Post-hurricane recovery and long-term viability of the Alabama beach mouse

Matthew R. Falcy [a,*], Brent J. Danielson [b]

[a] Ecology and Evolutionary Biology, Iowa State University, United States
[b] Department of Ecology, Evolution and Organismal Biology, Iowa State University, United States

ABSTRACT

The spatial configuration of habitat and the frequency of disturbances through time could have interacting effects on population viability. With this in mind, we assessed the rate of post-hurricane recovery and long term viability of the Alabama beach mouse (*Peromyscus polionotus ammobates*). We collected detection/nondetection data across the range of the Alabama beach mouse for four years subsequent to hurricanes Ivan and Katrina, and then fit a dynamic patch occupancy model to these data using hierarchical Bayesian methods. We converted remotely sensed data into habitat classes, and then mapped site survival probability over the entire range of the species. These estimates were then used to parameterize a spatially-explicit population viability analysis. Our occupancy modeling demonstrates that the probability of patch occupancy increased from 0.16 to 0.67, with occupancy in the surveyed patches approaching an asymptote by the third post-hurricane summer. The viability analysis suggests that extinction probability increases nonlinearly with monotonic increases in both habitat loss and hurricane frequency. Extinction risk is sensitive to the regularity of catastrophic hurricanes; consecutive hurricanes dramatically increase extinction risk, further suggesting that the effect of global climate change on hurricane regimes may have a large effect on the probability of long-term persistence. A mild interaction between habitat loss and hurricane frequency occurs when extinction probability is relatively low, but disappears as extinction probability increases. Our results indicate that extinction risk is a complex function of multiple interacting drivers.

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1. Introduction

Extinction risk is a frequently used metric in environmental management and decision making. Often that risk is expected to be a function of one, overwhelmingly important, driver such as a form of major disturbances or habitat loss, or some biotic issue such as invasive species or disease. However, extinctions may ultimately be the result of multiple factors acting in a multiplicative or synergistic fashion, which complicates assessment of persistence times (e.g., Vuilleumier et al., 2007; Brook et al., 2008). Classic examples include specialized butterflies with shrinking ranges impacted by fire (e.g., Swengel, 1996; Charrette et al., 2006). Species with reduced ranges due to habitat loss tend to have smaller population sizes, and therefore face increased risk from disturbances than larger populations. We modeled anthropogenic habitat loss and the frequency of major disturbances that may be a product of global climate change in order to better understand this

synergy on the risk of extinction of an endangered species. The rate of post-disturbance population recovery is a critical uncertainty in such assessments. The Alabama beach mouse (*Peromyscus polionotus ammobates*) provided an opportunity for us to obtain empirical estimates of the rate of post-hurricane recovery.

Beach mice along the northeastern coast of the Gulf of Mexico are a group of endangered subspecies that face continued loss of habitat due to anthropogenic development. They also face severe hurricane disturbances that may be increasing in both frequency and intensity (Emanuel, 2005; Trenberth, 2005; Webster et al., 2005). These subspecies prefer lightly vegetated, low primary dunes that begin immediately behind the high-tide surf zone. To a much lesser degree, they also use the scrub dune habitat immediately inland of the primary dune field which has a higher elevation and is dominated by woody shrubs. Densities of mice in the scrub are normally much less than in the primary dunes (Pries et al., 2009). These lower densities in the scrub have justified substantial conversion of the scrub into condominiums, private residents, golf courses, and other developments that are by and large not compatible with beach mouse productivity while primary

* Corresponding author.
  E-mail address: mfalcy@gmail.com (M.R. Falcy).

dunes have been, to a large extent protected from development and anthropogenic disturbances.

Yet, it is these protected primary dunes that are most susceptible to hurricanes, and in 2004 and again in 2005, the entire historic range of Alabama Beach Mouse was hit by hurricanes Ivan and then Katrina, eliminating almost all of the primary dunes and heavily damaging the scrub habitat. Overall, approximately 90% of Alabama beach mouse habitat was suspected to have been significantly damaged or destroyed by these hurricanes (USFWS, 2005). As a species, beach mice have survived hurricanes by persisting in low densities in the remains of scrub habitat until the primary dunes reform and become inhabitable, which can be 5–10 yrs. However, once extensive tracts of scrub habitat have now been largely developed. Beginning in the 1950s, but with much greater losses of habitat in the late 1980s and 1990s, scrub habitat has been reduced to small, isolated patches scattered along the landward borders of the beach mouse's range.

While other factors like predation (Falcy and Danielson, 2013a) and competition (Falcy and Danielson, 2013b) may play an important role in the population dynamics of beach mice, we focus our model only on the effects of habitat loss and hurricanes because these were cited as causes of decline when *P. p. ammobates* was granted federal protection under the Endangered Species Act. The effects of hurricanes on beach mouse population density (Swilling et al., 1998) and spatial distribution (Pries et al., 2009) have already been documented. Here, we use occupancy modeling to estimate of the rate of spatial recovery of the Alabama beach mouse following the catastrophic hurricanes of 2004 and 2005. Furthermore, population viability analyses (PVA) of the Alabama beach mouse have already been performed (Oli et al., 2000; Traylor-Holzer, 2005), but here we develop a spatially-explicit PVA parameterized with occupancy estimates to examine whether the risk of extinction from more frequent hurricanes is expected to be exacerbated by additional habitat loss.

2. Methods

Techniques for simulating occupancy dynamics of populations on binary landscapes of suitable and unsuitable habitat are relatively well-developed (Sjögren-Gulve and Hanski, 2000; Moilanen, 2004). However, many species do not occur on binary landscapes, and the importance of marginal habitats on population dynamics is well documented (Weigand et al., 2005; Falcy and Danielson, 2011). Occupancy models can be fit to data that were collected from investigator-defined sampling units, and covariates can be used to infer occupancy at un-surveyed locations (Royle and Dorazio p. 89). A challenge to inference and simulation of occupancy models when patches are not discrete concerns assumptions of the degree of spatial independence of site colonization and site survival. We address this issue by relating spatial variation in survival probabilities to local habitat conditions derived from remotely-sensed data, grouping regions of spatially-dependent survival, and then finding a colonization function that results in empirically observed occupancy rates at locations where detection/nondetection data were collected.

2.1. Beach mouse surveys

We conducted detection/non-detection surveys for the Alabama beach mouse every summer from 2006 through 2009. All survey sites were located in or to the west of the Perdue Unit of the Bon Secour National Wildlife Refuge (Fig. 1), where commercial and residential developments have had the greatest impact on habitat connectivity. Survey sites were either along public right-of-ways or on privately held property where access had been granted. The number of sites falling into the latter category increased throughout the duration of the study because the U.S. Fish and Wildlife Service, while promulgating the federal Endangered Species Act, included a monitoring-access clause in the permits it issued to landowners applying for permission to modify their parcel's landscape. During the summer of 2006, we were able to survey just 31 sites; by summer of 2009, 61 sites were included in our surveys.

Surveys were conducted with Sherman live traps. Traps were deployed at a density of approximately one per 225 m², with the total number of traps per site ranging from four to 32, depending on site size. Traps were set in the evening and then checked for beach mice in the early morning. Individuals were then released at the point of capture. Each site was surveyed once per year over five consecutive nights, with rare exceptions due to inclement weather.

2.2. Dynamic occupancy model

We adopted a hierarchical Bayesian approach to occupancy modeling because the resulting posterior probability distributions of latent process parameters can be easily used to simulate uncertainty in population viability analysis (Wade, 2002). The hierarchical approach to fitting dynamic occupancy models (Royle and Kéry, 2007; Royle and Dorazio, 2008; Link and Barker, 2010) to data requires two submodels: A state process submodel describes how occupancy status changes through time, and an observation submodel describes imperfection in the observation of that process. The observation model is important because the focal species may be present yet remain undetected during a survey. The observation model describes this uncertainty:

$$Y_{j,i,t}|z_{i,t} \sim \text{Bernoulli}(p_t z_{i,t}) \quad \text{for}$$
$$j = 1, 2, \ldots 5 \text{ temporal replicate surveys},$$
$$i = 1, 2, \ldots 61 \text{ survey sites, and}$$
$$t = 1, 2, 3, 4 \text{ years of observations}$$

where $y \in \{0, 1\}$ for nondetection and detection, respectively and $z \in \{0, 1\}$ for absence and presence, respectively.

The state model describes the ecological processes that drive occupancy dynamics. Following Royle and Kéry (2007) and Royle and Dorazio (2008), we use an auto-logistic formulation of change in occupancy through time because the probability of site occupancy at a given time, ψ_t, depends on whether or not the site is occupied at time $t - 1$. The state model for the first year that a site was sampled is simply:

$$z_{i,1} \sim \text{Bernoulli}(\psi_1) \quad \text{for } i = 1, 2, \ldots 61 \text{ sites}.$$

The true occupancy status (z) of sites during subsequent years is the net result of interannual survival (Φ) and colonization (γ) probabilities:

$$z_{i,t}|z_{i,t-1} \sim \text{Bernoulli}(\pi_{i,t}) \quad \text{for } t = 2, 3, 4$$

where

$$\pi_{i,t} = \gamma_{t-1}(1 - z_{i,t-1}) + \Phi_{t-1} z_{i,t-1} \tag{1}$$

Hence, the probability of occupancy at time t depends on either colonization (γ) or survival (Φ), depending on whether the site was previously unoccupied ($z_{i,t-1} = 0$) or occupied ($z_{i,t-1} = 1$), respectively. Covariate coefficients (β) can then be estimated from the equation:

$$\text{logit}(\pi_{i,t}) = \gamma_{t-1}(1 - z_{i,t-1}) + \Phi_{t-1} z_{i,t-1} + \omega_1 \beta_1 Cov1_i z_{i,t-1}$$
$$+ \omega_2 \beta_2 Cov2_i z_{i,t-1} + \cdots + \omega_4 \beta_4 Covn_i z_{i,t-1} \tag{2}$$

Note that all covariates in Eq. (2) are placed on survival ($z_{i,t-1}$) but not colonization ($1 - z_{i,t-1}$) because we are interested in using the covariates to predict the former but not the latter. Each