

Functional habitat connectivity for beach mice depends on perceived predation risk

Elliot B. Wilkinson · Lyn C. Branch ·
Deborah L. Miller

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Abstract Landscape features that promote animal movement contribute to functional habitat connectivity. Factors that affect the use of landscape features, such as predation risk, may alter functional connectivity. We identify factors important to functional habitat connectivity by quantifying movement patterns of the Santa Rosa beach mouse (*Peromyscus polionotus leucocephalus*) in relation to landscape features and by examining how ambient perceived predation risk, which is altered by moon phase, interacts with landscape features. We use track paths across the sand to relate the probability that beach mice cross gaps between vegetation patches to gap width, patch quality, landscape context and moon phase. Overall activity levels were lower during full versus new moon nights, demonstrating that beach mice respond negatively to moonlight. Gap crossing was more likely during new moon nights (25 % of gaps crossed vs. 7 % during full moon nights), and

across narrower gaps (<8.38 m) that led to larger vegetation patches (>11.75 m²). This study suggests that vegetation recovery is necessary for functional connectivity in post-hurricane landscapes commonly inhabited by beach mice and provides initial guidelines for restoring landscape connectivity. More broadly, this study highlights the importance of considering predation risk when quantifying landscape connectivity, as landscape features that facilitate connectivity when predation risk is low may be ineffective if predation risk increases over time or across space.

Keywords Functional connectivity · Predation risk · Beach mice · Gap crossing · Landscape restoration · Fragmentation · Animal movement · Santa Rosa Island · Florida

Introduction

As habitats are fragmented by natural or anthropogenic disturbance, movement among remnant habitat patches during foraging and dispersal becomes more important to population dynamics (Kadoya 2009 and references therein), distribution patterns (Ricketts 2001) and gene flow (Walker et al. 2007). The ability of organisms to move through fragmented habitats often is examined as a function of structural connectivity, or the amount and spatial configuration of suitable habitat in the landscape (Tischendorf and

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E. B. Wilkinson (✉) · L. C. Branch
Department of Wildlife Ecology and Conservation,
University of Florida, Gainesville, FL 32611, USA
e-mail: ebwilkinson@yahoo.com

D. L. Miller
Department of Wildlife Ecology and Conservation, West
Florida Research and Education Center, University of
Florida, Milton, FL 32583-1713, USA

Fahrig 2000). Recent work has shown that identifying landscape features that promote movement allows an understanding of connectivity from the perspective of the organism (functional connectivity; Taylor et al. 1993; Kindlmann and Burel 2008). Identifying landscape features that contribute to functional connectivity can improve predictions of animal distributions, population dynamics and gene flow in fragmented landscapes (Bélisle 2005; Stevens et al. 2006), and contribute to restoration and management strategies (Chetkiewicz et al. 2006).

Landscape features are associated with costs and benefits that influence animal movement, including risk of predation and benefits of resource acquisition (Brown and Kotler 2004; Bélisle 2005; Verdolin 2006). Intrinsic characteristics of landscape features that may affect costs and benefits of movement include patch size and quality (Uezu et al. 2005), matrix composition (Verbeylen et al. 2003; Castellon and Sieving 2006), gap size (Bright 1998), landscape context (Bélisle et al. 2001) and combinations of these factors (Rizkalla and Swihart 2007; Dancose et al. 2011, among others). Factors extrinsic to the landscape, such as individual energetic state (Turcotte and Desrochers 2003) or competitors (Turgeon et al. 2010) also affect relative costs and benefits that landscape features pose to movement and thus can be important to defining functional connectivity (Bélisle 2005). Ample evidence indicates that predation risk affects animal movement decisions (Lima and Dill 1990). Studies that address the importance of predation risk to functional connectivity often assume that predation risk is high in certain landscape elements such as gaps within a corridor, low quality habitat patches, and matrix habitat (Bélisle and Desrochers 2002; Hein et al. 2003; Castellon and Sieving 2006). In most cases the focal study organisms are found to avoid landscape elements putatively associated with high predation risk (but see Hein et al. 2003). However, predation risk does not vary independently from the landscape elements investigated in these studies and relative contributions of landscape elements and predation risk to functional connectivity are difficult to ascertain. An important issue that remains to be addressed is whether temporal or spatial variation in predation risk affects the degree to which landscape elements facilitate movement.

In this study we characterize functional habitat connectivity for the Santa Rosa Island (SRI) beach

mouse (*Peromyscus polionotus leucocephalus*) by quantifying movement patterns in relation to landscape features, and ask whether variation in perceived predation risk associated with moon phase affects the degree to which landscape elements facilitate movement. We use track paths of mice across the sand in both new and full moon nights to identify open sand gaps that are crossed between vegetation patches under different levels of perceived predation risk. We examine gap crossing behavior of mice in the context of well developed hypotheses from theoretical and empirical studies that propose movement patterns can be explained by (1) costs of movement such as mortality risk or travel costs, (2) benefits of increased resource acquisition, or (3) a balance between these costs and benefits (Lima and Dill 1990).

As a result of previous hurricanes, habitat on SRI comprises dune fragments that survived hurricanes surrounded by open sand, vegetation patches of different sizes and spatial configurations, and swale wetlands (Pries et al. 2009). Beach mice must repeatedly cross open sand gaps between vegetation patches during nightly foraging for seeds and insects. Recent work has demonstrated that intense selection from mammalian and avian predators such as coyotes, foxes, cats, owls and raptors maintains cryptic coat coloration that enhances survival of beach mice crossing open sand (Vignieri et al. 2010). Like other small mammals, beach mouse perception of predation risk during foraging depends on nocturnal illumination that varies through time (moon phase; Bowers 1988; Wolfe and Summerlin 1989; Orrock et al. 2004; Falcy and Danielson 2007) and across space (artificial lighting; Bird et al. 2004). In such instances, perception of predation risk may track actual predation risk, as efficiency with which predators capture small mammals is known to increase with the level of nocturnal illumination (Brown and Kotler 2004). Damage from storm surge across the length of SRI allows the study of movement behavior in replicate landscapes consisting of dune fragments surrounded by vegetation patches of different sizes and configurations. As a result, our study can address the simultaneous impacts of different gap widths, patch sizes and configurations on movement behavior under the different levels of perceived predation risk associated with moon phases. In addition, the fine sand and sparse vegetation cover on SRI make beach mouse tracks highly visible and allow precise tracking of

movement paths in relation to landscape features. No other small mammal species with similar tracks are found on this landscape (Wilkinson et al. 2012). Our study is based on the natural behavior of individuals embedded in different landscapes rather than translocated individuals that may exhibit non-typical movement behaviors (Bélisle 2005 and references therein; Heidinger et al. 2009).

We used our cost-benefit framework to develop a set of predictions about the probability of gap crossing based on potential costs and benefits that landscape features pose to movement under varying predation risk. We did not assess the functional connectivity of the landscape as a whole, as such characterizations at the landscape level can be prone to equating movement with functional connectivity when in fact overall resource availability is driving movement (Bélisle 2005). We focused instead on observations of gap crossing in replicate landscapes that enabled us to capture local variation in the costs and benefits that each landscape feature poses to movement. We predicted that gap width would influence gap crossing because it defines the amount of time mice are exposed to heightened predation risk and therefore influences the cost of moving through the landscape (Kotler et al. 1991; Longland and Price 1991). Second, we predicted that patch quality would influence gap crossing because patch quality influences cost:benefit ratio associated with movement (e.g., food and cover for a given level of risk, Lima and Dill 1990), especially during periods of heightened predation risk (Bowers 1988; Leaver and Daly 2003; Rizkalla and Swihart 2007). Third, we predicted that landscape context would affect gap crossing because use of a vegetation patch may depend on other habitat nearby (additional resources) or position within the matrix of non-habitat (travel costs or increased exposure to predation; Ricketts 2001; Castellon and Sieving 2006; Druce et al. 2006; Deconchat et al. 2009). Further, we predicted that changes in perceived predation risk with different levels of ambient light would alter animal response to gap width, patch quality and landscape context (Bright 1998; Rizkalla and Swihart 2007). Despite the potential for predation risk to modify costs associated with movement, the issue of whether perceived predation risk influences the relative importance of different landscape features to movement across an inhospitable matrix is largely unknown (but see Rizkalla and Swihart 2007).

Methods

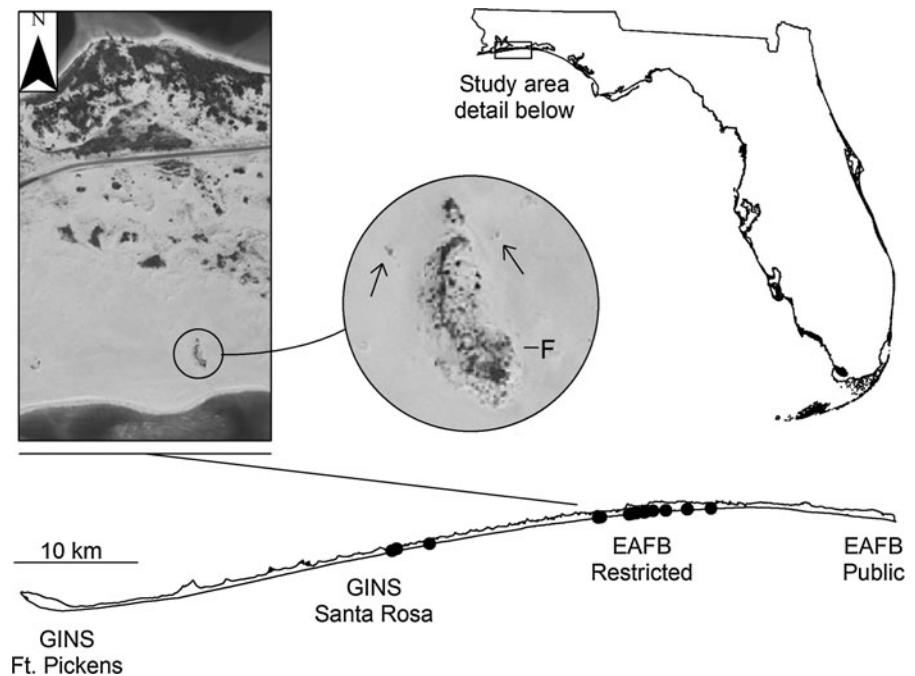
Study system

Beach mice are subspecies of the oldfield mouse (*Peromyscus polionotus*) that are unique to coastal landscapes of Florida and Alabama (Pries et al. 2009). This study focuses on the Santa Rosa beach mouse (*P. p. leucocephalus*). Our study was conducted on SRI, a barrier island in NW Florida, on undeveloped sections of the island managed by Eglin Air Force Base and Gulf Islands National Seashore (Fig. 1). This island has been damaged extensively by hurricanes Opal (1995), Georges (1998), Ivan (2004) and Dennis (2005), resulting in a 68 % loss of pre-storm dune area near the Gulf of Mexico (Pries et al. 2009). The landscape is characterized by a mosaic of sand flats caused by storm surge and wind erosion, vegetation patches entraining sand to form new dunes, grassy and woody dune fragments that survived recent hurricanes, and swale wetlands (boxed photo; Fig. 1). Each of our 14 study sites, which began 9–166 m from the gulf, was comprised of a dune fragment that survived hurricanes from 1995 to 2005. Dune fragments were surrounded by scattered vegetation patches with open sand gaps between them (circle detail; Fig. 1). For our study sites, we used dune fragments separated by more than 175 m, which was over seven times the median nightly foraging distance (25.11 m) of *P. p. leucocephalus* determined from a radio telemetry study (Branch et al. 2011). During the period of this study (April–September 2008), mouse density ranged from about 5–14 mice/ha (mean \pm SE June 2008 = 9.3 ± 2.6 , September 2008 = 7.2 ± 1.1) on 4 trapping grids that encompassed similar habitat on SRI (Branch et al. 2011). Densities of mice were not measured at the 14 sites in this study, but presumably exhibited similar patterns to the grids.

Sampling design

At each of our 14 study sites, we followed tracks of beach mice emerging from dune fragments on new and full moon nights in order to (1) determine whether overall activity patterns varied with moon phase and (2) identify factors important to functional habitat connectivity on new and full moon nights. Observations were limited to ± 3 days on either side of peak new and full moon nights to control ambient light

Fig. 1 Map of SRI in northwest Florida, USA, showing locations of study sites (black circles) and undeveloped areas including Gulf Islands National Seashore (GINS) Ft. Pickens and Santa Rosa units, and Eglin Air Force Base (EAFB) Restricted and Public sections. An example study site (circle) is shown on an aerial photograph taken in January 2007. Each site comprises a dune fragment (*F*) in habitat heavily damaged by hurricanes near the Gulf of Mexico and vegetation patches around the fragment (marked with arrows)



levels, which corresponded to moon face illumination of <25 % (new moon) or >75 % (full moon). Observations at a given site were conducted during subsequent moon phases, which minimized the possibility of changes in mouse density between new and full moons. The moon phase for initial observations was chosen randomly. To measure overall activity patterns on new and full moon nights, we recorded number of paths emerging from dune fragments, as well as number of open sand gaps crossed between vegetation patches within 40 m of dune fragments (Table 1). This distance was large enough to encompass the median foraging distance of *P. p. leucocephalus* and small enough to be logistically feasible.

A vegetation patch was defined as any area with vegetation that had accumulated at least 15 cm of sand above the storm surge overwash plain and was separated from other vegetation patches by ≥ 1.5 m of open sand (thus defining a minimum gap width). To define available gaps we mapped the network of all possible straight-line connections between vegetation patches that did not intersect another vegetation patch. We defined gaps in this manner based on the assumption that beach mice cross open sand between vegetation patches in approximately a straight line. To examine our assumption of straight-line movement, we measured tortuosity of beach mouse tracks. We

staked flags every 2 m along track paths ($n = 217$) to facilitate measurement of total path length. Track paths for measurements of tortuosity were defined as a continuous set of mouse tracks extending at least 4 m. Comparisons of straight line and total path length indicated that tortuosity was near 1, which characterizes straight-line movement (arc-chord ratio; full moon = 1.09 ± 0.01 SE, $n = 53$; new moon = 1.14 ± 0.03 , $n = 164$).

Sand tracking

To ensure that all tracks followed were from the previous night and to facilitate detection of gap crossing, we used utility brooms to remove existing tracks and sweep a smooth surface (track pad) around the dune fragment and other vegetation patches within 40 m of the fragment the afternoon before data were to be collected. In addition, we enhanced our ability to follow tracks by sweeping track pads in concentric circles spaced 10 m apart in a bull's eye pattern out to 40 m from the dune fragment. Tracks were followed until they were 40 m from the dune fragment or were lost in dense vegetation (49 % of tracks). In order to standardize conditions for observing tracks, we recorded data only after clear nights, when sand was dry and smooth, and when

Table 1 Local and landscape variables measured for analysis of functional connectivity in hurricane-damaged habitats

Landscape feature	Measure	Description
Open sand gap	Gap width	Width (m) of open sand gap between the patch of origin and the destination patch (smallest distance between proximate edges).
Vegetation patch ^a	Patch size	Elliptical area (m ²) calculated from length and width of destination patches or patches of origin at their longest and widest points.
	Vegetation cover	Coverage categories representing percentage of vegetation cover in destination patch estimated visually in the field: 0 (0 %), 1 (1–15 %), 2 (15–30 %), 3 (31–45 %), 4 (46–60 %), 5 (61–75 %), 6 (76–90 %), 7 (>90 %).
	Vegetation height	Tallest vegetation (m) in destination patch, measured from plant base to tip of living growth.
	Sand height	Height of sand buildup around destination patches (m), measured as vertical height above the flat overwash plane.
Landscape context of vegetation patch	Neighboring patches	Number of patches within 10 m of particular destination patch.
	Distance to dune fragment	Distance (m) to nearest woody scrub dune or mixed grassy/woody dune fragment that survived all recent storm surge overwash, measured as edge to edge distance from the destination patch to the dune fragment. Dune fragments were identified from post-hurricane mapping conducted by Pries et al. (2008).
	Distance to swale wetland	Distance (m) from the edge of a destination patch to low-lying swale area. Swale boundaries were identified from jurisdictional wetland mapping conducted by Cardno-Entrix Inc. according to Florida Department of Environmental Protection guidelines (Gilbert et al. 1995).
Predation risk	Moon phase	Observations occurring within 3 days of either new (low light and predation risk) or full moon (high light and predation risk).

^a All vegetation patches within 40 m of a dune fragment were included in the analysis. See “Methods” for a full definition of vegetation patches

current/overnight wind conditions were not likely to have affected tracks.

Measurement of local and landscape variables associated with gap-crossing

For gaps that were crossed and not crossed, we recorded gap width, characteristics of vegetation patches at either end of the gap, and landscape context of vegetation patches (Table 1). We measured gap width as the straight-line distance between proximate edges of vegetation patches. In the case that a gap was not crossed and the patch at the end of the gap could not be determined by track direction, the target patch for analysis was chosen randomly from the two possible patches bracketing the gap. This same method was used in rare instances when mice turned around in the middle of a gap and did not cross. Our measures of vegetation patches were based on the assumption that larger or more densely vegetated patches, taller vegetation, or more sand accumulation around vegetation are of higher quality for beach mice and that these characteristics offer perceptual cues about patch

quality to mice (Zollner and Lima 1999). Vegetation provides food and cover from predators, and accumulated sand provides a substrate for burrowing. To assess the influence that landscape context may have on functional connectivity, we measured the number of neighboring vegetation patches within 10 m of each vegetation patch, as well as distances of each patch from two key features of the landscape: dune fragments and swale wetlands (Table 1). Dune fragments and vegetation patches provide food resources and burrow sites for beach mice (Pries et al. 2008). The importance of swale wetlands to beach mice is unknown, but they may contain plant and insect resources during dry periods (Blair 1951).

Analysis

To assess differences in overall activity levels under different levels of perceived predation risk, we used paired *t* tests to compare (1) the number of paths leaving each dune fragment and (2) the number of gaps crossed around each fragment between new and full moon nights. The number of paths leaving dune

fragments was log transformed ($\log x + 1$) to meet assumptions of normality. Total numbers of paths leaving dune fragments and gaps crossed around dune fragments on new and full moon nights also are reported and are based on raw data summed across replicate dune fragments.

We used two modeling approaches to explain variation in gap crossing (crossed or not crossed) as a function of our explanatory variables (Table 1), while taking into account subsampling within each replicate study site (i.e., multiple observations of gap crossing around each dune fragment). First, we used Generalized Linear Mixed Models (GLMM) to test predictions developed from theoretical and empirical understanding of movement behavior and our study system. The hierarchical approach of GLMMs allows variation among subsamples in space or time to be specified in the error structure of the model, thus reducing the problems associated with pseudoreplication (Crawley 2007). However, correctly specifying the content and form of mixed models can be difficult when data are hierarchical, increasing the possibility of overlooking important interactions or combinations of variables (De'ath and Fabricius 2000). Therefore we also used classification tree analysis, which is a non-parametric approach to analysis of subsampled data that uses cross-validation of independent training and test datasets to determine model performance. Classification trees are useful for conservation and restoration because they identify specific levels of each factor that most influence the response variable (Vayssières et al. 2000).

Generalized linear mixed models

We constructed 73 candidate models representing biologically relevant predictions about factors affecting gap crossing probability. Although costs and benefits that individual landscape features pose to movement are known from prior empirical and theoretical studies, the relative importance of these features to movement is difficult to predict in systems where the natural history of the focal species is not fully understood. Thus, we took an exploratory approach to model construction and evaluated whether gap crossing by beach mice is related to (1) costs of movement (models contained variables for gap width, moon phase, distance to dune fragment, and distance to swale wetland), (2) benefits of resource acquisition

and/or cover from predators (models contained patch quality variables and number of neighboring patches), or (3) a balance of costs of movement and benefits of resource acquisition (models contained gap width, moon phase, patch quality and landscape context variables). To incorporate the possibility that different levels of ambient light would alter animal response to gap width, patch quality and landscape context, we developed additional models that included the interaction of moon phase with these landscape features (Bowers 1988; Bird et al. 2004; Orrock et al. 2004; see Supplementary Materials for details).

To account for sources of variation associated with the sampling design, we included random terms and covariates in our mixed models. Random terms were included in each model for repeated measures within site (Measure|Site) and Julian date (1|Julian date). The Measure|Site term controls for temporal autocorrelation across repeated measures within each site as well as variation in gap crossing behavior between sites. The 1|Julian date term controls for seasonal effects and similar weather patterns in temporally clustered observations. We controlled for the effect of origin patch size on gap crossing probability by including origin patch size as a covariate in the analysis. The size of the patch of origin is needed as a covariate to control for the possibility that larger patches may be associated with greater numbers of mice available to cross gaps or that mice in larger patches have a decreased incentive to cross gaps because of higher resource return rate (Brown and Kotler 2004). Finally, we developed a spatial autocovariate to account for spatial dependence in gap crossing responses within sites. Inclusion of the spatial autocovariate in models successfully accounted for spatial dependence in gap crossing, as seen by a lack of spatial dependence in model residuals (see Supplementary Materials).

To explain variation in gap crossing as a function of variables in each model, we used R package “lme4” (function glmer; Bates et al. 2011), specifying a binomial error structure with a Logit link function. Non-normal variables were log or square-root transformed as appropriate, and all variables were z-standardized before analysis. We tested for multicollinearity in each of our models with variance inflation factors (VIF; Chatterjee et al. 2000), all of which exhibited VIF's < 2. We assessed model performance using AICc (Akaike's information criterion corrected for small sample size). We evaluated

evidence supporting competing models with Akaike weights (w_i) and used model averaging to provide conservative estimates of model parameters and generate confidence intervals based on unconditional standard errors (Burnham and Anderson 2002). Model-averaged estimates were based on models falling within the 95 % confidence set as defined by Akaike weights (Burnham and Anderson 2002).

Classification tree analysis

As with GLMMs, we used classification tree analysis to explain variation in gap crossing (crossed or not crossed) as a function of our explanatory variables (Table 1; De'ath and Fabricius 2000). With classification tree analyses, explanatory variables are split into binary groups by maximizing homogeneity in the response variable (in this case, gaps crossed vs. not crossed). The value of the explanatory variable that splits the response variable into the most homogenous groups possible (as measured by the Gini impurity index) is used to define the first split, and then the process is repeated on each resulting group until a tree is grown. Classification trees make no assumption about the underlying distribution of data and can incorporate both categorical and continuous data in explanatory variables (Breiman et al. 1984).

We used cross-validation of independent training and test subsets to determine the misclassification rate for trees of different sizes, and followed the Breiman et al. (1984) 1 SE rule to choose a tree of size i that was not too complex but fit the test subset well (low cross-validation error; see Supplementary Materials). We used percent correctly classified as an overall measure of predictive success (De'ath and Fabricius 2000; Pries et al. 2008; Davidson et al. 2009). In addition, we used Cohen's kappa statistic to determine overall significance of the optimal classification tree (R package "irr"; Gamer et al. 2011; Davidson et al. 2009).

Analysis of use versus availability of gaps and patches

To confirm that beach mice were not simply using gaps and patches of different sizes in proportion to their availability on the landscape, we conducted a resource selection analysis that tested whether frequency of use (i.e., gap size crossed or size of vegetation patch used) differed from availability in the landscape. We focused on new moon nights because

most gaps were crossed during this moon phase. This method required binning our data into categories to generate frequency data. Bin width was determined with Scott's rule (Scott 2009). We used package "adehabitat" in R to estimate Manly's selection index (w_i) with Type III analysis, which compared use and availability of landscape features separately for each of our 14 replicate landscapes (Manly et al. 2002; Calenge 2006).

Preference for a particular gap size and patch size may not be independent if characteristics of these features are associated as a result of storm erosion (e.g., small gaps associated with large patches). If this pattern held for our study area, we would expect larger patches to be visited more often after crossing narrower gaps. To explore this possibility, we used a Chi square test to determine whether the size of vegetation patches visited was independent of the width of the open sand gaps preceding them. Frequency data for this test also was generated with Scott's rule (Scott 2009).

Results

Overall activity levels of mice differed between full and new moon nights. Fewer paths exited dune fragments during full moon nights (53) than during new moon nights (164; $t_{13} = -6.25$, $P < 0.01$). Likewise, fewer gaps were crossed during full moon nights (67) than during new moon nights (239; $t_{13} = -5.26$, $P < 0.01$).

Generalized linear mixed models

A single model received the majority of support as the top model describing gap crossing by beach mice ($w_i = 0.93$), and no other models were competitive ($\Delta AICc < 2$). The top model included gap width, patch size, number of neighboring patches, moon phase and the two-way interactions between moon phase and other variables (Table 2). Wider gaps and increased nocturnal illumination (moon phase) were negatively associated with probability of gap crossing. The two-way interaction between these variables was positively associated with probability of gap crossing, indicating that the negative effect of gap width weakened during full moon nights. Probability of crossing gaps increased as the size of the destination

patch increased, but the number of neighboring patches within 10 m of the destination patch was negatively associated with gap crossing.

Classification tree analysis

The cross-validation plot indicated that a tree consisting of four branches fit the data while also minimizing the misclassification error rate (see Supplementary Materials). Moon phase and gap width were identified as the two most important factors influencing whether mice crossed open gaps to reach vegetation patches (Fig. 2). Our classification tree predicted that gaps would not be crossed during full moon, which was correct in 93 % of cases. No measured variable offered any further explanation of gap crossing patterns during full moon (i.e., the 7 % of the gaps crossed).

Multiple factors interacted to influence gap crossing during new moon nights. Beach mice crossed narrower gaps (<8.38 m) more frequently than wide gaps and moved to relatively large patches (>11.75 m²) more frequently than to small patches. This branching pattern correctly classified 79 % of

cases during the new moon (Fig. 2). The entire tree (including both full and new moon branches) correctly classified 86 % of cases, which was more than would be expected by chance (Cohen's kappa = 0.3, $z = 15.6$, $P < 0.001$).

Analysis of use versus availability of gaps and patches

Resource selection analysis indicated that smaller gaps and larger patches were used more often than their availability in the environment (and visa-versa, Fig. 3). Size of target patches visited was independent of width of the open sand gap preceding them ($\chi^2_{72} = 80.66$, $P = 0.75$).

Discussion

Moonlight had a large negative effect on movement in both GLMM and classification tree analyses. Beach mice crossed only 7 % of available gaps during full moon nights, as opposed to 25 % on new moon nights.

Table 2 Model averaged parameter estimates for predictor variables in the top model describing gap crossing by the Santa Rosa Beach Mouse (*Peromyscus polionotus leucocephalus*) on SRI, Florida

Parameter ^a	Standardized estimate ^b	Unconditional standard error ^c	95 % CI ^d
Gap width (GW)	-1.10	0.10	-1.29, -0.89
Patch size (PS) ^e	0.71	0.09	0.53, 0.89
Neighbor patches (NP)	-0.34	0.09	-0.52, -0.16
Moon phase (MP) ^f	-0.74	0.11	-0.96, -0.53
MP × GW	0.28	0.10	0.08, 0.47
MP × PS ^e	0.01	0.09	-0.17, 0.19
MP × NP	0.08	0.09	-0.10, 0.26
Spatial autocovariate	0.65	0.09	0.49, 0.83
Origin patch size covariate	0.58	0.08	0.42, 0.74

^a Fixed parameters contained within the top model as ranked by AICc (see Supplementary Materials for complete model set, rankings and influence of random terms)

^b Model-averaged estimates based on models falling within the 95 % confidence set as defined by Akaike weights (Burnham and Anderson 2002). The 95 % confidence set included two models, which together accounted for 99.9 % of the evidence supporting our models (w_{tot})

^c Calculated from model-averaged parameter estimates

^d Calculated from unconditional standard errors

^e Patch size and Moon phase*Patch size terms were only present in one model from the 95 % confidence set. As a result, we based the model-averaged parameter estimate, unconditional standard error and 95 % CI for these variables on the full model set. Including models outside the 95 % confidence set is unlikely to have biased model-averaged parameter estimates because these models received <0.1 % of the total support for models (w_{tot} ; see ^b above)

^f Full moon was the reference category

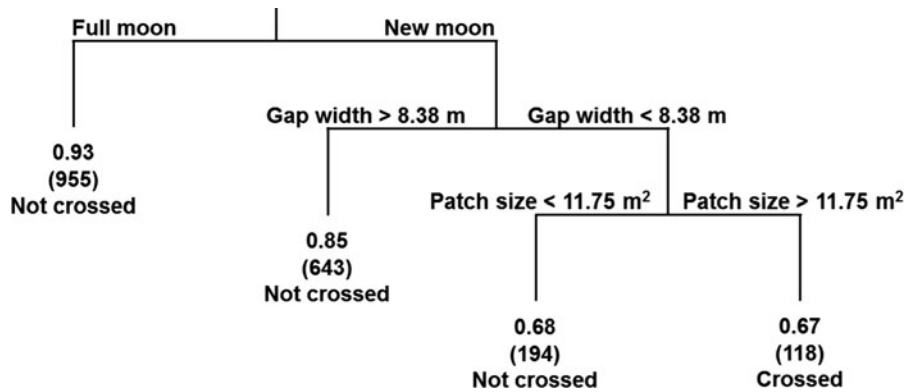


Fig. 2 Classification tree relating probability of gap crossing by beach mice to landscape features and perceived predation risk. *Categories* or *numbers* on top of each branch indicate the value of the explanatory variable that, when used to split the response variable, leads to maximum homogeneity of resulting

groups. The end of each branch is labeled according to whether gaps in this group were predominantly crossed or not crossed. *Numbers* at the end of each branch indicate the proportion of observations in that group correctly classified. The total number of observations (gaps) in each group is listed within *parentheses*

Overall activity as measured by the numbers of paths leaving dune fragments also was lower during full versus new moon nights. These patterns lend additional support to previous studies showing that beach mice use nocturnal illumination to gauge ambient predation risk and minimize the costs of movement (Bird et al. 2004; Falcy and Danielson 2007).

In most cases, behavior of beach mice on the landscape corresponded to our predictions based on

costs and benefits that each landscape feature should pose to movement. For instance, the strong negative association between probability of crossing gaps and gap width is consistent with greater predation risk while crossing open sand gaps (Kotler et al. 1991; Longland and Price 1991). Likewise, we expected that larger vegetation patches would provide more resources or refuge from predators, and observed a positive association between destination patch size and gap crossing probability (Lima and Dill 1990). Support for the role of food and cover in influencing behavioral decisions is provided by experiments demonstrating that foragers are more willing to risk predation to deplete resource patches when resource quality in the patch is high and when resource patches are in or near vegetation that provides cover from predators (Verdolin 2006). Larger vegetation patches also could result in greater risk to mice because large patches could harbor more terrestrial predators (Lima and Dill 1990). However, the gap-crossing behavior of mice indicates that they did not perceive such a risk. The positive effect of origin patch size on gap crossing likely resulted from increased numbers of mice present to cross gaps rather than an increase in the incentive for mice to cross gaps. Larger origin patches could decrease the propensity of mice to cross open sand gaps because of higher resource return rates in larger patches (Brown and Kotler 2004). However, if this were the case, the effect of this covariate would have been closer to zero or negative. Other measures of patch quality such as vegetation cover, vegetation height and sand height contributed less to explaining

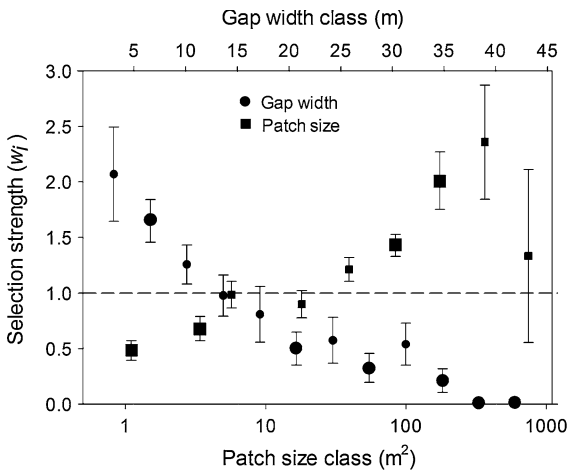


Fig. 3 Preference of beach mice for different sized open sand gaps (*circles*) and vegetation patches (*squares*) during new moon nights. Mean selection strengths (\pm SE) for classes that are significantly different than expected based on availability are indicated with *larger symbols*. Note that patches in the largest size category were found at only 3 sites as opposed to 7–14 sites for all other patch size categories, resulting in a large error and lower confidence for selection strength in this category

gap crossing behavior, suggesting that beach mice were less able to perceive these features or were less likely to associate them with benefits of movement (e.g., resources, refuge, mating opportunities; Zollner and Lima 1999).

Measures of landscape context did not affect gap crossing in ways that were clearly related to costs and benefits associated with movement. For instance, increasing the number of neighboring patches can increase the potential for resource acquisition and benefits associated with crossing to a particular destination patch (Castellon and Sieving 2006). In our study the number of neighboring patches within 10 m of a destination patch had a negative effect on gap crossing probability. This pattern may occur because an abundance of neighboring patches is perceived by mice as risky habitat because large amounts of vegetation cover may conceal predators (Verdolin 2006). However, this explanation is contrary to the observation that mice do not appear to perceive large patches of vegetation as risky. The negative effect of neighboring patches is more likely to have occurred because increasing local patch availability leads to decreasing likelihood that a given patch will be visited. In addition, we expected that beach mice would be less likely to cross to destination patches positioned further from dune fragments or swale wetlands because of higher travel costs and exposure to predation (Druce et al. 2006). However, neither of these measures of landscape context contributed to explaining gap crossing behavior.

Gap crossing behavior was not simply a function of availability of different sized gaps and patches in the landscape, as beach mice used narrow gaps and larger vegetation patches more than the availability of these features in the landscape. The fact that mice avoided the largest gaps and actively sought out large vegetation patches suggests that vegetation recovery is necessary for functional connectivity in post-hurricane landscapes. Our data provide initial guidelines on maximum gap width and minimum vegetation patch size for restoration aimed at improving landscape connectivity for beach mice (Tischendorf and Fahrig 2000). The importance of both gap width and patch size was not a function of these variables behaving as a compositional set, which would be expected if increases in open sand gaps led to proportional decreases in vegetation patch size as hurricane damage increased. Instead, the size of vegetation patches

visited was independent of the width of the open sand gap crossed to reach the patch.

Functional connectivity is defined by behavioral responses to landscape features during movement (Tischendorf and Fahrig 2000; Kindlmann and Burel 2008). The results of this study indicate that functional connectivity may not be static, and may instead depend on perceived predation risk associated with nighttime illumination. Probability of gap crossing was negatively associated with increased nocturnal illumination (full moon) and longer gaps. However, the negative effect of gap width weakened during full moon nights, as indicated by a positive gap width \times -moon phase interaction in GLMM analysis. Likewise, classification tree analysis indicated that gap width was the most important landscape feature contributing to gap crossing during new moon nights, but had little explanatory power during full moon nights. These patterns suggest that beach mice responded to increased nocturnal illumination by lowering their overall exposure to risk by crossing fewer gaps (Fraser and Huntingford 1986) rather than by altering which landscape elements they used or increasing their selectiveness for particular landscape elements (Leaver and Daly 2003). If foraging patterns during full moon nights are a function of perceived predation risk, our study indicates that risk avoidance behaviors may reduce connectivity and enhance sensitivity to fragmentation.

This study highlights the importance of considering factors that alter perceived predation risk when quantifying landscape connectivity from the perspective of an organism. Numerous factors can alter perceived predation risk, including introduction of artificial light (Bird et al. 2004) or changes in abundance of native or introduced predators (With 2002). Landscape features that facilitate connectivity when perceived predation risk is low may become ineffective if perceived predation risk increases over time or across space. As a result, conservation actions intended to facilitate animal movement may not be effective unless they are based on studies conducted across a range of landscapes with different predation risks.

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