on frontal dunes on Santa Rosa Island, Florida, before (Eglin Air Force Base; above the diagonal) and after (Eglin Air Force Base and Gulf Islands National Seashore; below the diagonal) Hurricane Ivan.

Variable	Dune area (ha)	Dune height (m)	Dune habitat within 200 m (ha)	Dune habitat within 1 km (ha)	Distance to nearest occupied dune (m)	% woody cover[a]	% herbaceous cover[a]	East–west coordinate (UTM; m)
Dune area (ha)		0.31	0.17	−0.09	−0.33	—	—	−0.02
Dune height (m)	0.43		−0.05	0.07	0.18	—	—	0.48
Dune habitat within 200 m (ha)	0.11	−0.32		0.37	−0.64	—	—	0.07
Dune habitat within 1 km (ha)	0.47	0.05	0.24		−0.47	—	—	0.26
Distance to nearest occupied dune (m)	−0.04	0.01	−0.62	−0.08		—	—	0.35
% woody cover	0.30	−0.04	−0.07	0.38	0.14		—	—
% herbaceous cover	0.32	−0.12	−0.13	0.49	−0.23	−0.61		—
East–west coordinate (UTM; m)	0.43	0.04	−0.05	0.69	0.10	0.14	0.30	

[a] Information on vegetation for frontal dunes was not collected before Hurricane Ivan made landfall.

Appendix II

Correlations for habitat and landscape variables measured on scrub dunes on Santa Rosa Island, Florida, before (above the diagonal) and after (below the diagonal) Hurricane Ivan.

Variable	Dune area (ha)	Dune height (m)	Dune habitat within 200 m (ha)	Dune habitat within 1 km (ha)	Distance to nearest occupied dune (m)	% woody cover	% herbaceous cover	East–west coordinate (UTM; m)
Dune area (ha)		0.55	0.46	0.26	−0.17	0.24	−0.20	0.28
Dune height (m)	0.55		0.46	0.31	−0.14	−0.18	−0.07	0.46
Dune habitat within 200 m (ha)	0.27	0.06		0.74	−0.39	−0.11	0.09	0.49
Dune habitat within 1 km (ha)	0.19	0.16	0.78		−0.41	−0.09	0.01	0.69
Distance to nearest occupied dune (m)	−0.15	−0.10	−0.38	−0.45		0.10	0.05	−0.17
% woody cover	0.07	0.08	−0.28	−0.17	0.17		−0.39	0.04
% herbaceous cover	−0.16	−0.03	0.01	−0.12	0.03	−0.07		−0.05
East–west coordinate (UTM; m)	0.25	0.23	0.48	0.70	−0.46	−0.08	−0.13	

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