Enhancing the area–isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal

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Abstract. Conservation of species in fragmented landscapes often is guided by spatially realistic metapopulation theory. However, convincing cases of metapopulation dynamics are uncommon, especially for vertebrates. Moreover, there is concern that the patch area and isolation paradigm for metapopulations is an oversimplification for heterogeneous landscapes. We tested predictions from metapopulation theory for a rare wetland mammal (round-tailed muskrat, *Neofiber alleni*) and asked whether it was necessary to use a habitat-informed version of the area–isolation paradigm that included patch quality and matrix heterogeneity. In each of two years, we surveyed 457 isolated wetlands in central Florida, USA, for presence–absence of *Neofiber* and evaluated logistic regression models of patch occupancy, extinction, and colonization. We documented metapopulation dynamics in which patch occupancy was constant between years (26% of patches occupied) due to balanced local extinctions ($n = 45$) and recolonizations ($n = 46$). *Neofiber* was both habitat and dispersal limited. Local extinctions were related negatively to patch area, patch quality (cover of maidencane grass, *Panicum hemitomon*), and distance to nearest roadside ditch. Patch colonization depended on patch area, patch quality, and spatial connectivity to potential source wetlands. Despite the importance of patch quality, *Neofiber* did not exhibit a habitat-tracking metapopulation on an annual time scale. Cost–distance modeling suggested effective distances that included high costs for moving through forested matrix habitats generally were better than Euclidean distances for predicting patch colonization and occupancy. Two dominant land uses were tied to turnover dynamics: cattle grazing decreased habitat quality of wetlands, and presence of pine (*Pinus* spp.) plantations decreased functional connectivity. The simple area–isolation paradigm was not adequate for characterizing spatial dynamics of the *Neofiber* metapopulation. Nevertheless, we contend that the metapopulation approach remains a useful conservation framework for many species if landscape heterogeneity is embraced and explicit effects of land-use practices on turnover processes are considered.

Key words: central Florida, USA; connectivity; cost–distance modeling; dispersal; extinction; habitat heterogeneity; matrix; metapopulation; Neofiber alleni; *patch occupancy; round-tailed muskrat; wetland.*

Introduction

Species conservation in fragmented landscapes often is based on predictions from spatially realistic metapopulation theory (Hanski 1994, Sjögren-Gulve and Ray 1996, Hokit et al. 1999, Hames et al. 2001). However, debates are ongoing regarding whether the patch area and isolation paradigm for metapopulations is an adequate conceptualization of fragmented landscapes and the utility of this paradigm for conservation (Baguette 2004, Shreeve and Dennis 2004, Pellet et al. 2007). An extreme imbalance exists between theoretical models and field investigations for metapopulations. However, if land-management practices are to be based on concepts from metapopulation theory, a solid empirical foundation

must be built and the importance of habitat complexity not captured by the area–isolation paradigm must be understood. The area–isolation paradigm may require incorporation of habitat heterogeneity and consideration of linkages between land use and turnover dynamics for metapopulation approaches to have consistent applications to biodiversity conservation (Sjögren-Gulve and Ray 1996, Fleishman et al. 2002, Thomas and Hanski 2004, Schooley and Branch 2007).

Classical metapopulation theory as formalized in the model of Levins depicts species inhabiting subdivided habitat and persisting regionally due to symmetry in local extinctions and recolonizations across patches (Hanski 1994). However, empirical evidence for classical metapopulations remains meager (Harrison and Taylor 1997, Baguette 2004). The requisite high rate of patch turnover and extinction–colonization equilibrium rarely have been demonstrated, in part because many metapopulation studies rely on a single-year snapshot of patch occupancy and cannot investigate extinction–colonization dynamics and their determinants (Clinchy

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et al. 2002). Also, studies of classical metapopulations can be unrepresentative if conducted near the periphery of geographic ranges of the species where population dynamics are atypical (Baguette 2004, Antonovics et al. 2006; but see Hanski 2004). Classical metapopulation theory developed into a spatially realistic version in which sizes and explicit spatial locations of habitat patches are considered (Hanski and Gaggiotti 2004). Spatially realistic metapopulation theory often has been applied with a binary, patch-matrix perspective and with an emphasis on how patch size affects extinction risk and how patch isolation affects colonization success (Hanski 1994, Wiens 1997). Such theory is most appropriate for species in highly fragmented landscapes (Hanski 2004). A recent analysis of multiyear occupancy data for 10 species revealed shaky support for the area–isolation paradigm derived from spatially realistic metapopulation theory (Pellet et al. 2007). Patch area was not a strong predictor of extinction risk due to a weak correlation between patch area and population size, and connectivity generally did not improve predictions of colonization.

Although metapopulation ecology and landscape ecology have been reluctant partners historically, a coupling of metapopulation approaches with landscape heterogeneity is underway (Wiens 1997, Thomas and Hanski 2004, With 2004, Armstrong 2005, Schooley and Branch 2007). Some failures of the area–isolation paradigm to predict behavior of populations in patchy environments is likely due to the lack of integration of habitat quality into measurements of patch area and connectivity (e.g., Pellet et al. 2007). Suitable patches often are not homogeneous and habitat quality influences population size, probability of extinction, and availability of dispersers (Hokit et al. 1999, Fleishman et al. 2002, Franken and Hik 2004). Also, matrix habitat is heterogeneous and may affect the ability of organisms to move among patches (Ricketts 2001), altering rates of demographic rescue and recolonization (Brown and Kodric-Brown 1977). Ecologists are attempting to integrate matrix quality with Euclidean distances to derive more functional measures of landscape connectivity for predicting colonization and occupancy (Moilanen and Hanski 1998, Roland et al. 2000, Verbeylen et al. 2003, Schooley and Wiens 2005). Patchily distributed species might even form habitat-tracking metapopulations in which habitat dynamics are of overriding importance, extinctions are due to deterministic population declines related to deterioration of habitat patches, and colonizations follow increases in patch quality (Thomas 1994, Snäll et al. 2003, Pita et al. 2007). This perspective of metapopulations differs from classical metapopulation theory in which local extinctions are caused by demographic and environmental stochasticity and result in empty but suitable patches available for recolonization (Thomas 1994, Thomas and Hanski 2004).

We investigated spatial dynamics of round-tailed muskrats (*Neofiber alleni*) by integrating habitat hetero-geneity into the area–isolation paradigm of metapopulations. We evaluated statistical models of patch occupancy, extinction, and colonization; tested predictions from spatially realistic metapopulation theory; and determined whether data on habitat quality improved these predictions. We addressed two of the potential weaknesses of metapopulation studies in that we conducted our research at the core of the geographic range of the species (Lefebvre and Tilmant 1992), and we used multiyear data to test the assumption that patch turnover processes were in equilibrium. A key feature of our study was a large sample size (457 wetlands) that allowed us to identify determinants of extinction and colonization events and unravel how these turnover processes contribute to patch occupancy patterns (Bulman et al. 2007). We adopted a mosaic approach to landscapes by emphasizing matrix heterogeneity, functional connectivity, and dispersal constraints. Finally, we investigated whether land-use practices were related to distribution dynamics of round-tailed muskrats with a goal of providing practical management recommendations for this species of conservation concern.

METHODS

Study system

The round-tailed muskrat (adult ≈ 250 g) is a semi-aquatic, nocturnal, secretive herbivore that prefers shallow marshes with emergent vegetation (Birkenholz 1963, Lefebvre and Tilmant 1992). In central Florida, the diet of round-tailed muskrats is primarily maid-encane (*Panicum hemitomon*) stems and roots, and muskrats often use maidencane to build lodges (Birkenholz 1963). Round-tailed muskrats use multiple rest sites (lodges or burrows) within their small home ranges that average ≈2000 m^2 (Schooley and Branch 2006). Local populations of this enigmatic wetland species can fluctuate dramatically, partly in response to flooding and drought (Birkenholz 1963). Round-tailed muskrats can breed year-round depending on environmental conditions and produce four or five litters per year (Birkenholz 1963). Timing of dispersal is unknown, but absence of a discrete breeding season suggests dispersal could occur throughout the year. Direct estimates of dispersal capacity are lacking for the species. *Neofiber* is a monospecific genus with a geographic distribution restricted to Florida and southern Georgia (Lefebvre and Tilmant 1992, Bergstrom et al. 2000). The round-tailed muskrat has been proposed as a species of Special Concern in Florida because of presumed population declines caused by wetland losses (Lefebvre and Tilmant 1992), and it is a threatened species in Georgia (Bergstrom et al. 2000).

We conducted our research on a 19 500-ha area in the southern portion of Avon Park Air Force Range (hereafter Avon Park; 15 km east of the town of Avon Park, Florida). Most suitable habitat for round-tailed muskrats consisted of geographically isolated (Tiner 2003), freshwater, seasonal wetlands surrounded by a

terrestrial matrix (Fig. 1). These depression marshes are also termed flatwoods marshes, seasonal ponds, flag marshes, and wet prairie (Kushlan 1990). Such wetlands typically dry out for part of spring (March–May), refill mainly due to summer rains (June–September), and are generally shallow (water depth <50 cm). Depression marshes often have concentric rings of plant zones due to hydroperiod and water depth (Kushlan 1990). At Avon Park, outer zones typically were dominated by shrubby St. John's wort (*Hypericum fasciculatum*), middle zones by maidencane grass, and inner zones by pickerelweed (*Pontederia cordata*). Other common species included *Juncus effusus*, *Spartina bakeri*, *Rhynchospora inundata*, *Sagitteria lancifolia*, *Aristida* spp., *Andropogon virginicus*, *Eriocaulon decangulare*, and *Cladium jamaicense*.

Besides depression marshes, the only other suitable habitat for round-tailed muskrats occurred as small patches within two large floodplain complexes (Arbuckle and Kissimmee marshes) located on the edges of our study area (Figs. 1 and 2). Field surveys from February 2003 indicated that both marshes were internally heterogeneous and included much non-suitable habitat. Hence, these floodplains contained some potential sources for dispersers, which we will consider when we measure patch connectivity, but they should not be viewed as large homogeneous areas that would act as mainlands to the depression marshes that we surveyed for muskrat occupancy.

We identified 457 suitable habitat patches (depression marshes) from low-altitude aerial photographs (1:4800) taken when wetlands were inundated and easily classified. We then digitized the wetlands in ArcView GIS (Version 3.2, ESRI, Redlands, California, USA) and verified their presence via ground reconnaissance. Many marshes were small (median = 0.94 ha) but their area was variable (0.04–73.81 ha). Nearest-neighbor distances between marshes averaged 312 m (85–1435 m). Depression marshes covered only 4.6% of the landscape (Fig. 1).

The study area is flat (12–24 m above sea level) except for a central, xeric scrub ridge (42 m asl). Nevertheless, matrix habitat is diverse due to soils, drainage, fire history, and other land uses. Treeless habitat comprised of nonforested flatwoods and Florida dry prairie is divided by forested flatwoods (*Pinus palustris*, *P. elliottii* var. *densa*), slash pine plantations (*P. elliottii* var. *elliottii*), oak scrub (*Quercus* spp.), oak hammocks, Bahia grass pastures (*Paspalum notatum*), and swamps (Fig. 1). These land-cover types also were identified from low-altitude aerial photographs, field verified, and digitized in ArcView.

Land use

Intensity of cattle grazing in freshwater marshes could affect habitat quality for round-tailed muskrats because cattle prefer maidencane grass and can reduce its abundance (Kalmbacher et al. 1984, Long et al. 1986,

U.S. Soil Conservation Service 1987, Kushlan 1990). At Avon Park, 412 (90%) of our 457 wetlands were located in areas that receive moderate, rotational grazing by cattle (hereafter termed "moderate"). Another 11 wetlands were surrounded by Bahia grass pastures where cattle were aggregated densely during portions of the year ("heavy"). Finally, 34 wetlands were located within areas where cattle had been excluded since at least 1994 ("ungrazed"). Most (94%) of these ungrazed wetlands occurred in a single 1410-ha block. We evaluated habitat quality of wetlands (see *Wetland traits and landscape position* below) and occupancy rates of wetlands in relation to grazing pressure (ungrazed, moderate, heavy).

Slash pines are planted in blocks of ~35 ha as part of forest management at Avon Park (Fig. 1). These plantations are characterized by canopy cover that is denser than that of naturally occurring pine flatwoods. Moreover, plantations create unusually sharp boundaries with adjacent open habitat. Because round-tailed muskrats primarily are a species of open habitat, we hypothesized that muskrats avoid heavily forested areas while dispersing. Hence, we expected that any influence of pine plantations on muskrats would be detected as a negative effect on colonization of vacant wetlands and subsequent occupancy patterns.

Survey procedures

We surveyed 457 depression marshes for occupancy of round-tailed muskrats during fall and winter in each of two years. In 2002–2003, surveys were conducted from 3 July to 15 February, but most (86%) were carried out after 30 September. In 2003–2004, surveys were conducted from 30 September to 22 January. We surveyed wetlands in a quasi-random manner; strictly random sampling was impossible due to constraints from military activities. Occupancy of wetlands by round-tailed muskrats was based on presence of their distinctive spherical to dome-shaped lodges built of tightly woven vegetation and positioned just above water level (Birkenholz 1963, Bergstrom et al. 2000). We searched wetlands for muskrat lodges by walking adjacent belt transects oriented parallel to the long axis of the wetland and initiated in vegetation zones dominated by emergent grasses and forbs. Spacing between observers (~2–6 m) was dictated by vegetation thickness and allowed for a thorough inspection of intervening habitat.

Schooley and Branch (2005) present more details on our survey techniques. Here, we summarize our assessment that indicated that we had a detection probability near 1.0 with a single visit, and that it was valid to treat survey results as presence–absence data (MacKenzie et al. 2003, Gu and Swihart 2004). We minimized and evaluated the potential for false absences in several ways. First, we conducted surveys when wetlands were inundated and muskrats used lodges instead of burrows (Schooley and Branch 2005, 2006). Next, we searched
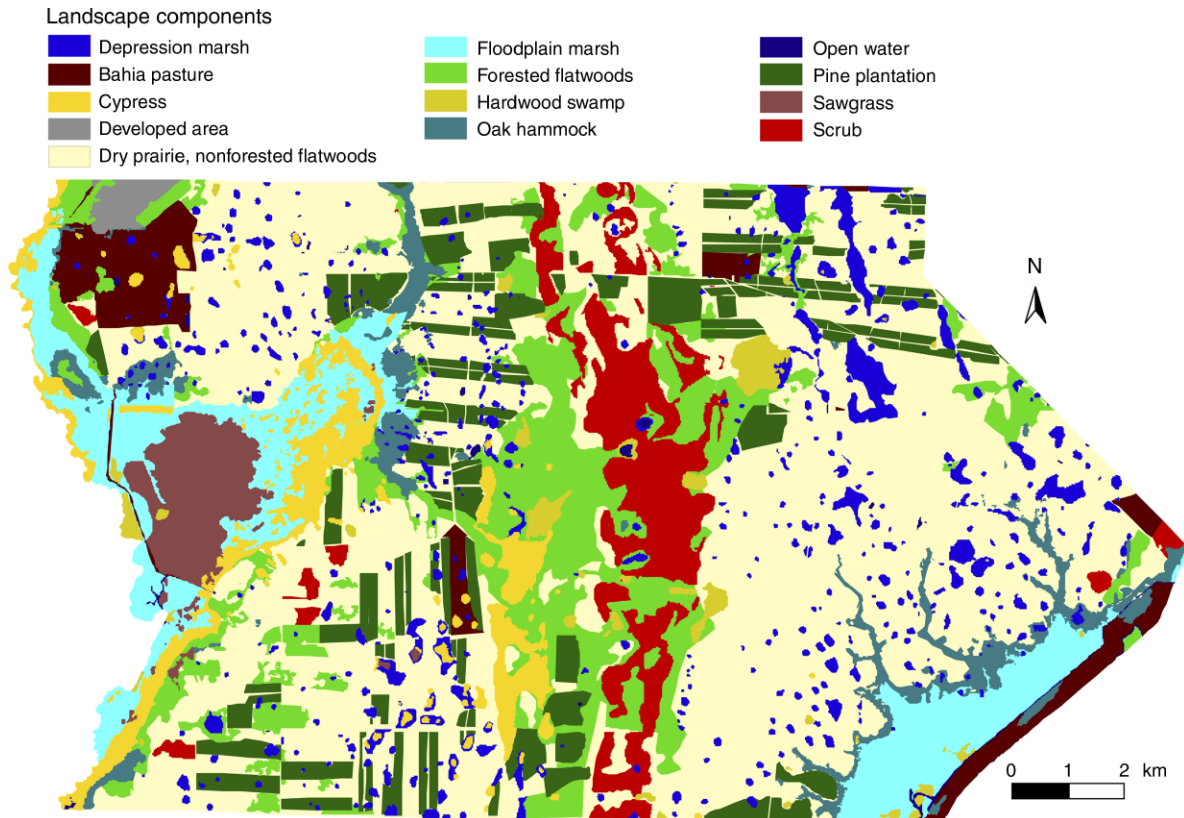
FIG. 1. Map of land-cover classes for the Avon Park study area (Avon Park Air Force Range; 15 km east of the town of Avon Park, in central Florida, USA). Depression marshes ($n = 457$) were surveyed for presence of round-tailed muskrats (*Neofiber alleni*) in a landscape with heterogeneous matrix habitat.

entire wetlands during 84 initial surveys and established that two trained searchers required ≤30 min to find a lodge, given that one would be found. We then standardized our occupancy surveys to ≥2 searchers (variable in relation to wetland size) for a limit of 30 min. This time limit resulted in partial searches for wetlands classified as unoccupied for 16% of the surveys in 2002–2003 and for 22% in 2003–2004. We extended the search time beyond 30 min (mean = 46 min, maximum = 106 min) for another 84 surveys to verify that the time limit was adequate for detecting presence of round-tailed muskrats in larger wetlands. We found sign of muskrats during the extended time, and not during the first 30 min, at only one wetland (1.2%). Finally, we resurveyed a random sample of 30 wetlands in 2003–2004 that were classified as vacant during the first visit that year, using an increased sampling effort on the second visit, to estimate the probability of false absences (Moilanen 2002). We detected no sign of wetland occupancy by round-tailed muskrats during any of our revisits.

When animal signs are used to determine site occupancy, false presences could arise if sign outlasts the individuals that produced the sign. We conducted a survival study of marked muskrat lodges that indicated

lodges encountered during our fall–winter surveys represented occupancy from the current survey year, and not the previous one (Schooley and Branch 2005).

Wetland traits and landscape position

Wetland area was measured with ArcView 3.2 (ESRI, Redlands, California, USA). We defined habitat quality of wetlands as an index of maidencane grass cover. We identified plant zones as continuous areas typically dominated by one or two species. For each plant zone dominated or co-dominated by maidencane, we assigned a cover rank from visual estimates in the field: 1 (<5%), 2 (5–20%), 3 (21–40%), 4 (41–60%), 5 (61–80%), 6 (81–100%). We then added 0.5 to each rank if the zone was pure maidencane (i.e., no co-dominant species). Next, we expressed each rank as a proportion of the maximum (rank/6.5), multiplied this proportion by the proportion of wetland covered by the zone, and then summed these area-weighted ranks across plant zones. The resulting index ranged from zero (no maidencane zones) to one (entire wetland in pure maidencane with an estimated cover of 81–100%). For analyses, habitat quality for each patch equaled the two-year average of the maidencane index.
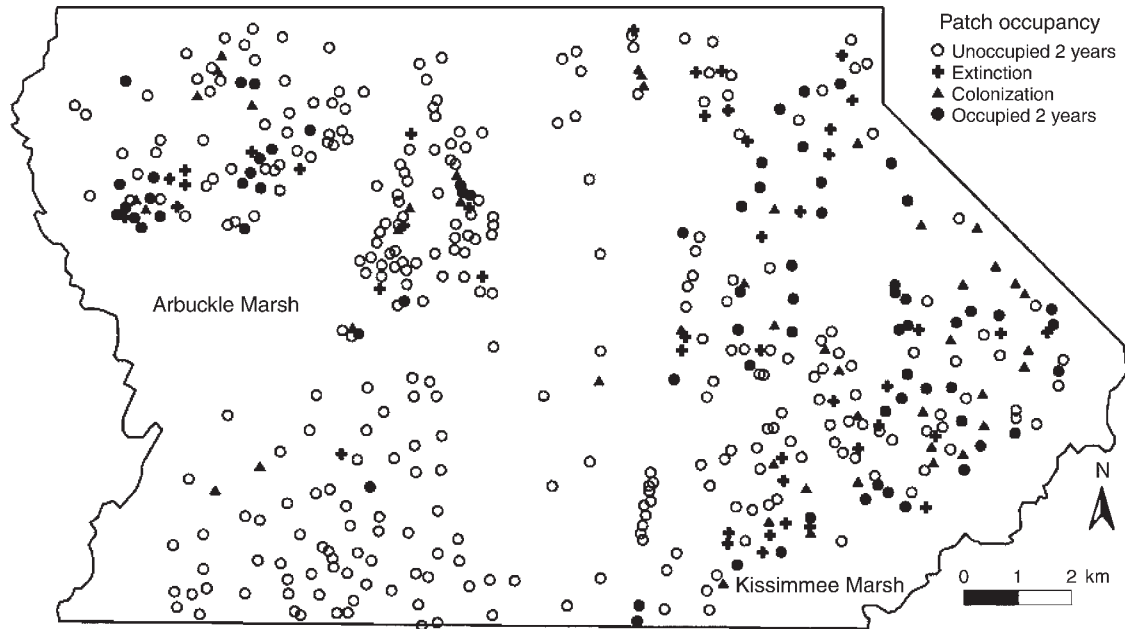
FIG. 2. Distribution patterns of round-tailed muskrats among 457 wetlands that were surveyed in each of two years (2002–2003 and 2003–2004). Muskrats were absent in both years from some wetlands (open circles) and present in both years at other wetlands (solid circles). Spatial turnover between years included local extinctions (crosses) and colonization of vacant wetlands (triangles).

Initially, we considered the spatial coordinates (Universal Transverse Mercators, UTMs) of wetland centers as predictor variables to account for broad-scale, linear spatial trends in response variables. However, we excluded from analyses the east coordinate because it was correlated ($r = 0.60$, $P < 0.001$, $n = 457$) with our measure of patch connectivity (defined in the following section). Other predictor variables did not exhibit strong multicollinearity (all $r < 0.28$). The north coordinate ("northing") was centered to its mean prior to analyses. Finally, because waterways may function as dispersal corridors for round-tailed muskrats (Birkenholz 1963, Mauritzen et al. 1999), we measured the distance between each wetland center and the nearest rain ditch along a road (minimum = 2 m, maximum = 1891 m). Most main roads had rain ditches that formed a hydrological network that was intermittent but generally intact throughout the summer rainy season.

Spatial connectivity

We used a patch connectivity metric typical of the incidence function model (IFM; Hanski 1994, Moilanen and Nieminen 2002) that considers distances to and characteristics of multiple, potential source populations. We calculated connectivity using only source patches within a specified buffer radius from each target patch because our study area was not an isolated patch network and thus an edge adjustment was necessary (see also Schooley and Wiens 2005). We used a buffer radius of 2 km because only 2% of vacant wetlands located >2 km from a source population ($n = 50$) were colonized

between years. Connectivity (S_i) of patch i included a negative exponential dispersal kernel and was defined as

$$S_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij}) A_j'^b \qquad (1)$$

where p_j is the likelihood that patch j was occupied during the previous year and thus could serve as a source patch, α is a parameter that scales the effect of distance on migration, d_{ij} is the distance (km) between centers of patches i and j (for $d_{ij} \leq 2$ km), A_j' is the "effective area" of patch j, and b is a scaling parameter relating abundance to effective area.

Most studies of patch occupancy represent a single-year snapshot and set p_j equal to zero for unoccupied patches and to 1.0 for occupied patches (e.g., Hanski 1994, Hokit et al. 1999). We had two years of data and thus set p_j equal to zero for patches unoccupied in both years, p_j equal to 0.5 for patches occupied in one year, and p_j equal to 1.0 for patches occupied in both years. This weighting scheme makes sense because of the biology of the species (i.e., dispersal might occur throughout the year). A patch that was unoccupied in Year 1 but occupied in Year 2 was colonized sometime between surveys, but the exact timing is unknown. The best estimate is that the patch became occupied halfway between surveys and was therefore a source patch for 50% of the year ($p_j = 0.5$). The same logic can be applied to patches that went extinct between the annual occupancy surveys; they were sources for part of the year. We estimated α as 0.5 by using logistic regression

to model colonization of patches in 2003–2004 as a function of $\exp(-\alpha d)$, where d was the distance to the nearest potential source patch (Hokit et al. 2001), and selecting the value of α that minimized the deviance of the model fit. Because habitat quality had a strong effect on wetland occupancy (see *Results: Determinants of patch occupancy*), we used "effective area" in Eq. 1 instead of patch area (A_j). Effective area (A_j') for patch j was calculated as $Q_j A_j / Q^*$, where Q_j was the habitat quality of patch j and Q^* was the maximal habitat quality of any patch (Hanski 1994, Hokit et al. 2001). Emigration is unlikely to scale linearly with (effective) patch area, setting b equal to 1.0 is a tenuous assumption, and a value of 0.5 is a more reasonable expectation (Moilanen and Nieminen 2002). We assumed a value of 0.5 for b in Eq. 1.

Potential source patches existed outside of our study area in most directions, except for the south boundary that abutted private agricultural land with few, if any, wetlands suitable for muskrats. Hence, our connectivity measure would have been biased low for some edge wetlands (<2 km from boundary) if we made no correction. For each wetland, we measured the proportion of the 2 km radius buffer that occurred within our study area and then divided S_i by this proportion to produce an edge-corrected connectivity metric (C_i). This correction included the reasonable assumption that suitable habitat within each buffer was distributed similarly within and outside of the study area. We did not correct connectivity for buffers that extended beyond the southern boundary. Although our edge correction substantially changed a few wetlands, most buffers were within the study area (median proportion inside = 0.95), and estimates of S_i and C_i were correlated ($r = 0.96$, $P < 0.001$, $n = 457$). Hence, the correction was a necessary but minor fine tuning.

Matrix habitat and cost–distance modeling

To examine effects of a heterogeneous matrix on functional connectivity (Roland et al. 2000, Ricketts 2001, Schooley and Wiens 2005), we used cost–distance modeling (Ferreras 2001, Chardon et al. 2003, Verbeylen et al. 2003). We modified our connectivity metric (C_i) by replacing Euclidean distances (d_{ij} in Eq. 1) with effective distances calculated with the PATHMATRIX software (Ray 2005) and ArcView. In this approach, cost grids are created by assigning a movement cost to each matrix type and then least-cost paths are calculated among patches. Accumulated cost along the least-cost path represents an effective distance that integrates Euclidean distance with differential resistances of matrix elements.

Our cost surfaces were based on the land-cover map (Fig. 1) that we converted into a raster grid (30 × 30 m cells). We combined three marsh types (depression, floodplain, sawgrass [*Cladium jamaicense*]) and used 11 land-cover types (Table 1). Ideally, resistance values are assigned to habitats using empirical data on habitat-

TABLE 1. Sets of movement costs for different land-cover classes (see Fig. 1) used in cost–distance modeling of spatial connectivity for round-tailed muskrats (*Neofiber alleni*) in central Florida, USA.

	Resistance sets		
Land-cover class	R1	R2	R3
Marsh†	1	1	1
Open water	1	5	1
Cypress swamp	1	20	1
Hardwood swamp	1	20	1
Dry prairie, not forested	1	5	1
Oak hammock	1	20	1
Forested flatwoods	1	20	50
Scrub	1	20	1
Pine plantation	1	20	50
Bahia pasture	1	5	1
Developed area	1	100	1

Note: Predictive abilities of resistance sets were compared with logistic regression models of wetland occupancy and spatial turnover.

† This class includes depression marsh, floodplain marsh, and sawgrass.

specific movement rates or preferences (Ferreras 2001, Schooley and Wiens 2004, Stevens et al. 2004). For species of conservation concern lacking such information, multiple sets of resistance values can be assigned to represent alternative hypotheses of landscape structure that then can be evaluated with empirical data on occupancy (Chardon et al. 2003, Verbeylen et al. 2003) or turnover. We created three resistance sets (Table 1). We always assigned a value of 1.0 for marsh habitats, which allowed these wetlands to serve as stepping stones for dispersal. For set R1 (Euclidean), all resistances were set to 1.0 to represent a homogenous matrix and to approximate Euclidean distances between patches. Set R2 (Open connectance) emphasized low resistances for treeless habitats, especially Florida dry prairie, compared to forested and scrub habitats. For resistance set R3 (Pines as barriers), we assigned high costs for forested flatwoods and pine plantations to represent these pine woods as potential dispersal barriers.

Regression models of occupancy, extinction, and colonization

We evaluated an increasingly complex series of regression models for predicting distribution patterns and extinction–colonization dynamics for round-tailed muskrats. Our candidate set of 56 models contained various combinations of five predictor variables: patch area, habitat quality, north coordinate, distance to roadside ditch, and one of the spatial connectivity metrics (C_{R1}, C_{R2}, C_{R3}). We started with two patch-level models for wetlands (area, area + quality) and then created a total of eight base models by adding landscape position variables (northing or ditch or northing + ditch) to the patch-level models. We created 16 new models by adding Euclidean connectivity (C_{R1}) and then connectivity plus an area–connectivity interaction term to the

base models. We generated the final 32 models by replacing C_{R1} with either C_{R2} or C_{R3}. Hence, each of the three connectivity metrics occurred in 16 models in a balanced fashion.

We used ordinal logistic regression to model patch occupancy with a multinomial probability distribution and cumulative logit link function (Proc Genmod; SAS 2002). The response variable was number of years a wetland was occupied (0, 1, 2). Next, we evaluated factors affecting spatial turnover between years by using binary logistic regression to model state-transition probabilities that occupied patches went extinct and that vacant patches were colonized (Sjögren-Gulve and Ray 1996). We used a binomial probability distribution and logit link function (Proc Genmod; SAS 2002). For all analyses, we report "max-rescaled" coefficients of determination for discrete models (Nagelkerke 1991, SAS 2002).

For each data set, we used a model-selection procedure based on Akaike Information Criterion (AIC) to select the best model and rank the others (Burnham and Anderson 2002). We used the AIC_c criterion corrected for small-sample bias for all analyses except for the models of extinction probability in which we used $QAIC_c$ that also allowed for overdispersed data. We present results as AIC differences ($\Delta_i = AIC_i -$ minimum AIC) so that the best model has $\Delta_i = 0$. Models with $\Delta_i \leq 2$ have substantial support (Burnham and Anderson 2002). We also report Akaike weights (w_i) that are normalized relative likelihoods that model i is the best model, and we use summed Akaike weights (Burnham and Anderson 2002) to compare support for the three different cost–distance resistance sets (Table 1).

Logistic regression assumes spatial independence among model residuals, and positive spatial dependence reduces true degrees of freedom and inflates measures of correlation strength (Lichstein et al. 2002, Fortin and Dale 2005). Therefore, we constructed Moran's I correlograms (Fortin and Dale 2005) using residuals from all models with substantial support and evaluated them for evidence of autocorrelation. Residual diagnostics are not well-developed for ordinal methods (O'Connell 2006), so for occupancy we evaluated residuals from binary logistic regression models in which the response variable was coded as unoccupied in both years (0) vs. occupied in one or two years (1). We calculated P values for Moran's I values at each lag distance with a Monte Carlo randomization procedure using 999 permutations (Sawada 1999). We tested for significance of particular lag distances using a progressive Bonferroni correction with an overall α of 0.05 (Lichstein et al. 2002, Fortin and Dale 2005).

Predictive performance of occupancy model

Evaluating predictive ability is important for habitat models applied to species conservation. For binary logistic regression models, receiver operating characteristic (ROC) curves are effective for quantifying model accuracy (Fielding and Bell 1997, Pearce and Ferrier 2000). A ROC curve plots the true positive fraction (sensitivity) vs. the false positive fraction (1 − specificity) for a wide range of thresholds. Area under the ROC curve (AUC) is a single measure of accuracy that ranges from 0.5 (no discrimination) to 1.0 (perfect discrimination). For example, an AUC value of 0.8 means that 80% of the time a random selection from occupied wetlands will have a higher predicted score than a random selection from unoccupied wetlands (Fielding and Bell 1997). Using predictors from the best ordinal logistic regression model, we evaluated two binary logistic regression models by combining response variable categories. For ROC 1, we tested a model in which the response was coded as unoccupied in both years (0) vs. occupied in one or two years (1). For ROC 2, we tested a model in which the response was coded as unoccupied in both years or occupied in only one year (0) vs. occupied in both years (1). We constructed ROC curves using a cross-validation approach for data partitioning that approximates a jackknife procedure (SAS 2002).

Analysis of habitat tracking

To test whether our system represented a habitat-tracking metapopulation, we determined if extinction and colonization probabilities were related to changes in habitat quality of patches between years ($\Delta_{qual} = $ [2003–2004 maidencane index] − [2002–2003 maidencane index]). For each turnover process, we used a likelihood ratio test to compare the best model as identified by our AIC-based selection procedures (reduced model) to a model with the same predictors plus Δ_{qual} (full model).

RESULTS

Round-tailed muskrats occupied 117 (25.6%) of the 457 wetlands in 2002–2003 and 118 (25.8%) of the wetlands in 2003–2004 (Fig. 2). This cross-year constancy in patch occupancy occurred despite substantial spatial turnover in which local extinctions ($n = 45$) and colonizations ($n = 46$) were nearly in balance. Of the 117 wetlands occupied in 2002–2003, 38.5% went extinct by 2003–2004. Of the 340 wetlands vacant in 2002–2003, 13.5% were colonized by the next year. Much turnover occurred within a restricted scale so that broadscale distribution patterns were similar between years (Fig. 2).

Determinants of patch occupancy

Of the 457 wetlands, 64% were unoccupied in both years, 20% were occupied in one year, and 16% were occupied in both years. All highly ranked models ($\Delta AIC \leq 2$) predicting occupancy of wetlands by round-tailed muskrats included patch area, habitat quality, spatial connectivity, and an area × connectivity interaction (Table 2). Wetland occupancy was related positively to patch area, quality, and connectivity (Fig. 3A–C). A positive interaction between connectivity and wetland

TABLE 2. Ranking of ordinal logistic regression models for predicting occupancy of 457 wetlands by round-tailed muskrats in central Florida during two years.

Model	K	Log-likelihood	AIC$_c$ Δ_i	w_i
$A, Q, C_{R2}, A \times C_{R2}, Y$	7	−300.92	0.00	0.59
$A, Q, C_{R2}, A \times C_{R2}, Y, D$	8	−300.68	1.60	0.27
$A, Q, C_{R2}, A \times C_{R2}$	6	−304.16	4.42	0.06

Notes: The response variable was the number of years each wetland was occupied (0, 1, 2). Models with $\Delta_i \leq 5$ are presented. K = number of explanatory variables + 2, $\Delta_i = \text{AIC}_{ci} - \text{minimum AIC}_c$, and w_i are Akaike weights. Main effects include patch area (A), habitat quality (Q), connectivity (C), northing (Y), and distance to roadside ditch (D). Subscripts for connectivity refer to particular resistance sets used to quantify cost and distances for matrix habitats (see Table 1).

area indicated that patch size was more important for wetlands that were relatively connected and likely to have been reached by dispersers. The northing coordinate occurred in the top two models (Table 2) indicating a broadscale pattern of occupancy not captured by other predictor variables. Distance to nearest rain ditch occurred in a competitive model (second ranked, Table 2), but the addition of ditch distance to the top model did not improve model fit by much (see log-likelihoods, Table 2). The best model explained considerable variation in patch occupancy by muskrats ($R^2 = 0.45$). The simple area–isolation model (patch area + C_{R1}), which is most often applied to metapopulations, was not adequate for our system ($w_i \leq 0.00$, $\Delta\text{AIC} = 121.06$, $R^2 = 0.21$).

Grazing pressure was associated negatively with both habitat quality (Fig. 4A; ANOVA, $F = 24.69$, $P < 0.0001$, df = 2, 454) and patch occupancy (Fig. 4B; logistic regression, Wald chi-square = 25.03, $P < 0.0001$, df = 2). Land use created relevant heterogeneity in patch quality for muskrats.

The R2 connectivity metric (Open connectance) was supported strongly in patch occupancy models (Table 2). The sum of Akaike weights for models with C_{R2} was 0.999, and connectivity based on Euclidean distances had no support (Fig. 5). Because Akaike weights are relative measures that depend on the model set, we also examined summed weights for a reduced set containing only models with Euclidean connectivity (C_{R1}) or the Pines as barriers metric (C_{R3}). The sum of Akaike weights for the Euclidean metric was 0.00, and the sum of weights for the Pines as barriers metric was 1.00. Hence, abilities of the spatial connectivity metrics to predict patch occupancy can be clearly ranked (Open connectance > Pines as barriers > Euclidean).

We did not detect strong positive autocorrelation for residuals from any of the competitive ($\Delta\text{AIC} \leq 2$) logistic regression models of occupancy (Moran's I values ≤ 0.10 for all lag distances). These results regarding autocorrelation held for models of extinction and colonization presented below (see Appendix A for correlograms of top models for each response variable).

The receiver operating characteristic (ROC) plots (see Appendix B) indicated that the best occupancy model
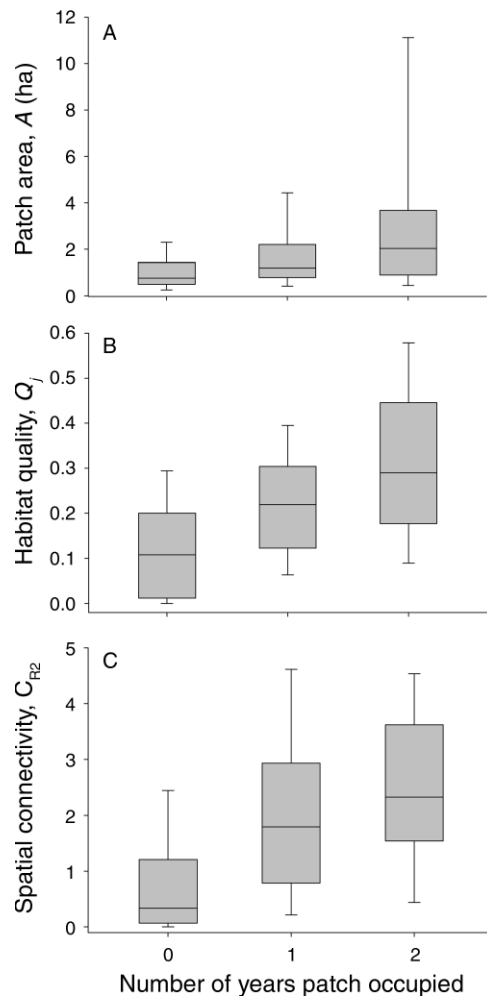

FIG. 3. Box plots of relationships between key predictor variables and patch occupancy for round-tailed muskrats. Occupancy was related positively to (A) patch area, (B) habitat quality of wetlands as indexed by cover of maidencane grass, *Panicum hemitomon*, and (C) spatial connectivity modified by matrix structure. C_{R2} represented Open connectance and was the best predictor of occupancy (see Table 2). Shaded boxes are bounded by 25th and 75th percentiles; horizontal lines within boxes are medians; and whiskers indicate 10th and 90th percentiles.
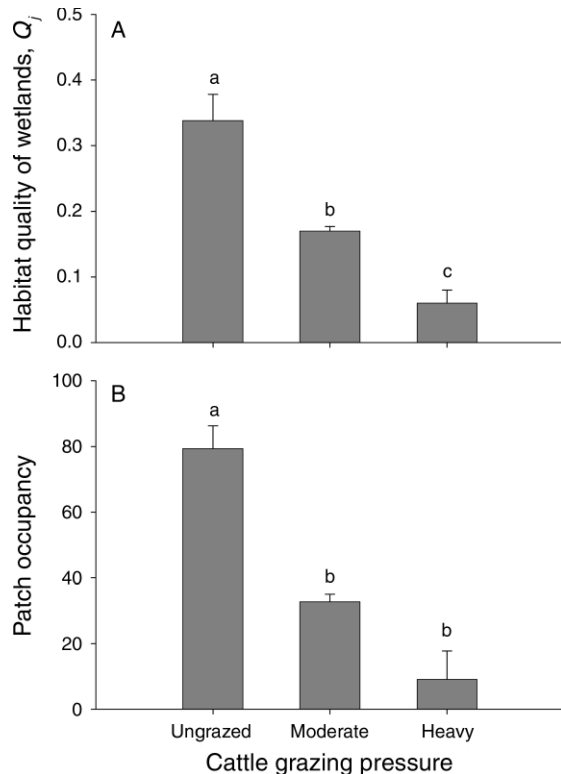
FIG. 4. (A) Association between habitat quality of wetlands and cattle grazing pressure. Bars are means (+SE); group differences are indicated by different lowercase letters (Tukey test, $P < 0.05$). (B) Relationship between occupancy of wetlands by round-tailed muskrats and grazing pressure. Occupancy indicates wetlands occupied in at least one of two years. Group differences based on contrasting odds ratios are indicated by different lowercase letters.

had good predictive ability when the response was coded as binary (area under the ROC curve; AUC = 0.86 for ROC 1, AUC = 0.87 for ROC 2). An AUC value between 0.70 and 0.90 indicates a reasonable discrimination capacity that is suitable for many uses (Pearce and Ferrier 2000).

Environmental correlates of extinction and colonization

All competitive models for explaining extinction risk included patch area, habitat quality, and distance to ditch (Table 3). Local extinctions of round-tailed muskrats were most likely in small wetlands with poor-quality habitat (Fig. 6) and in wetlands closer to roadside ditches (regression coefficient from top model = −0.0013; 95% CL [−0.0025, −0.0002]). Evidence of a rescue effect was inconclusive (Brown and Kodric-Brown 1977). Although two competitive models for extinction included a connectivity metric, the top-ranked model had no connectivity metric but had a similar log-likelihood to other competitive models (Table 3). Moreover, the eight base models without connectivity had a summed Akaike weight of 0.34, whereas these models had summed weights of zero for colonization

and occupancy. There also was little evidence that any particular cost–distance resistance set was most useful for predicting extinctions (Fig. 5). The highest ranked extinction model explained a moderate amount of variation ($R^2 = 0.25$).

Competitive models for predicting colonization events always included patch area, habitat quality, connectivity, and an area × connectivity interaction (Table 3). Round-tailed muskrats colonized wetlands that were relatively large (colonized mean = 2.1 ha, 95% CL [1.5, 2.7] vs. vacant mean = 1.2 ha, 95% CL [1.0, 1.4]), high quality (0.23 [0.19, 0.27] vs. 0.13 [0.12, 0.14]), and well-connected (Fig. 7). Among connectivity metrics, most support was for C_{R3}, which contained high resistance for pine forests and plantations. This resistance set was in three of the four competitive models (Table 3) and had the highest Akaike weights summed across models ($w_i = 0.61$; Fig. 5). Euclidean connectivity (C_{R1}) was the second best metric for predicting colonization (Table 3, Fig. 5). There was only moderate support for landscape position variables (northing, distance to ditch) in the colonization models (Table 3). The highest ranked model explained 34% of the variation in colonization probability.

Annual habitat tracking

Extinction and colonization events were unrelated to changes in habitat quality of patches between two years. The reduced model for extinction probability without Δ_{qual} (top model in Table 3) had an adequate fit when compared to the full model with the habitat change variable included ($\chi^2 = 0.17$, df = 1, $P = 0.68$). Extinction risk was not associated positively with decreases in habitat quality. Likewise, the reduced model for colonization probability (top model in Table 3) fit the
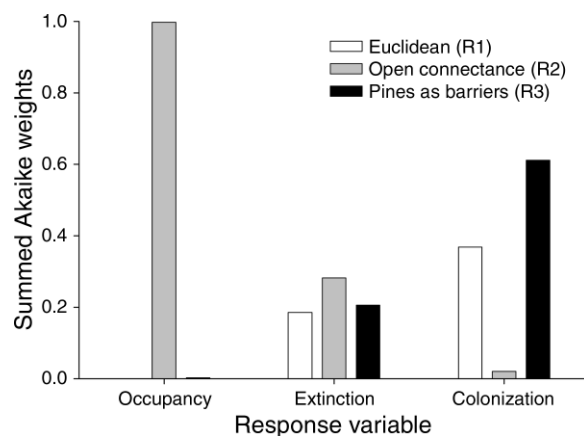

FIG. 5. Relative importance of three cost–distance resistance sets of matrix habitat (R1, R2, R3) for predicting patch occupancy and spatial turnover for round-tailed muskrats. Movement costs for matrix habitats for each resistance set are provided in Table 2. Resistance sets with high values of summed Akaike weights have the most support for a particular response variable (occupancy, extinction, colonization).

TABLE 3. Ranking of logistic regression models of extinction–colonization dynamics of round-tailed muskrats in isolated wetlands.

			AIC$_c$‡	
Process and model†	K	Log-likelihood	Δ_i	w_i
Extinction				
A, Q, D	4	−65.84	0.00	0.19
A, Q, C_{R2}, D	5	−65.15	1.02	0.11
A, Q, C_{R3}, D	5	−65.59	1.76	0.08
Colonization				
$A, Q, C_{R3}, A \times C_{R3}$	5	−100.02	0.00	0.26
$A, Q, C_{R1}, A \times C_{R1}$	5	−100.48	0.93	0.17
$A, Q, C_{R3}, A \times C_{R3}, Y$	6	−99.46	0.95	0.16
$A, Q, C_{R3}, A \times C_{R3}, D$	6	−99.87	1.78	0.11

† Models with $\Delta_i \leq 2$ are presented. K = number of explanatory variables + 1; $\Delta_i = \text{AIC}_{ci} - $ minimum AIC$_c$; and w_i are Akaike weights. Main effects include patch area (A), habitat quality (Q), connectivity (C), northing (Y), and distance to roadside ditch (D). Subscripts for connectivity refer to particular resistance sets used to quantify costs and distances for matrix habitats (see Table 1).

‡ Extinction was evaluated with QAIC$_c$, and colonization with AIC$_c$.

data well relative to the full model that included Δ_{qual} ($\chi^2 = 0.22$, df $= 1$, $P = 0.64$). The chance that a vacant wetland was colonized between years was unrelated to yearly shifts in habitat quality.

The lack of evidence for annual habitat tracking was not due to static habitat quality. Although habitat quality of wetlands was correlated between years ($r = 0.66$, $P < 0.0001$, $n = 457$), many wetlands either increased or decreased in quality. For occupied wetlands in which extinctions could have occurred (mean quality $= 0.28$, $n = 117$), 25% decreased in quality by ≥ -0.07 and 10% decreased by ≥ -0.20. For unoccupied wetlands in which recolonizations were possible (mean quality $= 0.14$, $n = 340$), 25% increased in quality by ≥ 0.11 and 10% increased by ≥ 0.22.

DISCUSSION

Metapopulation dynamics

Categorizing a system as either a metapopulation or not is unproductive because populations often exhibit mixed spatial structures at different spatiotemporal scales (Hanski 1997, Harrison and Taylor 1997, Thomas and Kunin 1999), but considering how closely a system resembles a classical metapopulation is useful for identifying practical approaches for conserving rare species in fragmented landscapes (Hanski 1997). Our study provided compelling evidence for metapopulation dynamics for a wetland mammal (round-tailed muskrat, *Neofiber alleni*) and documented high rates of turnover and balanced extinction–recolonization as predicted by classical metapopulation theory. Few studies have provided convincing examples of metapopulation processes for small mammals (Lambin et al. 2004). Interestingly, species that demonstrate metapopulation structure and dynamics include semiaquatic water voles

in Europe (*Arvicola terrestris* and *A. sapidus*) that have similar ecologies to round-tailed muskrats. The distribution of *A. sapidus* among isolated ponds is related to local habitat quality and to landscape factors including isolation (Fedriani et al. 2002). *Arvicola terrestris* inhabits patchy riverbank habitat and exhibits population turnover with extinction related to population size and recolonization related to isolation and habitat quality (Telfer et al. 2001, Lambin et al. 2004).

We recognize that the turnover equilibrium observed for round-tailed muskrats might not last over longer time scales. Moilanen (2000) cautioned that extinction–colonization stochasticity could lead to observing unequal numbers of extinction and colonization events during a short study period even if metapopulation size had no long-term trend. The reverse is true also. Our muskrat metapopulation could be non-equilibrial despite the balance that we observed during two years with normal rainfall patterns. Broad-scale responses to climatic variability could create synchronous population dynamics among patches and reduce metapopulation persistence (Hanski 1997, Stapp et al. 2004). For instance, our study area was directly impacted by hurricanes Charley, Frances, and Jeanne during the 2004 hurricane season that occurred after our field sampling had ended, and it is unknown whether patch occupancy equilibrium was maintained.

Our muskrat-wetland system included key aspects typical of a situation in which spatially realistic metapopulation theory should apply (Hanski 1994, Hanski and Gaggiotti 2004). Round-tailed muskrats occupied discrete patches that covered <5% of the landscape
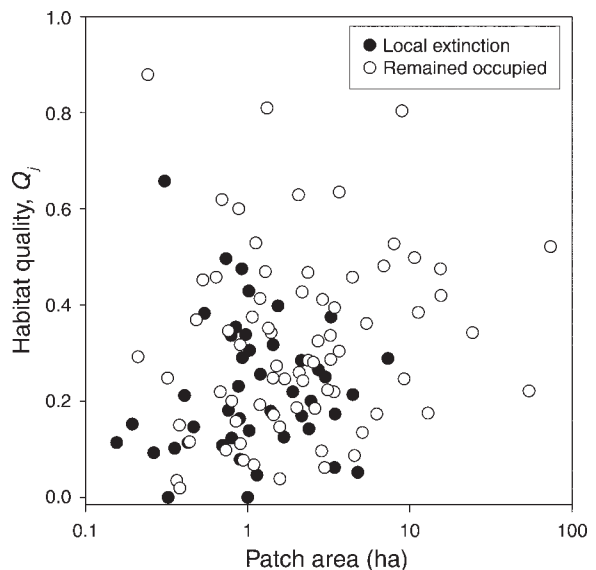

FIG. 6. Effects of habitat quality and patch area (note the log scale) on probability of local extinctions of round-tailed muskrats. Each circle represents a depression marsh ($n = 117$) that was occupied by muskrats in 2002–2003 and resurveyed in 2003–2004.
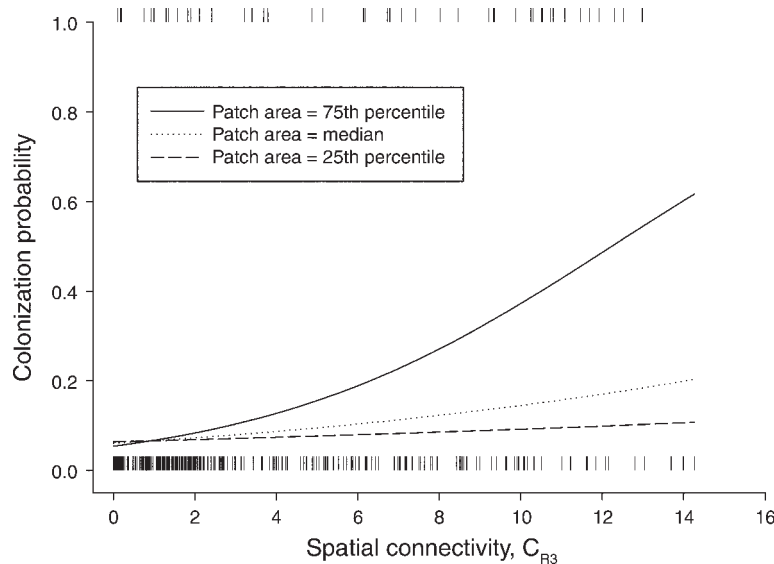
FIG. 7. Interaction between spatial connectivity and patch area for predicting colonization of vacant wetlands ($n = 340$) by round-tailed muskrats. Predicted probabilities are from the best logistic regression model (Table 3) in which habitat quality was held constant. Lines represent predictions for patch sizes equivalent to the 25th percentile (dashed), median (dotted), and 75th percentile (solid) of the patch-size distribution. Vertical dashes represent observed colonization events (at probability = 1) or continued vacancies (at probability = 0). Spatial connectivity integrates Euclidean distances to source patches with high costs for dispersing through pine habitats in the matrix.

mosaic. Radio tacking of adult muskrats indicated that wetlands, at least high quality ones, contained local breeding populations (Schooley and Branch 2006). Extinction risk was related negatively to patch size. However, we expect that even large patches had a non-trivial risk of local extinction over relevant time scales and that mainland–island dynamics were not dominant. A subpopulation went extinct within a 7.3-ha wetland that was larger than 96% of the wetlands. Likewise, large populations (thousands of individuals) of round-tailed muskrats in central Florida (Birkenholz 1963) and southern Georgia (Bergstrom et al. 2000) were reduced to only a few individuals due to drought and other unidentified factors. In our study, muskrat dispersal was spatially restricted and colonization probability was related negatively to (effective) distances to other source wetlands.

Despite this close matching between predictions from spatially realistic metapopulation theory and dynamics of our muskrat metapopulation, the patch area and isolation paradigm that adopts a binary view of landscapes was inadequate. The occupancy model that included solely patch area and Euclidean connectivity had no support (see also Pellet et al. 2007). These two key variables formed an initial template, but habitat quality of suitable patches and matrix heterogeneity had to be incorporated into the area–isolation framework to understand spatial incidence patterns for round-tailed muskrats.

Habitat effects on turnover and occupancy

Local extinctions and patch occupancy depended on combined effects of patch area and patch quality

(Fleishman et al. 2002, Franken and Hik 2004, Bulman et al. 2007), which likely set upper limits to muskrat abundances. There was limited evidence that extinction risk was related to patch isolation, and a predictive model with no spatial connectivity metric performed comparatively well. Thus, we did not detect a strong rescue effect in which dispersers from wetlands within dispersal range might bolster small populations before they went extinct (Brown and Kodric-Brown 1977, Hanski 1994). However, matrix characteristics not incorporated into our connectivity measures influenced extinction probability. Wetlands close to roadside rain ditches were more likely to go extinct than those farther from ditches. We can only provide two general hypotheses regarding this outcome because the outcome was opposite to our a priori prediction. First, ditches might function as movement corridors for muskrats, but instead of increasing colonization their main effect could be to increase emigration from wetlands. Emigration from small, isolated populations can decrease population growth rates and increase extinction risks for small mammals (Andreassen and Ims 2001, Crone et al. 2001, Gundersen et al. 2001). Lack of mates and other Allee effects might promote dispersal by the last individuals remaining in a patch (Andreassen and Ims 2001). Second, ditches and associated structures could increase predation pressure and extinction risk for muskrats. Ditches could function as conduits for predators such as semiaquatic snakes, and fences and power lines along roads could provide perches for hunting hawks and owls, which are important predators of *Neofiber* (Birkenholz 1963). Additionally, presence of red im-

ported fire ants (*Solenopsis invicta*) is related positively to roads in Florida, and invasive fire ants prey on small mammals (Forys et al. 2002). For a sample of our wetlands in 2003–2004, fire ants occurred in at least 39% of the wetlands ($n = 121$), and 19% of abandoned muskrat lodges ($n = 387$) housed fire ant colonies (R. L. Schooley and L. C. Branch, *unpublished data*). Future investigations of matrix effects should consider interactions among landscape disturbances such as roads and ditches, invasive species, and metapopulation processes for native wetland species.

Colonization of vacant wetlands by round-tailed muskrats depended on size and quality of target patches. A positive relationship between colonization probability and local habitat quality indicated dispersers were actively selecting habitat (Telfer et al. 2001, Stamps et al. 2005) or had higher initial survival following immigration into good habitat. Colonizations of certain low-quality wetlands might have been ephemeral and might not have resulted in lasting sign of occupancy. Such wetlands still could function as important stepping-stone habitats (Semlitsch 2000).

Muskrats were a dispersal-limited species. Colonization and subsequent patch occupancy were related positively to spatial connectivity. Habitat potentially influenced functional connectivity in two ways. First, habitat quality of suitable wetlands was spatially autocorrelated up to 1 km (Schooley and Branch 2007). Because higher quality patches are likely to produce more dispersers, spatial autocorrelation created neighborhoods with high colonization potential and the opportunity for source–sink dynamics among clusters of patches (Schooley and Branch 2007). Second, matrix composition seemed to affect colonization because the cost surface with greatest support included high movement costs for pine habitats. The ranking of a competitive model for colonization that included simple Euclidean connectivity was surprising because Euclidean connectivity was not a useful predictor for patch occupancy. Collectively, our results suggest that scrub and forested habitat, especially pine forests, can reduce dispersal success for round-tailed muskrats either due to avoidance behavior at habitat edges (Haddad 1999, Schultz and Crone 2001, Allaye Chan-McLeod 2003) or increased predation risk. These inferences should be scrutinized further with experiments on movement behavior that also could clarify underlying mechanisms (Schooley and Wiens 2004, Stevens et al. 2004). More generally, our study demonstrated how multiyear data allow one to assess matrix effects separately for extinction, colonization, and occupancy.

Habitat tracking

Our measure of patch quality (maidencane cover) was an important determinant of extinction–colonization processes, but our system did not behave as a strict habitat-tracking metapopulation on an annual time step (Thomas 1994, Pita et al. 2007). Annual changes in other subtle aspects of habitat quality that we did not measure may have contributed to turnover dynamics. Also, deterministic changes in habitat quality over longer time scales may have reduced local population sizes below a threshold in which environmental and demographic stochasticity were more likely to cause patch extinctions. Many metapopulations probably exhibit aspects of habitat tracking and classical metapopulations at different temporal resolutions so that clear distinctions are difficult to construct (Thomas and Kunin 1999, Thomas and Hanski 2004).

Management implications and conclusions

Development of isolated wetlands within the United States is regulated mainly by wetland size, and the value of small wetlands could be underestimated if their roles in maintaining metapopulation connectivity and their positions along hydroperiod gradients are disregarded (Semlitsch and Bodie 1998, Gibbs 2000, Snodgrass et al. 2000). Our research highlights two key points related to potential values of small wetlands to biota. First, appraisal of wetland value based solely on patch area, without considering patch quality, is a myopic perspective. Second, we uncovered a positive interaction between patch area and spatial connectivity for all competitive models of colonization and occupancy (Tables 2 and 3). An area–connectivity interaction has been documented by several other fragmentation studies (e.g., Quintana-Ascencio and Menges 1996, Kehler and Bondrup-Nielsen 1999, Schooley and Wiens 2005). Hence, the value of a wetland patch depends not only on its effective size but also on its explicit positioning within the landscape mosaic, which affects its contribution to colonizations, metapopulation capacity, and network persistence (Ovaskainen and Hanski 2003).

We identified two land uses at Avon Park, cattle grazing and establishment of pine plantations, which represent previously unrecognized threats to round-tailed muskrats (Lefebvre and Tilmant 1992) and potentially to many marshland species. Effects of cattle grazing on wetland ecosystems have received little attention (Steinman et al. 2003), and grazing disturbances are not explicitly considered in conceptual models of plant community development for depressional wetlands (e.g., Kirkman et al. 2000). Nevertheless, there is a general recognition that overgrazing can degrade habitat quality for wetland fauna (Jansen and Healey 2003, Tiner 2003).

At Avon Park, spatial patterns of habitat quality and wetland occupancy by muskrats likely echo historical grazing regimes (Schooley and Branch 2007) because maidencane grass declines in abundance when exposed to cattle grazing (Kalmbacher et al. 1984, Long et al. 1986). In other wetlands, regulated cattle grazing can reduce cover of invasive plants and increase invertebrate diversity (Marty 2005). More focus is needed on effects of livestock grazing on biodiversity of isolated wetlands,

especially regarding potential thresholds in grazing intensity and comprehensive faunal responses.

Ecological consequences of plantation forests have been considered mainly for situations in which native forests are replaced by industrial plantations, and local effects are stressed more than landscape impacts (e.g., Hartley 2002). Even when landscape context effects are considered, forest-to-forest transitions are the customary setting. For example, conversion of matrix habitat from *Eucalyptus* forest to *Pinus radiata* plantations influenced frog communities in New South Wales, Australia (Parris and Lindenmayer 2004). Replacement of grasslands by plantation forests should have large effects on functional connectivity for species that prefer open environments because of the strong structural contrast created between habitats (Haddad et al. 2003). Our results indicated that pine forests can decrease connectivity for round-tailed muskrats. We expect that many marshland and grassland species could respond similarly and that maintaining connectivity for these species will require keeping uninterrupted expanses of open habitat.

In conclusion, a metapopulation approach should be useful for conserving many species in subdivided landscapes if habitat heterogeneity is included at multiple levels. Criticisms directed at the simple area–isolation paradigm of metapopulations can be partially deflected through use of a habitat-informed version of the paradigm. Coupling land-use practices to habitat heterogeneity and extinction–colonization processes will be crucial if conservation and restoration practices are to benefit from metapopulation theory.

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APPENDIX A

Evaluation of the assumption of spatial independence of residuals from logistic regression models used to predict patch occupancy and turnover for round-tailed muskrats (*Neofiber alleni*) in isolated wetlands in central Florida, USA, 2002–2004 (*Ecological Archives* A019-069-A1).

APPENDIX B

Receiver operating characteristic (ROC) curves based on the best logistic regression model of wetland occupancy by round-tailed muskrats (*Ecological Archives* A019-069-A2).