

ANTHROPOGENIC ENVIRONMENTAL CHANGE AND HABITAT
OCCUPANCY BY RIPARIAN MUSKRATS IN A MIDWESTERN
LANDSCAPE

BY

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THESIS

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ABSTRACT

Increased urban land cover and more intensive agriculture in the Midwest have changed the landscape for wildlife species. Distributions of semi-aquatic mammals such as muskrats (*Ondatra zibethicus*) may respond to environmental changes including increased urbanization, alteration of hydrology, introduction of invasive species, and changes in predator communities. The response of muskrat populations to landscape and local-scale changes is important for the conservation of this economically-valuable furbearer species. I completed multiple surveys for occupancy by muskrats at 90 sites in central Illinois in 2007 and 2008. Sites were stratified based on urbanization levels. Occupancy was determined by presence of tracks, scat, and feeding sign in 200-m stream segments that approximated a home-range scale. I calculated detection probabilities to determine the likelihood of false absences. The per-survey detection probability was 0.79 (SE = 0.04) in 2007 and 0.76 (SE = 0.04) in 2008. Detection was related positively to Julian date and negatively to wood debris abundance. Muskrats occurred more often at sites with a greater percentage of developed landcover, as well as in wider and deeper streams that drained more area. Year-to-year turnover was explained by water availability and measures of stream size. Although invasive reed canary grass was the dominant species at an average of 2.3 (SE = 0.20) out of 5 habitat sampling stations per site, it did not affect site occupancy or turnover. Occupancy patterns may be related to lower predation risk near human development and in wider, deeper streams. Overall, muskrat distribution was related to local and landscape variables and was insensitive to some aspects of environmental change.

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General Introduction

“There is a reasonably strong consensus that land use change is now, and for some decades will remain, the single most important of the many interacting components of global change affecting ecological systems” (Vitousek 1994).

The Illinois landscape has experienced drastic changes since the first settlers arrived in the early 1800s (Urban 2005). Historically, >58% of the state was tallgrass prairie, but by 1980 <0.01% was prairie with >90% of the converted land in agriculture (Iverson 1988). Flatter areas, especially the Grand Prairie region of east-central Illinois, experienced the most conversion to row crop agriculture (Mankin and Warner 1997). Land-use change did not stop with “taming” of the prairie. Consolidation of small farms between 1900 and 1950 resulted in further habitat loss as field borders and fencerows were plowed under (Mankin and Warner 1997). Over the last few decades, urbanization has further altered the character of the landscape.

Aquatic and riparian habitats in the Grand Prairie region have experienced major alterations over the past 150 years. Erosion and gully formation were a huge problem in the late 1800s, leading to improved land-conservation practices such as contour planting, installation of grass waterways, and tile drainage (Knox 2001). Passage of the Drainage Act and Levee Acts in 1879 by the Illinois legislature allowed small farmers to coordinate construction of ditches and levees and channelization of streams to increase productivity of seasonally-flooded lands

(Urban 2005). An estimated 59 to 90% of Illinois wetlands were drained between 1820 and 1997, with most of this conversion (87%) for agriculture (Iverson 1988; Urban 2005). Over 20 million hectares of farmland in the Great Lakes Region were tile-drained between 1870 and 1980 for row crop agriculture (Freeman et al. 2007). Approximately 90% of cropland in Illinois is tile-drained, consisting of almost 4 million hectares and 35% of the state (Zucker and Brown 1998).

Urbanization

Land-use change in the Grand Prairie region also has involved increasing urban and suburban development. As urban areas in Midwestern states such as Illinois have grown, the impact of human development on wildlife also has increased. Proximate causes of changes in wildlife populations in urbanizing habitats are varied and may include habitat loss and fragmentation (Crooks et al. 2004), direct mortality from roads and contact with humans (Guichón and Cassini 1999; Clevenger et al. 2001), decreases in predator abundances (Baker and Harris 2007), and increased rates of zoonotic diseases and competition from non-native species (Niemelä 1999). Randhir and Ekness (2009) suggest that non-fish vertebrate diversity is negatively associated with urban land cover percentages above 10-12%. Mammals may be more sensitive to urbanization than other taxa (Randhir and Ekness 2009). Species display a variety of responses to urbanization. Some species behaviorally avoid developed areas (Buij et al. 2007), some species continue to live near humans but have lower reproductive success

(Rodewald 2003), and other species adapt to the available resources and thrive (“urban adaptors” and “urban exploiters”; McKinney 2006).

Land use and hydrology

Effects of changing land-use patterns on watersheds can be highly variable (Knox 2001). Many Midwestern streams have become flashier over the past 30 years, in part, due to increases in agricultural tile drainage and urbanization (Baker et al. 2004). Hydrological alterations that result in more severe high and low flow events cause direct mortality and may act as “ecological bottlenecks” for riverine and riparian species (Poff et al. 1997).

Effects of human activities on stream habitats vary between urban and rural environments. In urban areas, pollution, loss of stream habitat due to storm drainage systems, and increase in impervious surfaces threaten the function and biodiversity of stream ecosystems (Hirsch et al. 1990). Impervious surfaces decrease the lag time between rainfall events and peak stream flow (Paul and Meyer 2001). Flashier flows cause bank incision and channelization and an eventual drop in the water table (Groffman et al. 2003). Storm drainage systems, sewage effluent, and outflow from retention ponds result in higher baseflows in urban areas (Changnon and Demissie 1996; Poff et al. 1997). Goldstein et al. (2007) found that changes in stream width and depth were correlated positively with increases in human population.

In rural watersheds, tile drainage and channelization of streams result in fewer kilometers of headwater streams, decreased groundwater recharge, and decreased baseflow by quickly routing water downstream. Highly modified rural streams also experience increased flashiness, entrenchment, and greater peak flows (Changnon and Demissie 1996; Poff et al. 1997; Knox 2001).

Channelization of existing streams and dredging drastically changed the watersheds of Central Illinois. For the six watersheds that are partially within Champaign County, on average 95% of the first order streams have been channelized to the extent that a distinction is rarely made between ditches that were created by dredging and those that were originally streams (Urban 2005). Despite the various threats, riparian areas serve as important corridors and habitat for wildlife in Illinois (Mankin and Warner 1997).

Invasive reed canary grass

Invasive species threaten biodiversity and ecosystem function (Vitousek 1994; Maskell et al. 2006). Approximately 27% of Illinois flora is non-native (Spyreas et al. 2004). Disturbance and channelization increase invasive species risk (Kercher and Zedler 2004; Maskell et al. 2006). Reed canary grass (*Phalaris arundinacea*) is an invasive plant causing concern in Illinois. Although this species is native to the state, today the reed canary grass found in Illinois is primarily a European genotype which was planted as forage and erosion control (Kercher and Zedler 2004). Reed canary grass was a dominant species at 43% of

central Illinois wetlands surveyed for the Illinois Critical Trends Assessment Program (CTAP) and at 29% of wetlands statewide (Spyreas et al. 2004). In wetlands, reed canary grass outcompetes other wetland plants under multiple disturbance regimes (Kercher and Zedler 2004). Drainage ditches in central Illinois are susceptible to invasive species such as reed canary grass because they have a history of disturbance and channelization, fertile soils, adequate water availability, and they are effective conduits for spread of seeds (Lavoie and Dufresne 2005). In Wisconsin, increases in reed canary grass along the banks of a river island in Chippewa River corresponded to severe declines in the populations of several native floodplain plants (Barnes 1999). Reed canary grass has high levels of alkaloids and is suspected to be of poor quality forage for native herbivores (Miller and Nelson 1995; Illinois Department of Natural Resources 2005).

Study species

My research focuses on the muskrat (*Ondatra zibethicus*), a common semi-aquatic rodent native to most of North America (Willner et al. 1980). In Illinois, the muskrat is an economically important furbearer species. During the 2006-2007 trapping season in Illinois, 50,483 muskrat pelts were sold at a combined value of \$335,712 (Bluet 2008). Muskrats also have been listed as a Species of Special Conservation Concern under the Illinois Comprehensive

Wildlife Conservation Strategy due to concerns about declines in riparian muskrat populations (CWCS; Illinois Department of Natural Resources 2005).

Musk rats have broad habitat preferences and will inhabit shallow wetlands, ponds, small lakes, streams, drainage ditches, and rivers (Nadeau et al. 1995). Although muskrats typically construct lodges of cattails (*Typha* spp.) or other reeds, especially in wetlands and ponds, at low population densities and in riparian systems muskrats tend to use bank burrows for shelter and as natal dens (Messier and Virgl 1992; Nadeau et al. 1995). In riparian habitats, muskrat burrows are generally located in slow-moving reaches (Nadeau et al. 1995). Slope and soil type impact the location, construction, and longevity of bank burrows (Willner et al. 1980). Musk rats are vulnerable to direct and indirect mortality during flooding events (Errington 1937a; Errington 1941; Willner et al. 1980; Proulx et al. 1987; Thommes 1992; Nadeau et al. 1995).

The diet of muskrats is diverse and may consist of cattails, arrowhead (*Sagittaria* spp.), smartweeds (*Polygonum* spp.), burr marigold (*Bidens laevis*), aster species, goldenrod (*Solidago* spp.), grasses and occasionally frogs, fish, aquatic insects and shellfish (Errington 1941; Convey et al. 1989). Muskrat occasionally use upland habitat (Clough 1987) and will feed on corn, alfalfa, and other row crops in agricultural areas (Errington 1937b; Arta 1959; Errington et al. 1963). In Illinois, muskrats consume cattails, goldenrod, sweet clover (*Melilotus* spp.), broom sedge (*Andropogon* spp.), willow (*Salix* spp.), soft-stem bulrush (*Scirpus validus*), stonewort, (*Chara* spp.) and eel grass (*Vallisneria americana*; Arta 1959). Diet plasticity may allow this species to occupy a wide geographic

range and may decrease its susceptibility to invasive plants such as reed canary grass. However, little is known about responses by muskrats to non-native vegetation.

Muskrats typically produce two to four litters per year consisting of three to twelve young (Boutin et al. 1988). Litters are born between April and late September with length of the reproductive season correlated with latitude (Beer 1950; Stewart 1974). The young are born in burrows or lodges and are weaned at approximately four weeks of age. By 14-16 days old, young muskrats are capable of diving, and presumably of leaving the den (Errington 1939). Their high fecundity may be offset by high rates of depredation by coyotes (*Canis latrans*), mink (*Neovison vison*), and hawks (Haydon et al. 2001). Mink populations cycle with muskrat populations across large portions of their overlapping ranges (Viljugrien et al. 2001). Predation risk for muskrats may decrease along the rural-to-urban gradient as predator populations decline with increased road and housing density.

Habitat modeling and objectives

Previous efforts to model muskrat habitat preferences in riparian systems have generally focused on local habitat characteristics. Nadeau et al. (1995) used muskrat sign to determine presence of muskrats in 235 sections of shoreline (60 m each) spread throughout different habitat types including fast-and-slow flowing streams and rivers, lakes, bogs, and beaver (*Castor canadensis*) dam ponds in

James Bay, Quebec. Muskrats were most likely to occur in slow-flowing streams and rivers and had their lowest occurrence in fast-moving rivers and streams, but water depth was unrelated to muskrat presence (Nadeau et al. 1995). However, in that study all sites were >0.48 m deep at 2 m from the shore. Moreover, detection probability was not estimated using multiple surveys, so the potential problem of false absences was not dealt with in the habitat model (MacKenzie et al. 2002).

Little is known about the spatial distribution and habitat use of riparian muskrats in agricultural-dominated landscapes. Over the past 100 years, tile drainage, loss of hedgerows and riparian buffers, increases in corn-soybean monocultures (Urban 2005), spread of invasive plants (Spyreas et al. 2004), and increased urbanization (Mankin and Warner 1997) have drastically altered the agricultural landscapes in Illinois. Effects of these anthropogenic changes on muskrat populations are unknown. The goal of this project was to identify local and landscape factors that affect site occupancy by riparian muskrats in the Grand Prairie Region of Illinois. Chapter 2 describes a multi-year occupancy model (MacKenzie et al. 2002) for muskrats that accounts for imperfect detection during presence-absence surveys. The model includes spatial turnover for muskrats, in addition to static incidence patterns, to gain a clearer picture of habitat suitability for riparian muskrats in a changing environment.

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Introduction

Globally, wildlife diversity is threatened by anthropogenic environmental impacts. Habitat loss and spread of invasive species due to land-use changes are two of the most serious problems (Vitousek 1994). In parts of the Midwestern USA, >90% of the original habitat has been converted to agriculture and urban land cover, leaving the remaining wildlife habitat fragmented and degraded (Iverson 1988; Illinois Department of Natural Resources 2005). Land-use changes have altered compositions of wildlife communities with predator species such as coyotes (*Canis latrans*) increasing in agricultural areas relative to in urban sites (Gosselink et al. 2003).

Urban areas in the Midwest have increased in size over the past century, including smaller cities far from major metropolitan centers. For example, the population of Champaign, Illinois, a moderate-sized college town, increased 9% between 1990 and 2007 (United States Census Bureau 2002). Urbanization gradients represent a complex interplay between abiotic and biotic factors that affect wildlife species (McDonnell and Pickett 1990). Proximate causes of changes in wildlife populations in urbanizing habitats are varied and include habitat loss and fragmentation (Crooks et al. 2004), direct mortality from roads and contact with humans (Guichón and Cassini 1999; Clevenger et al. 2001), decreased predator abundances (Baker and Harris 2007), increased rates of zoonotic diseases (Gómez et al. 2008) and competition from non-native species (Niemelä 1999). Although some species are negatively affected by urbanization,

other species are urban adapters that take advantage of resources available near human development (McKinney 2006). Urban adapters have common characteristics such as behavioral plasticity, relatively small size, and broad diets (Ditchkoff et al 2006; Hunter 2007).

Aquatic habitats in both urban and rural watersheds have been highly modified by humans (Knox 2001). In regions of the Midwest, 90% of wetlands were drained by the late 1900s (Urban 2005). Most remaining habitat for aquatic and semiaquatic species occurs in riparian systems that also have been highly modified by humans. Urban streams are impacted by pollution, loss of stream habitat due to storm drainage systems, and increases in baseflow caused by outflow from waste-water treatment plants and retention ponds (Hirsch et al. 1990; Changnon and Demissie 1996; Poff et al. 1997). Agricultural watersheds have been heavily tile-drained and channelized resulting in reduced headwater streams, decreased groundwater recharge, lower baseflow, and increased flashiness and peak flows (Changnon and Demissie 1996; Poff et al. 1997; Knox 2001). Over the past 30 years, increases in impervious surfaces in urban watersheds and tile-drained acreage in agricultural watersheds have created shorter lag times between rainfall events and peak stream flow (Baker et al. 2004). These changes in stream hydrology, which result in more severe high and low flow events, may act as “ecological bottlenecks” reducing individual fitness for riverine and riparian species (Poff et al. 1997).

Invasive species threaten biodiversity and ecosystem function in highly modified landscapes (Vitousek 1994; Maskell et al. 2006). A European genotype

of reed canary grass (*Phalaris arundinacea*) that was planted for forage and erosion control has become the dominant species at 43% of wetlands in central Illinois (Kercher and Zedler 2004; Spyreas et al. 2004). In riparian habitats, increases in reed canary grass correspond to severe declines in the populations of native floodplain plants (Barnes 1999). Reed canary grass contains high levels of alkaloids and low levels of digestible dry matter and thus is suspected to be poor quality forage for native herbivores (Miller and Nelson 1995; Illinois Department of Natural Resources 2005). Monotypic stands of reed canary grass can negatively affect abundance and diversity of various taxa including small mammals and moths (Semere and Slater 2007; Schooler et al. 2009).

Occupancy models are a valuable tool for evaluating effects of landscape-level changes on wildlife because they require only presence-absence data to make inferences about habitat relationships and can be less costly and time intense than alternatives (Lebreton et al. 1992; Wintle et al. 2005; Lopez and Pfister 2001; Yoccoz et al. 2001). To avoid biases related to imperfect detection of species during a single survey, occupancy modeling employs multiple surveys at the same sites to allow for simultaneous estimation of detectability and site occupancy (MacKenzie et al. 2002; 2006). Previous studies have evaluated the applicability of occupancy modeling to a range of survey techniques and a wide variety of taxa from salamanders (Bailey et al. 2004) to forest elephants (*Loxodonta cyclotis*; Buij et al. 2007).

I used occupancy modeling to ask how muskrats (*Ondatra zibethicus*) have responded to environmental change, including urbanization and invasion by

reed canary grass, in riparian habitats in the Grand Prairie region of central Illinois. Muskrats are a good species for asking such questions because they potentially occur across entire urbanization gradients, respond to variation in measurable habitat quality (Nadeau et al. 1995), and are herbivores that should be sensitive to changes in plant community composition. Improved knowledge of habitat suitability for muskrats also can guide management for this species that is an economically important furbearer and has been listed as a Species of Special Conservation Concern in Illinois due to perceived population declines (Illinois Department of Natural Resources 2005).

I examined whether past land-cover modification and variation in local habitat characteristics affected distribution patterns of riparian muskrats across an urban-rural gradient. This is the first study that accounts for imperfect detection while creating a predictive habitat model for muskrats. Specific objectives were to determine (1) if detection probability for muskrats varied in relation to survey-specific covariates; (2) if local habitat characteristics were an important cause of heterogeneity in occupancy probability; and (3) if site occupancy was related to anthropogenic habitat alterations including urbanization and the spread of non-native reed canary grass. Because muskrats should be sensitive to stream flashiness and low water levels, I predicted that larger streams with more water permanence would have greater occupancy by muskrats. I also predicted that occupancy by muskrats would be related positively to urbanization due to higher stream baseflows, their life history as urban adapters, and reduced predation risk

at sites with more human development. Finally, I expected that dominance of sites by reed canary grass would negatively affect muskrats.

Methods

Study area

My research was conducted in the Grand Prairie Region of Illinois within a 7854-km² area (Fig. 1) centered upon Champaign, Illinois (40°05' N, 88°15' W). This region contains portions of five watersheds: Sangamon, Moultrie, Embarras, Wabash, and Vermilion. Streams within the study area range from first-order headwater streams to a fifth-order stream (Sangamon River). Elevations range from 188 to 236 m, and stream gradients are primarily <1%. Streams varied from <1 to 30 m in wetted channel width. Land cover in the Grand Prairie Region is dominated by row crop agriculture (80%, primarily corn and soybeans), forest (5%), and pasture and grassland (4%). Dominant riparian vegetation included reed canary grass, smooth brome grass (*Bromus inermis*), giant ragweed (*Ambrosia trifida*), and goldenrod (*Solidago* spp.). Common riparian forest trees and shrubs included elm (*Ulmus* spp.), silver maple (*Acer saccharinum*), box elder (*Acer negundo*), black walnut (*Juglans nigra*), and honeysuckle (*Lonicera* spp.). Twelve incorporated towns within the study area have population sizes >2,500 people and therefore meet the US Census Bureau definition of urban (United States Census Bureau 2002). The region has a humid

continental climate with total precipitation between July 1 and October 31 averaging 346 mm (SE = 10) between 1907 and 2007. In 2007, 261 mm of rain were recorded in Urbana between July 1 and October 31. During the same period in 2008, 503 mm of rain were recorded. Precipitation data were collected at the Illinois State Water Survey weather station in Urbana (<http://www.isws.illinois.edu/data/climatedb/>). Average monthly temperatures range from a high of 23.8° C in July to a low of -3.5° C in January (Urban and Rhoads 2003).

Design of occupancy surveys

I conducted occupancy surveys for muskrats at 90 sites between mid July and late October in 2007 and 2008. Because occupancy methods are most effective when the sampling unit is designed to match either a population or a home-range scale (Royle and Nichols 2003), I surveyed 200-m reaches of wadeable streams (hereafter referred to as sites), which approximated the average linear home range of riparian muskrats (MacArthur 1980; Allen and Hoffman 1984; Brooks 1985; Brooks and Dodge 1986). Hence, I investigated distribution patterns and turnover dynamics of muskrats at the home-range scale. I used a stratified random sampling design to select the 90 sites; 50% were located within a 2-km radius of incorporated towns (>2500 people), and 50% were located outside of this urban buffer. Intermittent streams were retained for sampling

because some had evidence of use by muskrats. Sixteen sites (17.8%) were dry at the time of sampling in 2007, whereas only 3 sites (3.3%) were dry in 2008.

I used observations of scat, tracks, feeding sign, and burrows to indicate site occupancy by muskrats. Evidence of feeding sign, tracks, and scat can be collected faster than burrow data (Brooks 1985; Nadeau et al. 1995), so more effort was focused on locating these types of sign. During each survey, a single trained observer searched for sign on both sides of the 200-m stream reach. In 2007, six different observers conducted surveys but most surveys (95%) were performed by one of three observers. In 2008, three observers conducted all surveys. Each site received a minimum of one visit in which two independent observers conducted surveys, starting from opposite ends of the stream reach. I used a removal design (MacKenzie and Royle 2005) in which sites where muskrat sign was detected on either of the first two surveys were not revisited. If muskrat sign was not detected during the first two surveys, we returned for two additional surveys for a maximum of four surveys (MacKenzie and Royle 2005). We completed a total of 518 surveys (264 in 2007, 254 in 2008).

Detection covariates

I recorded survey-specific covariates for detection (Table 1) including observer, date, cumulative rainfall during the previous seven days, and the relative abundance of emergent woody debris and large rocks on a scale of 0-5 (0 = none, 5 = >1 item per 10 m of stream bank). Muskrats deposit scat in prominent

locations such as on top of logs and rocks (Brooks 1985; Rezendes 1999), so I predicted that detection probability would be greater where more of these surfaces were available. With one exception each year (both cases due to persistent inclement weather), we did not conduct surveys within two days of any rainfall event >1 cm to minimize the chance of sign being removed by rainwater and water-level fluctuations immediately prior to our surveys.

Local habitat conditions

At each site, I collected habitat data at five stations located 0, 50, 100, 150, and 200 m from the downstream end. At each station, I measured wetted channel width, thalweg depth (maximum cross-sectional depth), soil texture (Percent Sand) estimated using the feel method (Thien 1979), riparian buffer width, and type of riparian vegetation (Fitzpatrick et al. 1998; Table 1). I quantified several aspects of streambank morphology. I measured linear distances along the slope of the bank from the wetted edge to bankfull (Bankfull Height) and from bankfull to the top of the floodplain (Floodplain Height; Table 1). The bank angle was measured using a clinometer at the wetted edge (Bankfull Angle) and halfway between bankfull and the top of the floodplain (Floodplain Angle; Table 1). I estimated percent cover vegetation in four zones: submerged, emergent, from the wetted edge to bankfull, and from bankfull to the top of the floodplain (Table 1). I also recorded the dominant plant species in each of these zones and then determined the number of stations at each site dominated by reed

canary grass from the wetted edge to bankfull. Habitat data from all five stations in both years were averaged to create a single value for each covariate at each site.

Landscape covariates

I used the latest available data sources for the study area for landscape analysis. To delineate all land-cover types within a 500-m buffer around each site, I used land-cover data from the National Agricultural Statistics Service (NASS) for 2007 (USDA 2008) combined with data on nearest crop collected in the field and land-use category boundaries derived from digital orthoquadrangles (Illinois National Aerial Photography Program 2005). I calculated the percentage land cover in the following categories: Urban (includes buildings, maintained lawns, parking lots, roads, and railroads), Forest, Row Crop Agriculture, and Field (includes pastures, road edges, prairie, and unmaintained grasslands; Table 1). Because of collinearity, I focused on Urban. Riparian buffer widths that were >30 m were estimated in the field but confirmed in GIS using the digital orthophotography.

Although I designated areas as urban or rural for site selection, urbanization is better understood as a gradient (McDonnell and Pickett 1990). My sites encompassed the entire gradient of urban land cover from 0% to 98.7%. For a random sample of 30 sites, urban land cover within the 500-m buffers was highly correlated with building density ($r = 0.95$, $P < 0.0001$).

The drainage area for each site was calculated for the upstream subwatershed (Fitzpatrick et al. 1998; Table 1). I used existing subwatershed, elevation, and stream layers to manually delineate the subwatershed using the downstream extent of each 200-m site as the pour point (Illinois State Geological Survey 2003; US Environmental Protection Agency and the US Geological Survey 2005). Finally, I used spatial coordinates (Universal Transverse Mercator, UTM) for each site to assess any linear spatial patterns in response variables not accounted for by other predictors. I centered the coordinates prior to analysis (Table 1).

Occupancy modeling

To avoid multicollinearity, I examined correlations between predictor variables and used $r \geq 0.60$ as a criterion to avoid using pairs of correlated variables in further analysis. Thalweg depth, wetted width, and drainage area were correlated (all $r > 0.60$), so I used Principle Components Analysis (PCA) to create orthogonal principle components (PC). The first PC (SizePC), which accounted for 88.8% of the variation and was positively correlated with all three variables, was retained for use in subsequent analyses as a measure of stream size and water availability (see Graham 2003; Krishna et al. 2008). SizePC was correlated with riparian width ($r = 0.67$), therefore I omitted riparian width from all models containing SizePC. Measures of percent cover of vegetation in several zones (bankfull, floodplain, and channel) also were correlated (all $r > 0.60$). The

first PC (VegPC) accounted for 78.3% of the variation and was positively correlated with all three percent cover measures, so I included VegPC in subsequent models as a measure of vegetation cover (see Mortelliti and Boitani 2007).

I used occupancy modeling to evaluate the influence of covariates on detection (p), occupancy (ψ), colonization (γ), and extinction (ϵ). Occupancy modeling employs multiple surveys at the same sites to create a detection history with 1 representing that the species was detected and 0 representing non-detection (MacKenzie et al. 2005). Non-detection occurs when the species is present but not detected [$\psi \times (1-p)$] or when the species is not present ($1 - \psi$) (MacKenzie et al. 2005). Detection probability (p) is calculated and used to correct the naïve occupancy estimate to explicitly account for non-detection. Detection, occupancy, colonization, and extinction can vary among sites based upon survey-specific (for detection) and site-specific covariates which are incorporated into models using logit link functions (MacKenzie et al. 2005). Since occupancy modeling is an extension of capture-recapture theory, similar assumptions apply: (1) closed population within a defined season; (2) no false presences; (3) detection probability is independent among sites (MacKenzie et al. 2005; Bailey et al. 2004).

I created a set of 20 multiyear occupancy models based upon biological rationale and evaluated these models with PRESENCE 2.3 software (Hines 2006). PRESENCE uses Akaike's Information Criterion (AIC_c for small sample sizes) to identify the most parsimonious model from a set of models and to rank the rest

(Burnham and Anderson 2002). I evaluated 12 occupancy covariates, including the first PC for stream size and the first PC for vegetation cover, and four detection covariates. I compared models with a maximum of four covariates for ψ , two covariates for ϵ , and two covariates for p to avoid over-parameterization. I used a step-wise approach in which I first selected the best model for p via AIC_c and then modeled ψ , γ , and ϵ (Krishna et al. 2008). I built occupancy and colonization models with various combinations of covariates to investigate the relative importance of stream size, urban land cover, invasive species, streambank morphology, and local habitat characteristics on site occupancy and turnover for muskrats. Due to the small number of sites that went extinct between 2007 and 2008 ($n = 5$), I did not include covariates for local extinction (ϵ). Typically, the global model should be subjected to a goodness-of-fit test to assess whether it offers adequate explanatory value. However, such a test is not yet available for multiyear models (MacKenzie 2005; Hines 2006).

Results

In 2007, evidence of muskrats was found during ≥ 1 visit at 52 of 90 sites (naïve occupancy = 57.8%; Fig. 1). In 2008, muskrat sign was located during ≥ 1 visit at 62 of 90 sites (naïve occupancy = 68.9%; Fig. 1). Scats, tracks, and plant clippings were the most common types of sign detected in both years. Scats were found at 60% of occupied sites each year. Muskrat tracks were detected at 73% of occupied sites in 2007 and at 58% of occupied sites in 2008. More than one

type of sign was detected at 82.6% of occupied sites in 2007 and 69.4% of occupied sites in 2008.

Detection

Per-visit detection probability (p) was estimated from my best model as 0.79 (SE = 0.04) in 2007 and 0.76 (SE = 0.04) in 2008. The best model for detection of muskrats included Julian date and woody debris as covariates (Table 2). Julian date was related positively to detection probability (Fig. 2). Detection rates increased from 0.60 – 0.70 in July to ~0.85 by late October (Fig. 2).

Relative abundance of woody debris was related negatively to detection probability. No other models were highly competitive ($\Delta AIC_c < 2$, Table 2) and thus there was little evidence that observer and cumulative 7-day rainfall were important influences on detection probability.

Site occupancy

For 2007, site occupancy (ψ) for muskrats was estimated as 0.59 (SE = 0.09) after correcting for imperfect detection. For 2008, site occupancy was derived as 0.69 (SE = 0.06) using the estimates from the top model for 2007 occupancy, colonization, and extinction.

The best multiyear model contained four covariates for occupancy (ψ): SizePC, bankfull height, percent sand, and urban land cover (Table 3).

Occupancy probability was related positively to SizePC and approached an asymptote of 1.0 at SizePC of 1.4 (Fig. 3a). Occupancy probability was related positively to bankfull heights (Fig. 3b). Percent sand in bank soil samples ranged from 8 to 67%. Sandier soils were associated with lower occupancy probabilities (Fig. 3c). Urban land cover had a positive influence on site occupancy by muskrats (Fig. 3d). Other models were not highly competitive, including those that included dominance of reed canary grass (Table 3), which was the dominant species at an average of 2.3 (SE = 0.20) out of 5 habitat sampling stations per site (Range= 0-5).

Spatial turnover

Of 38 sites at which muskrats were not detected in 2007, muskrats were detected at 15 sites in 2008 (39.5%; Fig. 1). The best model for colonization (γ) included SizePC as the sole covariate (Table 3). Colonization events were more common at larger streams that drained larger areas (Fig. 4). Eighty percent of unoccupied sites with drainage areas larger than 10 km² ($n = 10$) were colonized in 2008. Apparent local extinctions occurred at only five sites. Three of the five local extinctions were located in the Moultrie watershed (Fig. 1).

Discussion

Occupancy modeling revealed that the spatial distribution and dynamics of riparian muskrats in the Grand Prairie Region were related to habitat factors at local and landscape scales. However, muskrats were not negatively affected by broad anthropogenic changes to their stream environments including urbanization and dominance by invasive reed canary grass. Muskrats may be among the species considered urban-adapters (Ditchkoff et al 2006).

Detection

Detection probability (p) on a single visit was <1.0 indicating that occupancy modeling was warranted for riparian muskrats. Detection probability was related positively to Julian date. As the field season progressed, more juvenile muskrats might have been active outside of their natal burrows, which could correspond to more sign. Stewart and Bider (1974) reported muskrat activity increased as summer progressed in Quebec. In other regions at the same latitude as my study area, muskrats have multiple litters with 25% of litters born in July and August (Errington 1937). Detection probability was related negatively to woody debris abundance. I predicted a positive relationship because muskrats frequently deposit scat on emergent rocks and woody debris (Brooks 1985; Rezendes 1999). This is opposite of our prediction and we have no explanation for this relationship.

Site Occupancy

Occupancy probability for muskrats increased as proportion of urban land cover at a site increased. This outcome is contrary to patterns reported for many riparian and riverine species. Decreased species richness for stream macroinvertebrate and fish communities has occurred when urban land cover was 8-33% (Paul and Meyer 2001). However, muskrats may be insensitive to processes that negatively affect fish and invertebrates such as sedimentation, pollution, and loss of the ripple-pool structure (Paul and Meyer 2001). Some characteristics that have made muskrats successful invaders in Europe should make them less sensitive to modifications of their environment by humans. For example, the species is capable of moving relatively long distances, living in locally dense populations, reproducing rapidly, and feeding on a broad diet (Danell 1996). Muskrats are relatively tolerant of pollution (Halbrook et al. 1993; Juhlin and Halbrook 1997). Connectivity of streams, presence of riparian buffers, and the ability to bypass roads via culverts could mitigate some negative effects of urbanization for stream-dwelling species (Dickman 1987; Clevenger et al. 2001; Mahan and O'Connell 2005; Randhir and Ekness 2009). Hydrologic characteristics of urban streams, including higher baseflow for a given wetted width, may favor urban muskrats (Hirsch et al. 1990; Chagnon and Demissie 1996). Conversely, rural muskrats (especially in headwaters) could be negatively affected by land conservation and agricultural drainage practices that lowered

water tables, decreased baseflow, and increased flashiness (Hirsch et al. 1990; Knox 2001; Baker et al. 2004).

Muskrats likely have lower predation risk in urban areas due to effects of urbanization on potential predators. Coyotes and red foxes (*Vulpes vulpes*) tend to avoid urban sites with foxes being more sensitive to human disturbance than are coyotes (Randa and Yunger 2006). In urban areas, coyotes concentrate foraging in woodlot edges and grassy old fields, whereas coyotes in rural agricultural areas forage almost exclusively along corridors such as drainage ditches (Atwood et al. 2004). Coyote home ranges are smaller in urban areas than in rural areas, and coyotes are less active and travel less distance each day compared to those with rural home ranges (McClennen et al. 2001; Atwood et al. 2004). The American mink (*Neovison vison*) is a key predator of muskrats in our system (A. Ahlers unpublished data). Little is known about mink response to urbanization in North America, but introduced populations of American mink in Europe avoid areas with human activity (Melero et al. 2008). Finally, trapping pressure may be lower for muskrats near urban areas due to human demographic trends resulting in a negative relationship between trapping participation rates and urbanization (Lischka et al. 2008; Poudyal et al. 2008).

Several caveats must be added regarding the relationship between site occupancy by muskrats and urbanization. First, my results pertain to medium and small urban areas and might not hold for larger cities that could have elevated levels of habitat disturbance. Second, many of my urban sites were located in the urban fringe and not within inner-city areas where hydrology and streambanks

could be modified to a greater degree. Third, rural sites were in human-dominated, agricultural areas and results could differ for urban-rural gradients that include more natural habitat.

My prediction that sites dominated by reed canary grass should have lower occupancy by muskrats was not supported. Although there is evidence that reed canary grass is of low nutritional value due to high levels of alkaloids and low digestible dry matter (Miller and Nelson 1995), I routinely witnessed muskrats carrying reed canary grass clippings that they presumably consumed, used as nesting material, or both. Floodplain fields dominated by reed canary grass have larger numbers of voles (*Microtus* spp.) than old fields dominated by weeds and shrubs, probably because voles are grassland specialists (Spyreas et al. 2009). Reed canary grass was historically cultivated as forage and most palatability studies have focused on livestock and have compared various non-native forage grasses to each other (Lavoie and Dufresne 2005). Further research is needed on the comparative nutritional value of native and introduced plants for muskrats and other native herbivores.

Site occupancy by muskrats was related positively to SizePC. Larger SizePC values indicated wider, deeper streams that drained a larger area and typically had more permanent flow and wider riparian corridors. As watershed size increases, streams become less flashy and less sensitive to localized changes in conditions such as storms (Poff et al. 1997; Baker et al. 2004). Sufficient and stable water levels can result in higher population growth rates for muskrats (Virgl 1997). Extreme changes in water levels and low water availability result in

lower food and cover availability that can increase muskrat mortality and reduce body condition and body fat reserves. (Allen and Hoffman 1984). Water level fluctuations also increase predation risk (Virgl 1997). Muskrats prefer water depths between 0.2 and 1.2 m in marshes and ponds (Bellrose and Brown 1941; Errington 1963; Earhart 1969), and water level is more important than food resources in muskrat habitat suitability models for marsh habitats (Virgl 1997). Muskrats may be at lower predation risk in streams with a larger SizePC where they are better able to take cover under water. Mammalian predators such as coyotes are less likely to enter deep water and thus have more access to terrestrial prey in riparian ecosystems where flow is low (Tigas et al. 2002; Zoellick et al. 2004). Moreover, larger streams have wider riparian corridors, which can positively affect water quality and wildlife dispersal and counteract negative impacts of row-crop agriculture and urbanization (Groffman et al. 2003; Lovell and Sullivan 2006).

The other two predictors in my best occupancy model, bankfull height and percent sand, may be important determinants of bank suitability for construction of muskrat burrows. Muskrat occupancy was higher at sites with greater bankfull heights, which is consistent with previous findings that banks less than 0.2 m are poor sites for muskrat burrows (Allen and Hoffman 1984; Brooks 1985). Percent sand was negatively related to muskrat site occupancy. Soil properties, including soil texture, can affect burrowing behavior by small mammals (e.g., Rhodes and Richmond 1985). Muskrats prefer clay-loam soils over sandy soils (Nadeau et al.

1995), and burrow longevity is negatively related to the percent sand in the soil (Allen and Hoffman 1984).

Spatial turnover

I reiterate that my sampling was conducted at a home-range scale so that patterns of local colonization and extinction may reflect year-to-year fluctuations in population density or changes in resource patch use (MacKenzie et al. 2005). Fifteen sites were colonized in 2008, and five sites became locally extinct between years. Colonization was best explained by SizePC; deeper and wider streams that drained greater areas had a greater likelihood of being colonized by muskrats. Weather patterns were drastically different between years causing greater water availability in 2008 relative to 2007. The increased rainfall resulted in increased water depths and may have benefitted muskrats living in marginal habitats where low flow exposes them to predators in years with typical or below-average rainfall. Due to the low number of local extinctions, I did not attempt to model extinction covariates. However, sites that experienced local extinctions tended to have smaller SizePC values compared with sites occupied in both years. Turnover dynamics mainly were driven by spatial patterns of water availability.

Conclusions

As landscapes become increasingly modified by humans, it is important that we not only identify wildlife species that are sensitive to ecosystem changes, but also species that can persist or even thrive in highly altered habitats. My research indicates that muskrats in the Grand Prairie region of Illinois were not negatively affected by urbanization and invasive reed canary grass on a landscape scale. Muskrats may even be urban adapters when occupying riparian habitat that remains relatively connected in urbanizing landscapes. Moreover, muskrats could benefit from higher baseflow in urban streams, which is reflected in patterns of riparian muskrat occupancy, colonization, and local extinction.

Table 1 Descriptions of covariates for detection, occupancy, and colonization models for riparian muskrats

Parameter	Covariate	Description
Detection	Date	Julian Date
	Debris	Relative abundance of coarse woody debris and emergent rocks (cobble or larger) on a scale of 1-5
	Rain	Cumulative rainfall during previous 7 days (cm)
	Observer	Observer recording presence-absence
Occupancy & Colonization	SizePC	First principal component from PCA containing wetted width, thalweg depth, and subwatershed drainage area
	VegPC	First principal component from PCA containing percent cover of vegetation in channel from wetted edge to bankfull, and from bankfull to floodplain
	Bk_Ht	Linear distance (m) along bank from wetted edge to bankfull
	Bk_Ang	Bank angle at wetted edge
	Fld_Ht	Linear distance (m) along bank from bankfull to floodplain
	Fld_Ang	Bank angle halfway between bankfull and floodplain
	Sub_Veg	Percent cover of submerged vegetation
	Urban	Percent developed land cover within 500-m buffer of site

Table 1 (cont.)

Parameter	Covariate	Description
	ReedC	Relative dominance of reed canary grass (wetted edge to bankfull)
	Sand	Percent sand in soil samples
	North	North-south distance (km) from site to center of study area
	East	East-west distance (km) from site to center of study area

Table 2 Ranking of detection (p) models for riparian muskrats in the Grand Prairie Region of Illinois based on Akaike's Information Criterion (AIC_c)

Model	ΔAIC_c	w_i	K	-2*LL
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Date, Debris})$	0	0.671	6	473.17
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Date})$	3.23	0.134	5	478.40
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Date, Rain})$	4.95	0.057	6	478.12
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Observer, Debris})$	5.42	0.045	9	472.59
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Observer, Date})$	5.79	0.037	9	472.96
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Debris})$	6.26	0.029	5	481.43
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9.68	0.005	4	486.85

Detection covariates included Julian date, woody debris, rainfall during previous seven days, and observer. ΔAIC_c = difference between AIC_c value for given model and best model in set. K = number of model parameters including occupancy (ψ), colonization (γ), and local extinction (ε). w_i = Akaike weights. LL is the log-likelihood. A 95% confidence set is presented (cumulative Akaike weights sum to ≥ 0.95) plus the base model with no detection covariates.

Table 3 Ranking of occupancy models for riparian muskrats in the Grand Prairie Region of Illinois based on Akaike's Information Criterion (AIC_c)

Model	ΔAIC_c	w_i	K	-2*LL
$\Psi(\text{SizePC}, \text{Bk_Ht}, \text{Sand}, \text{Urban}), \gamma(\text{SizePC}), \varepsilon(\cdot),$ $p(\text{Best})$	0	0.466	11	423.48
$\Psi(\text{SizePC}, \text{Bk_Ht}, \text{Sand}), \gamma(\text{SizePC}), \varepsilon(\cdot),$ $p(\text{Best})$	2.27	0.150	10	427.75
$\Psi(\text{SizePC}, \text{Bk_Ang}, \text{Sand}, \text{Urban}), \gamma(\text{SizePC}),$ $\varepsilon(\cdot), p(\text{Best})$	2.92	0.108	11	426.40
$\Psi(\text{SizePC}, \text{Bk_Ht}, \text{Bk_Ang}), \gamma(\text{SizePC}), \varepsilon(\cdot),$ $p(\text{Best})$	3.13	0.097	10	428.61
$\Psi(\text{SizePC}, \text{Bk_Ang}, \text{Sand}), \gamma(\text{SizePC}), \varepsilon(\cdot),$ $p(\text{Best})$	3.93	0.065	10	429.41
$\Psi(\text{SizePC}, \text{Urban}, \text{Sand}), \gamma(\text{SizePC}), \varepsilon(\cdot), p(\text{Best})$	4.67	0.045	10	430.15
$\Psi(\text{SizePC}, \text{Bf_Ang}, \text{ReedC}), \gamma(\text{SizePC}), \varepsilon(\cdot),$ $p(\text{Best})$	5.13	0.036	10	430.61
$\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{Best})$	39.69	0	6	473.17

Occupancy covariates used in model selection (see Table 1) included stream size (SizePC), bankfull height (Bk_Ht), percent sand (Sand), bankfull angle (Bk_Ang), and reed canary grass dominance (ReedC). $p(\text{Best})$ refers to the best detection model (see Table 2) that included Julian date and relative abundance of

Table 3 (cont.)

woody debris. ΔAIC_c = difference between AIC_c value for given model and best model in set. K = number of model parameters including occupancy (ψ), colonization (γ), and local extinction (ϵ). w_i = Akaike weights. LL is the log-likelihood. A 95% confidence set is presented (cumulative Akaike weights sum to ≥ 0.95) plus the base model without covariates for occupancy or colonization.

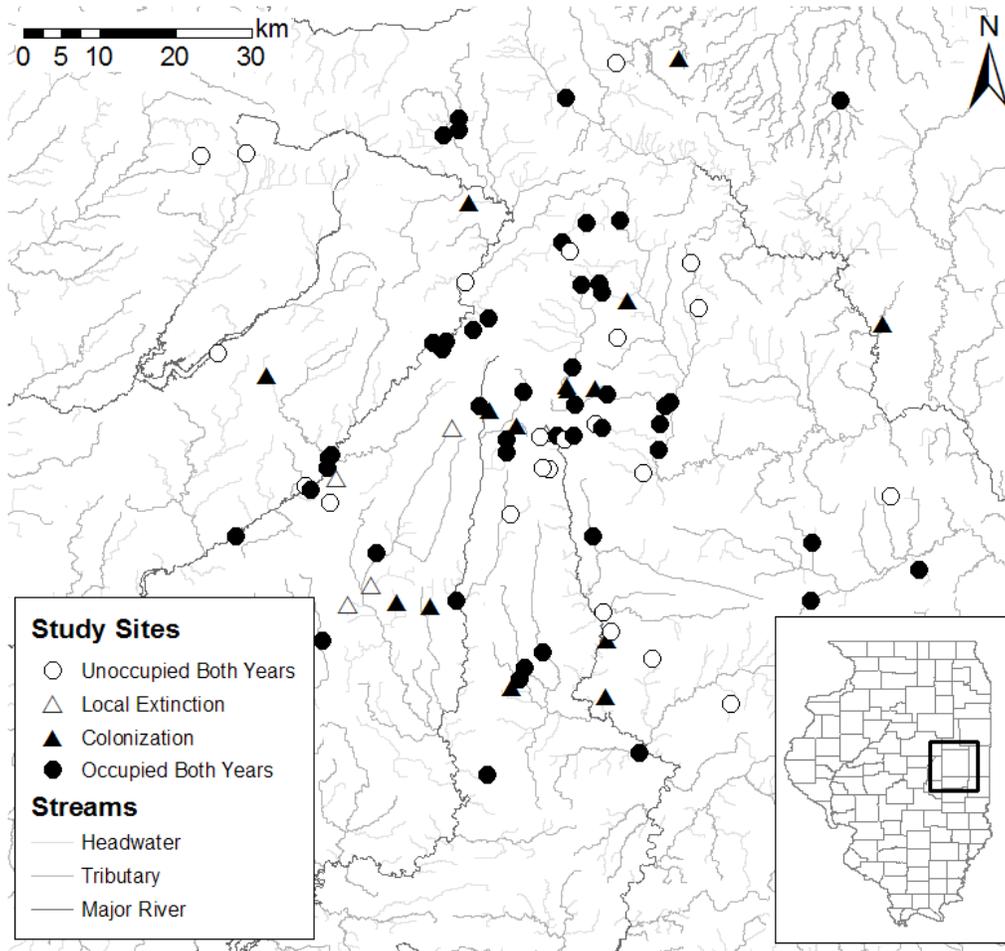


Fig. 1 Map of naïve occupancy and turnover for muskrats at riparian sites ($n = 90$) for 2007 and 2008. Inset shows location of study area in the Grand Prairie region of Illinois, USA. Each site was a 200-m stream segment. Four occupancy patterns were observed. Muskrats were 1) not detected in 2007 or 2008 (Unoccupied both years), 2) not detected in 2007 but present in 2008 (Colonization), 3) present in 2007 but not detected in 2008 (Local extinction), and 4) present in 2007 and 2008 (Occupied both years).

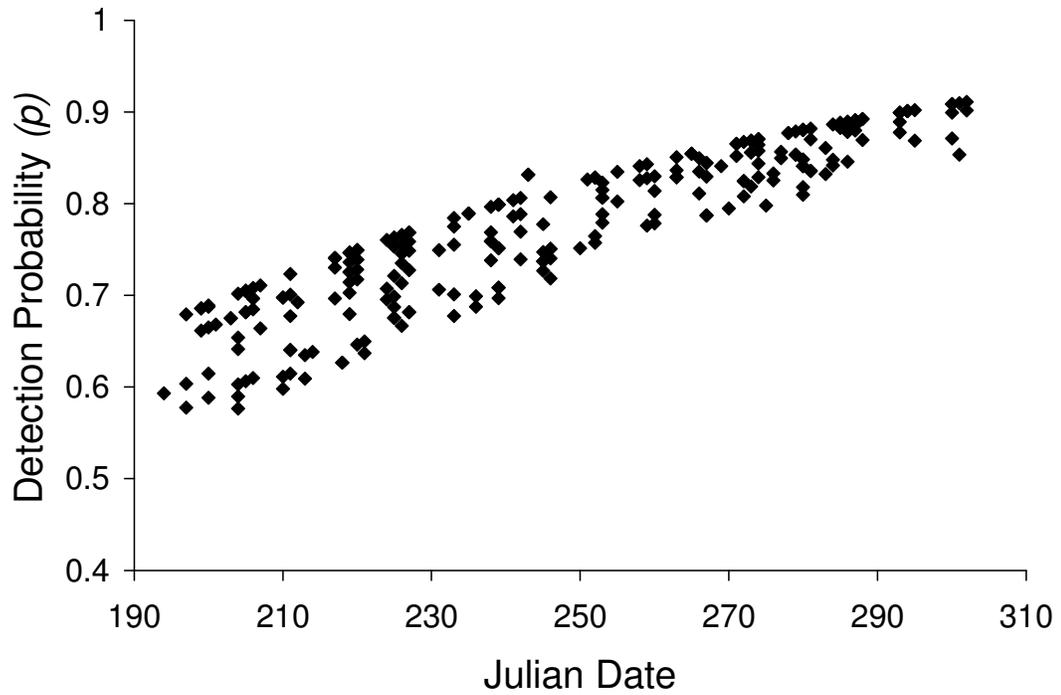


Fig. 2 Estimates of survey-specific detection probabilities (from the best detection model) in relation to Julian Date (JD). Surveys were conducted between July 13 (JD 194) and October 29 (JD 302) in 2007, and between July 17 (JD 199) and October 20 (JD 294) in 2008. Effect of woody debris on detection probabilities is accounted for in plotted values.

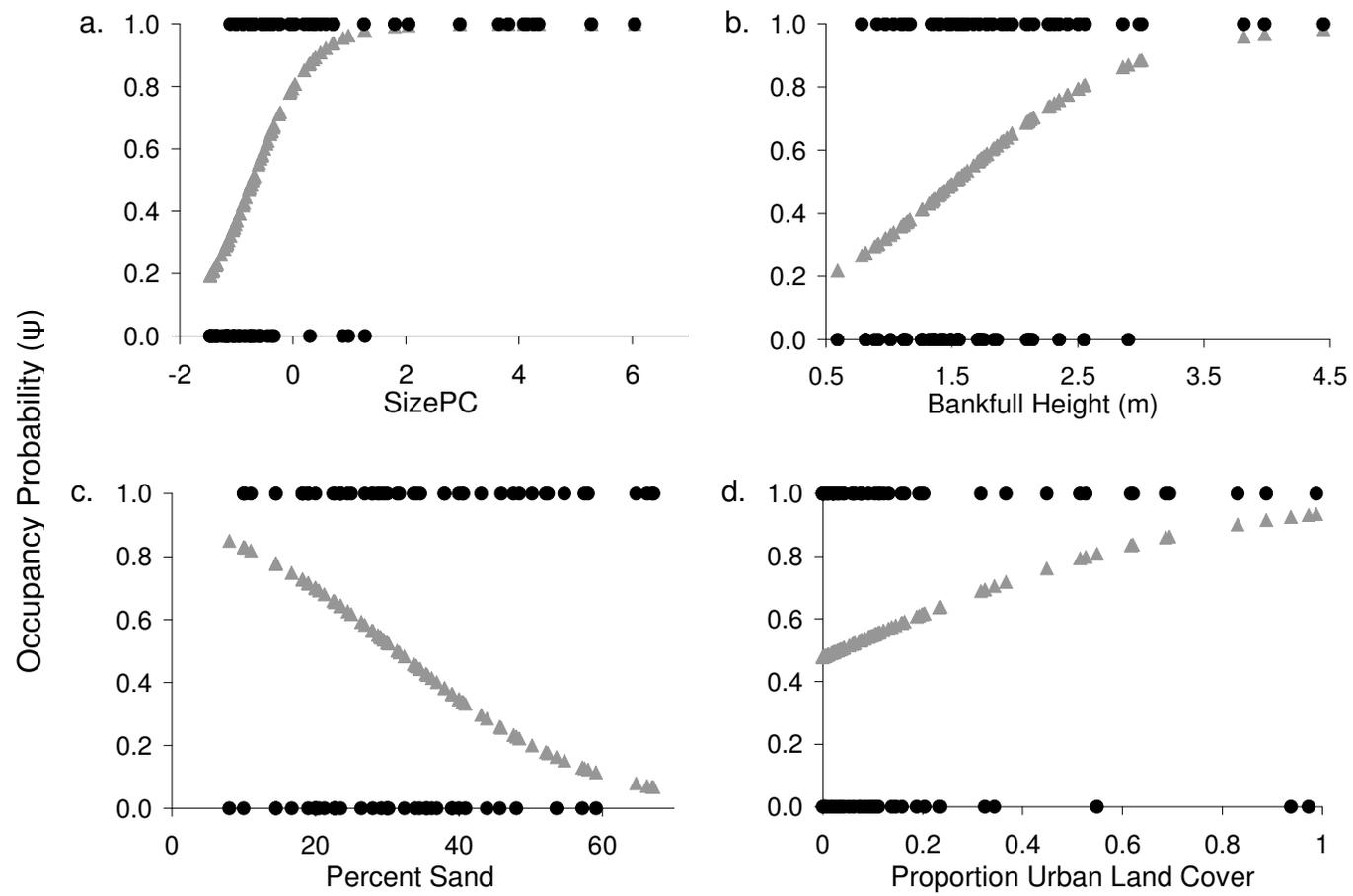


Fig. 3

Fig. 3 (cont.)

Relationships between occupancy probabilities (ψ) for muskrats and covariates from the top occupancy model (see Table 3). Gray triangles indicate predicted ψ for each variable when other covariates were held to their median values. Black circles indicate naïve occupancy for sites in 2007 (1 = occupied, 0 = unoccupied). (a) ψ was related positively to stream size (SizePC), (b) ψ increased with greater bankfull heights, (c) ψ was related negatively to percent sand in bank soils, and (d) ψ was related positively to urban land cover in surrounding landscape

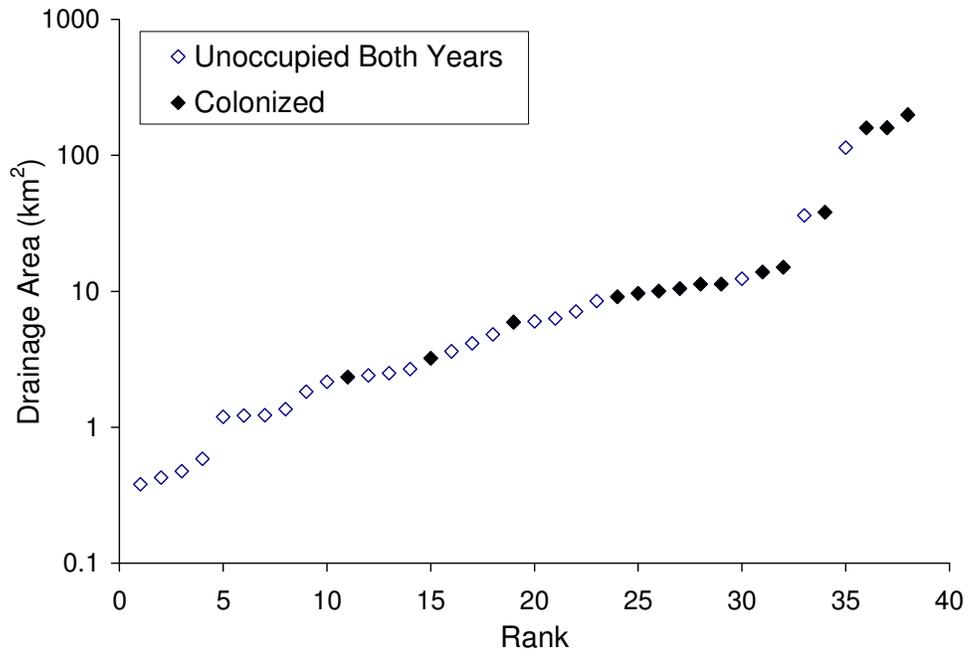


Fig. 4 Colonization of stream sites by muskrats in relation to subwatershed drainage area (plotted on a logarithmic scale). The 38 sites where muskrats were not detected in 2007 are arranged in rank order. Solid diamonds represent sites that were unoccupied in 2007 (naïve occupancy) but colonized in 2008. Open diamonds represent sites that were unoccupied in both years

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