Spatial Distribution of Round-tailed Muskrats on Dry Prairie Wetlands: Untangling Historical Landscapes and Current Land Use

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The round-tailed muskrat (*Neofiber alleni*) is a semi-aquatic, herbivorous, nocturnal, and enigmatic species (Birkenholz 1963, Lefebvre and Tilmant 1992) that occurs within wetlands embedded in dry prairie and other landscape associations. The species has a restricted geographic distribution and occurs mostly in Florida where it was proposed as a Species of Special Concern because of presumed statewide population declines due to wetland losses (Lefebvre and Tilmant 1992). Previous research has not investigated landscape-scale distributional patterns of round-tailed muskrats, although evidence that local populations fluctuate dramatically (Birkenholz 1963) suggests the potential for important spatial dynamics within wetland networks. Recently, we developed a predictive habitat model within a metapopulation framework that elucidated factors affecting extinction-colonization dynamics of round-tailed muskrats (Branch and Schooley 2005). We use the term metapopulation to refer to a collection of local populations that occur in discrete habitat patches and are connected by enough dispersal to allow for recolonization of patches following local extinctions (Hanski 1999). Here, we compare distributional patterns and spatial turnover of muskrats between wetlands located within the historical Florida dry prairie landscape (Bridges 2000, 2001) and other landscape types. Our results suggest that the distribution of round-tailed muskrats depends on landscape context and that dry prairie and other treeless associations might be important matrix habitats that facilitate recolonization of vacant wetlands and contribute to regional persistence.

Our study site was a 19,500-ha area in the southern portion of Avon Park Air Force Range in central Florida. Suitable habitat for round-tailed muskrats consisted of small (median ≈1 ha), geographically isolated, seasonal depression marshes. Matrix habitat between depression marshes was heterogeneous and included Florida dry prairie, pine flatwoods (*Pinus palustris, P. elliottii* var. *densa*), slash pine plantations (*P. elliottii* var. *elliottii*), oak scrub and hammocks (*Quercus* spp.), pastures, and swamps.

We surveyed 457 wetlands for occupancy of round-tailed muskrats during fall-winter of 2002-2003 and 2003-2004. Occupancy of wetlands by round-tailed muskrats was determined based on presence of their characteristic lodges (Birkenholz 1963). Schooley and Branch (2005) provided details of the survey procedure and an assessment of its reliability for determining site occupancy. Because we collected two years of occupancy data for muskrats, we could examine spatial dynamics of local extinctions and colonizations in addition to static patterns of wetland occupancy. We evaluated several patch-level traits as correlates of occupancy and turnover including wetland area and habitat quality. We used cover of maidencane grass (*Panicum hemitomon*) as a measure of a habitat quality because maidencane is a preferred species in diets of muskrats and a common substrate for their lodges (Birkenholz 1963). We also evaluated the importance of landscape-level traits including spatial connectivity, which was a metric that incorporated distances and effective sizes of neighboring occupied wetlands (Hanski 1994), and proximity to pine plantations (Branch and Schooley 2005). We provide descriptive statistics for these environmental correlates and test for differences in them between dry prairie and other landscapes combined using χ^2-tests for categorical data and Wilcoxon tests for continuous data.

Round-tailed muskrats occupied 26% of the 457 surveyed wetlands in 2002-2003 and again in 2003-2004. This temporal stability in wetland occupancy occurred despite considerable spatial turnover in which local extinctions and colonizations were nearly balanced (Branch and Schooley 2005). Hence, the study system possesses one of the key traits of a metapopulation (Hanski 1994, 1999), and understanding factors that influence extinction-colonization dynamics is central to understanding regional distributional patterns.

Muskrats were more likely to be present in wetlands within the historical dry prairie landscape (42.1% occupied in ≥1 yr, $n = 233$) compared to wetlands surrounded by other matrix habitats (29.0%, $n = 224$; $\chi^2 = 8.47$, $d.f. = 1$, $P = 0.004$). Rates of local extinctions between the two years were similar for wetlands embedded in dry prairie (36.2%, $n = 69$) and those located in other landscape types (41.7%, $n = 48$; $\chi^2 = 0.35$, $d.f. = 1$, $P = 0.55$). In contrast, colonization of vacant wetlands between years was greater in wetlands within dry prairie matrix (17.7%, $n = 164$) compared to wetlands surrounded by other matrix habitats (9.7%, $n = 176$; $\chi^2 = 4.67$, $d.f. = 1$, $P = 0.03$).

What factors were related to the greater colonization and occupancy rates of wetlands within the historical dry prairie landscape? In general, round-tailed muskrats are more likely to colonize larger wetlands and those of higher habitat quality (Branch and Schooley 2005). Wetland area did not differ between dry prairie areas ($\bar{x} = 1.97$ ha, SE = 0.35) and other habitats ($\bar{x} = 1.96$ ha, SE = 0.27; Z = 0.42, $P = 0.67$). However, habitat quality was greater for dry prairie wetlands ($\bar{x} = 0.20$, SE = 0.01) relative to wet-

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lands in other matrix types ($\bar{x}$ = 0.15, SE = 0.01; Z = -3.56, P = 0.001). This greater cover of maidencane grass in dry prairie wetlands might reflect differences in soils, topography, and hydrology between landscape associations, although the environmental factors that promote thick maidencane marshes are not well understood. Differences in habitat quality also might reflect land-use history given that cattle grazing can reduce habitat quality of wetlands (Branch and Schooley 2005). Most wetlands at Avon Park are subjected to managed, moderate grazing. However, 10.3% of the dry prairie wetlands were located within a pasture where cattle grazing had been excluded for 8 years, whereas only 3.6% of the wetlands within other matrix types were located in the ungrazed pasture.

Colonization of wetlands by round-tailed muskrats also is strongly related to their connectance to occupied wetlands that can serve as sources of dispersers (Branch and Schooley 2005). Wetlands in the historical dry prairie region had greater spatial connectivity ($\bar{x}$ = 4.11, SE = 0.17) than did wetlands surrounded by other habitats at Avon Park ($\bar{x}$ = 1.97, SE = 0.16; Z = -10.33, $P < 0.001$) as gauged by the connectivity metric that measured Euclidean distances to other occupied wetlands within the presumed maximum dispersal distance of muskrats. In addition, wetlands (whether occupied or not) were nearer to each other in the dry prairie landscape (1st nearest-neighbor distance, $\bar{x}$ = 277 m, SE = 7.4) compared to those situated in other areas ($\bar{x}$ = 348 m, SE = 13.7). Our analyses also implicate pine plantations as relative barriers to dispersal that negatively affect wetland colonization (Branch and Schooley 2005). Dry prairie wetlands were less likely to be next to pine plantations (10.3%) compared to wetlands located in other regions (31.3%; χ^2 = 30.68, *d.f.* = 1, $P < 0.001$). Finally, we found no evidence that rain ditches along roads functioned as movement corridors for muskrats because the distance between vacant wetlands and the nearest ditch was not an important predictor of wetland colonization (Branch and Schooley 2005).

Distributional patterns of round-tailed muskrats are sensitive both to wetland condition and to landscape connectivity. In our study area, in which suitable habitat patches are naturally fragmented and matrix habitat is heterogeneous, muskrats display spatial dynamics typical of metapopulations. The region that Bridges (2000, 2001) delineated as pre-settlement dry prairie contains wetlands with a relatively high rate of occupancy by muskrats (42%). Our analyses indicate that these incidence patterns mainly are related to greater recolonization of vacant wetlands in the historical dry prairie region compared to other matrix habitats such as pine flatwoods and scrub. Interpretation of these patterns is not straightforward, however, because current land uses are partially confounded with historical landscape associations. In particular, matrix effects on dispersal of muskrats likely reflect a mix of factors. Florida dry prairie represents a treeless habitat that should favor inter-wetland movement by round-tailed muskrats, which basically are a species of open habitat. Patch connectivity also is relatively high in the dry prairie landscape, which should increase dispersal success. These processes probably operate similarly today as in pre-settlement times. In addition, a key land use at Avon Park—the planting of pines in dense blocks—seems to reduce the functional connectivity of the landscape for muskrats. It is unclear whether this negative effect of plantations on muskrat colonization is due to vegetation structure *per se* or to increased predation risk in plantations, perhaps from increased perches for avian predators. Regardless of exact mechanisms, negative effects of pine plantations are reduced in the dry prairie region compared to other matrix habitats due to spatial patterns of land use at our site.

We suggest that relative effects of historical landscapes and current land-use practices can be unraveled fully only through adaptive management (Walters and Holling 1990) in which large-scale management actions are treated as 'landscape experiments' that assess alternative hypotheses and recognize uncertainties in ecosystem management. One such experiment could include removal of pine plantations in selected blocks and monitoring of wetland colonization by muskrats over time. Likewise, effects of grazing intensity on wetland quality and the spatial incidence of muskrats could be evaluated more rigorously via adaptive management.

The spatial structuring of round-tailed muskrat metapopulations requires that conservation practices for the species be applied at broad spatial scales. Maintenance of Florida dry prairie might be especially important to persistence of muskrats and other marshland species that must periodically travel across matrix habitat to reestablish populations in vacant patches. Management of the Florida dry prairie landscape should include considerations of these wetland-upland linkages and of how land-use practices might affect landscape cohesiveness.

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