

HABITAT SELECTION, SURVIVAL, AND DISEASE RISK OF SEMIAQUATIC
MAMMALS IN A HIGHLY ALTERED LANDSCAPE

BY

ADAM ALBERT AHLERS

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2015

Urbana, Illinois

Doctoral Committee:

Associate Professor James R. Miller, Chair
Associate Professor Robert L. Schooley, Co-Director of Research
Adjunct Professor Edward J. Heske, Co-Director of Research
Associate Professor Patrick A. Zollner, Purdue University

ABSTRACT

Landscape change in the Midwest, USA has resulted in drainage of most wetlands and isolated those that remain. Semiaquatic species occurring in this region must adapt to novel landscapes and mortality risks and variable environmental conditions. I used 6 years of presence-absence data and information from radiomarked individuals to evaluate habitat selection, survival, and disease risk of semiaquatic mammals in east-central, Illinois. Annual model-averaged occupancy estimates of stream sites were correlated positively to summer precipitation for both American mink (*Neovison vison*) and muskrats (*Ondatra zibethicus*) suggesting a possible climate-change effect. Factors interplaying across multiple scales influenced occupancy dynamics of mink in stream habitats. Stream sites closer to permanent wetlands had lower occupancy and colonization rates for mink. Occupancy and colonization rates for mink were higher at sites with deeper water, and colonization rates were related negatively to urban land cover. Additionally, mink were more likely to leave stream habitat if muskrats were not present and permanent wetlands were nearby, highlighting the importance of supplementary habitats and prey availability. As predicted, male mink were more likely to use terrestrial habitat than female mink. When integrating habitat use and known-fate survival analysis, I demonstrated that use of terrestrial habitat exposes mink to elevated risk of mortality. Weekly survival rates of mink were lower when using terrestrial habitat. Mink also had reduced survival during the mating season, males had lower weekly survival rates than females, and subadults had lower weekly survival rates than adults. My results also revealed that exposure risk of semiaquatic mammals to the parasite *Toxoplasma gondii* is likely facilitated by modified drainage practices common in agricultural and urban landscapes. My studies highlight how environmental change has affected habitat use, survival, and disease risk of semiaquatic mammals occurring in a human-dominated landscape.

From the desperate city you go into the desperate country, and have to console yourself with the
bravery of minks and muskrats.

– Henry D. Thoreau, *Walden*

ACKNOWLEDGEMENTS

I would like to thank my co-advisors, Ed Heske and Bob Schooley, for their input, guidance, and generous support on this project. Without their expertise, commitment, and extraordinary patience this work would not have been possible. My current and future success as an applied ecologist is directly related to their commitment to my education and training. Mark Mitchell graciously put up with my erratic trapping schedules and gave up most of his weekends and personal time to help me with surgeries each spring. The inspiration for the final chapter of this dissertation was born out of our hours of conversation while waiting for animals to recover from surgery. I sincerely thank all of the biologists who have worked on this project including Dave Ellington, Karla Griesbaum, Matt Ulrich, Ed Manofsky, Matt Nickols, Bob Caveny, Jess Cochran, Stacy Beyer, Joe Osbourne, Julia Nawrocki, Andrew Mathis, Lisa Cotner, and Pat Wolff. Thanks also go to committee members Jim Miller and Pat Zollner for helping me develop and refine my research questions.

I would especially like to thank my extremely supportive and patient family. My wife, Haley, provided continuous encouragement throughout my many years as a graduate student. She has selflessly put up with my crazy deadlines, unpredictable work schedules, and occasional writer's block. Thanks to my parents, Melvin and Kate, for teaching me the value of hard work and persistence. I also thank my family in Pathfinder Company (101st Airborne Division) for our shared lessons in selfless service, commitment, and leadership. I often recall our most challenging experiences when I need to put my academic life into perspective. And finally, my daughters, Madison and Emma. Your enthusiasm, energy, and love-of-life have inspired me throughout every step of this process.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION	1
Literature Cited.....	5
CHAPTER 2: SUMMER PRECIPITATION PREDICTS SPATIAL DISTRIBUTIONS OF SEMIAQUATIC MAMMALS	6
Abstract	6
Introduction	7
Methods	9
Results	14
Discussion	17
Literature Cited.....	21
Tables and Figures.....	27
CHAPTER 3: PREY DISTRIBUTION, CONTEXT, AND POTENTIAL LANDSCAPE SUPPLEMENTATION AFFECT OCCUPANCY DYNAMICS OF AMERICAN MINK IN STREAMS	33
Abstract	33
Introduction.....	34
Methods.....	37
Results.....	43
Discussion.....	45
Literature Cited	50
Tables and Figures	58
CHAPTER 4: TERRESTRIAL HABITAT USE IS RISKY FOR AMERICAN MINK (<i>NEOVISON VISON</i>) IN A HIGHLY MODIFIED LANDSCAPE.....	65
Abstract	65
Introduction	66
Methods	69
Results	75
Discussion	76
Literature Cited.....	80
Tables and Figures.....	88
CHAPTER 5: RISK FACTORS FOR <i>TOXOPLASMA GONDII</i> EXPOSURE IN SEMIAQUATIC MAMMALS IN A FRESHWATER ECOSYSTEM	93
Abstract	93
Literature Cited.....	100
Tables and Figures.....	103
CHAPTER 6: SUMMARY.....	105
Literature Cited.....	109

APPENDIX A:.....	112
Tables and Figures.....	113

CHAPTER 1

INTRODUCTION

Widespread agricultural production and urbanization have drained many natural wetlands (Brady and Flather 1994; Gutzwiller and Flather 2011; McCauley and Jenkins 2005). As a result, remaining habitat for semiaquatic species occurring in these modified landscapes include climate-sensitive riparian habitats that have dynamic flow regimes (Baker et al. 2004). Consequently, habitat quality in these areas is likely driven by local precipitation events (Ahlers et al. 2010). Species persistence in these highly altered regions requires successful adaption to novel landscapes, variable environmental conditions, and mortality risks.

Historically, the Grand Prairie region was comprised of tall-grass prairie and wetland habitats but has since been drained and converted for agricultural production (Urban 2005). For instance, in east-central Illinois, 85% of the landscape is devoted to row-crop agriculture and ~98% of historical wetlands have been drained (Suloway and Hubbell 1994; McCauley and Jenkins 2005). Currently, most available habitat for semiaquatic species is now located in highly altered small streams and agricultural ditches. Additionally, row crops (e.g., corn [*Zea mays*] and soybeans [*Glycine max*]) have typically replaced the natural riparian zones (Ahlers et al. 2010). My research focused on elucidating factors affecting the spatial distribution, habitat selection, survival, and disease risk of American mink (*Neovison vison*) and muskrats (*Ondatra zibethicus*) in this highly altered landscape.

In Chapter 2, I use six years of presence-absence data that span years of record-breaking floods and drought to investigate how mink and muskrat populations respond to future climate-change scenarios. Riparian habitat has flashy flow regimes (Baker et al. 2004; Ahlers et al. 2010) with habitat quality for semiaquatic species strongly determined by water depths. Water

depths in stream habitat can be diminished during drought, reducing protection from terrestrial predators and the availability of aquatic prey. I explicitly test if annual habitat occupancy rates for mink and muskrat can be explained by summer precipitation across years. I also comparatively assessed the broad extent of terrestrial habitat use between mink and muskrats. My results indicate a strong positive correlation between summer precipitation and annual habitat occupancy rates for both species. Also, I show that mink use terrestrial habitat more than muskrats. However, mortality risk was disproportionately greater for mink when moving through terrestrial areas. I discuss how semiaquatic species may be affected by the synergistic effects of habitat loss and climate change.

In Chapter 3, I investigated how local habitat quality, presence of muskrats, and landscape supplementation and context affect habitat occupancy and turnover dynamics of mink in stream habitat. My results suggest that factors interplaying across multiple scales influence occupancy dynamics of American mink in stream habitat in a highly modified landscape. I show that water depths are important for habitat occupancy dynamics by mink and that colonization of stream sites is negatively affected by the amount of urbanization surrounding stream sites. I also demonstrate that the presence of supplementary habitats (permanent wetlands) is important for habitat occupancy, colonization, and extinction of stream sites by mink. Additionally, my research suggests that muskrat presence and distance to permanent wetlands interact to influence motivation for movements between stream and wetland habitats by mink. I discuss how estimates of connectivity based on the spatial arrangement of habitats should consider similar interactions.

Anthropogenic landscape changes in the Grand Prairie region have generated a novel set of mortality risks for species occurring there. Semiaquatic mammals in this region may have to

move through terrestrial habitat to find supplementary resources (Chapters 2 and 3). In Chapter 4, I evaluate factors that could explain the degree of terrestrial habitat use for mink, and determine mortality risk factors including the relative risk of using stream versus upland habitats. My results indicate that male mink are more likely to use terrestrial habitat than females. Also, mink occurring in larger streams were less likely to use terrestrial habitat. While incorporating data on habitat use and known-fate mortality information, I show that mink using terrestrial habitat away from the stream edge are exposed to increased mortality risks in human-dominated landscapes. I discuss how the rapid rate of landscape change in the Grand Prairie region may have created an evolutionary time lag (Remeš 2000) as mink may not recognize the mortality risks associated with contemporary land uses. I also stress how future studies should focus on elucidating why semiaquatic species may use riskier habitats in highly altered landscapes.

A result of widespread agricultural production and urbanization is that most wetlands have been drained and natural riparian zones have been destroyed. Historically, these habitats have naturally filtered pollutants and pathogens from land-derived runoff to improve water quality. The parasite *Toxoplasma gondii* is a significant risk to human and wildlife health and can be transmitted to watersheds via *T. gondii* contaminated runoff from surrounding landscapes. In Chapter 5, I assessed risk factors for *T. gondii* exposure in semiaquatic mammals occurring in human-modified watersheds largely devoid of wetlands and natural riparian zones. My results show that *T. gondii* prevalence rates for mink and muskrats are ≥ 1.7 times higher than those of terrestrial mammals in this region, consistent with my watershed contamination hypothesis. Additionally, I demonstrate that muskrats positioned in larger sub-watersheds (and exposed to drainage from many more hectares) had higher exposure risks than muskrats positioned in smaller sub-watersheds. I discuss how landscape change in this region has likely facilitated

waterborne transmission of *T. gondii* and how altered drainage practices have likely affected exposure risk for semiaquatic mammals.

Literature Cited

- AHLERS A.A., R.L. SCHOOLEY, E.J. HESKE, AND M.A. MITCHELL. 2010. Effects of flooding and riparian buffers on survival of muskrats (*Ondatra zibethicus*) across a flashiness gradient. Canadian Journal of Zoology 88:1011-1020.
- BAKER, D.B., R.P. RICHARDS, T.T. LOFTUS, AND J.W. KRAMER. 2004. A new flashiness index: characteristics and applications to Midwestern rivers and streams. Journal of American Water Resources Association 40:503-522.
- BRADY, S.J., AND C.H. FLATHER. 1994. Changes in wetlands on nonfederal rural land of the conterminous United States from 1982-1987. Environmental Management 18:693-705.
- GUTZWILLER, K.J., AND C.H. FLATHER. 2011. Wetland features and landscape context predict the risk of wetland habitat loss. Ecological Applications 21:968-982.
- MCCAULEY, L.A., AND D.G. JENKINS. 2005. GIS-Based estimates of former and current depressional wetlands in an agricultural landscape. Ecological Applications 15: 1199-1208.
- REMEŠ, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? Oikos 91: 579-582.
- SULOWAY, L., AND M. HUBBELL. 1994. Wetland resources of Illinois: an analysis and atlas. Special publication 15. Illinois Natural History Survey, Champaign, Illinois, USA.
- URBAN, M.A. 2005. An uninhabited waste: transforming the Grand Prairie in nineteenth century Illinois, USA. Journal of Historical Geography 31: 647-665.

CHAPTER 2

SUMMER PRECIPITATION PREDICTS SPATIAL DISTRIBUTIONS OF SEMIAQUATIC MAMMALS

Abstract

Climate change is predicted to increase the frequency of droughts and intensity of seasonal precipitation in many regions. Semiaquatic mammals should be vulnerable to this increased variability in precipitation, especially in human-modified landscapes where dispersal to suitable habitat or temporary refugia may be limited. Using six years of presence-absence data (2007-2012) spanning years of record-breaking drought and flood conditions, I evaluated regional occupancy dynamics of American mink (*Neovison vison*) and muskrats (*Ondatra zibethicus*) in a highly altered agroecosystem in Illinois, USA. I used noninvasive sign surveys and a multiseason occupancy modeling approach to estimate annual occupancy rates for both species and related these rates to summer precipitation. I also tracked radiomarked individuals to assess mortality risk for both species when moving in terrestrial areas. Annual model-averaged estimates of occupancy for mink and muskrat were correlated positively to summer precipitation. Mink and muskrats were widespread during a year (2008) with above-average precipitation. However, estimates of site occupancy declined substantially for mink (0.56) and especially muskrats (0.09) during the severe drought of 2012. Mink are generalist predators that probably use terrestrial habitat during droughts. However, mink had substantially greater risk of mortality away from streams. In comparison, muskrats are more restricted to aquatic habitats and likely suffered high mortality during the drought. These patterns are striking, but a more mechanistic understanding is needed of how semiaquatic species in human-modified ecosystems will respond ecologically *in situ* to extreme weather events predicted by climate-change models.

Introduction

Many studies attempt to predict species' responses to climate change (1) and most focus on changes in geographic distributions (1-3) and potential *in situ* evolutionary adaptation (4-5). However, many animal species will need to make ecological adjustments within geographic range interiors, such as altering habitat selection, to deal with increased environmental stochasticity. These responses should have consequences for species persistence and may be affected by human alterations of the landscape. To understand how populations will respond to predicted climate-change scenarios, a necessary step is to investigate temporal variation in species occurrences relative to a range of weather conditions.

Climate change is increasing the variability of precipitation and frequency of extreme flooding and drought events (6-7). Species obligately associated with wetland and stream habitats are particularly at risk due to extreme fluctuations in water levels. As these climate-sensitive habitats become less stable, species dispersal (8), recruitment (9) and survival (9-12) could be compromised. Semiaquatic species might need to move to other suitable habitat patches to persist during times of environmental stress, but moving across terrestrial areas can be costly (13-14), especially in regions where agriculture and urbanization have destroyed linkages and reduced connectivity.

American mink (hereafter mink; *Neovison vison*) and muskrats (*Ondatra zibethicus*) are semiaquatic mammals that may be sensitive to increased variation in precipitation events. Both species are widely distributed throughout North America and are obligately associated with aquatic habitats, although the degree of this association differs between species. Muskrats are chiefly herbivores and most of their diet consists of wetland vegetation. Space use by muskrats is mostly restricted to the stream edge and movements >3 m away from water are rare (15).

Mortality from predation is high during drought conditions and likely due to the limited mobility of muskrats away from water and reluctance to leave established home ranges (16-17).

Additionally, increased flooding can reduce survival of young (18). Mink are generalist predators that forage in aquatic and terrestrial habitats (19). When aquatic prey (e.g., fish, amphibians, and crayfish) are unavailable, mink will forage more frequently in terrestrial areas (20), which could expose them to elevated risks. However, mortality risk for mink in terrestrial versus stream habitats is unknown.

I used 6 years of presence-absence data spanning years of record-breaking floods and drought to assess how mink and muskrats respond to conditions predicted to increase under climate-change scenarios. Specifically, I tracked annual changes in site occupancy for mink and muskrats in response to variable summer precipitation. I also radiomarked individuals to assess mortality risk for both species in terrestrial habitats as activity in these areas may become more common with increasing environmental variability. In my study system, > 90% of wetlands have been drained to accommodate agricultural production (20), thus limiting both species' distributions primarily to flashy streams and rivers. Species occurring in these human-dominated landscapes may be at an increased risk owing to the synergistic effects of habitat loss and climate change (22-23).

I hypothesized that mink and muskrat populations in my region would be sensitive to summer precipitation because droughts reduce habitat quality for semiaquatic mammals in streams. Droughts lower water levels and persistence of flow, thus reducing the protection from predation, and availability of aquatic prey, afforded by deeper water. Thus, I predicted habitat occupancy for both species would be correlated positively with summer precipitation across years. I assumed differences in annual occupancy rates for species reflected underlying patterns

of abundance (24-25). Because muskrats are more tightly associated with streams than are mink, I predicted negative effects of droughts would depress muskrat abundance more than mink abundance. I also assessed the extent of terrestrial habitat use by mink and muskrats and predicted mortality risk would be greater in terrestrial habitat than in stream habitat.

Methods

Study area

My study was conducted in east-central Illinois, USA. (40°12'N, 88°26'W) in a region that is intensely farmed and highly fragmented. This region has a humid continental climate with temperatures ranging from -8.5 to 30.0° C and experiencing ~175 cm of precipitation annually. Currently, 85% of the landscape is dedicated to corn (*Zea mays*, 45%) and soybean (*Glycine max*, 40%) production, and wetlands cover only 0.9% of the landscape (21, 26). Consequently, small streams and agricultural ditches that form narrow riparian corridors represent the primary habitat for semiaquatic mammals in the region. These habitats have dynamic flow regimes tied to local precipitation events (27-28). Climate models predict this region will experience a significant increase in the frequency of summer drought and spring flooding events (29-30), thus increasing flow variability and potentially affecting habitat quality for semiaquatic species. In 2008, the region experienced the 2nd wettest year on record (31). In 2012, the region experienced the 2nd driest January – July period on record (32; Figure 2.1).

Sampling design

I used a stratified-random sampling design to select 90 survey sites along riparian areas. All survey sites were located on property owned or controlled by private individuals, municipalities,

land trusts, or state agencies. I obtained permission from all landowners prior to surveys.

Contact information for the owners of these properties can be obtained from the corresponding author (AAA). Fifty percent of the sites ($n = 45$) were randomly chosen within a 2-km radius of incorporated cities (population size >2500), and the remainder ($n = 45$) were randomly chosen outside of this buffer. Each site was a 200-m stretch of wadeable stream (ranging from 1st to 5th order in size) and represented a potential resource patch for both mink and muskrats (33-36).

Median nearest-neighbor distance between sites was 2.5 km (range = 0.5 – 22.8 km).

Sites were surveyed by trained, independent observers for presence of mink (tracks and scat) and muskrats (tracks, scat, clippings and burrows) using a removal-design framework (37) from July to October, 2007- 2012. Each site was surveyed by two independent observers simultaneously, with each observer beginning their survey on opposite ends of the stream segment during each site visit (two surveys during one site visit; 35). Initially (2007-2008), surveys were developed to assess muskrat occupancy (removal design based on muskrat sign) and each site was surveyed twice for both species but not revisited if muskrat sign was detected (2 surveys). If muskrat sign was not detected during the first site visit, I conducted an additional site visit to survey for both species for a maximum of four surveys per site (35). From 2009-2012, if mink sign was not found during the first site visit (removal design based on mink sign), I conducted an additional site visit yielding a maximum of four surveys per site. For each year, I limited the time between site visits to ≤ 10 days. I randomly reduced the number of sites from 90 to 60 in 2009-2012 due to logistical constraints. The occupancy modeling approach that I used efficiently handles missing observations as created by my mixed removal design and reduction in number of sites (38). To reduce risk of sign being washed away by rain or rising water, I waited >2 days to survey sites that had experienced weather events with ≥ 1 cm of precipitation.

Overall, I conducted 1196 surveys (2007 = 276; 2008 = 282; 2009 = 130; 2010 = 160; 2011 = 162; 2012 = 186) that spanned ~239 km of wadeable stream.

Site occupancy analysis

I fit multi-season models using Program PRESENCE 6.9 to derive model-averaged annual estimates of site occupancy for each species given unique detection histories (38). For each model, I held initial occupancy (Ψ_{2007}) constant, let colonization (γ) and extinction (ϵ) vary by year, and varied survey-specific covariates for species detection (p). Because the goal of this analysis was to derive robust estimates of annual habitat occupancy for the region, I was not concerned with site-specific habitat variables important for individual site occupancy and turnover. Potential detection covariates included survey date, recent rainfall, observer effects, and amount of trackable surface along the stream edge (35-36). Additionally, I considered the amount of debris within the stream (emergent rocks and logs used for scat deposition by muskrats) in models of muskrat detection (35). Survey date (Date) was the day of the year when the survey was conducted (1-365). I acquired rainfall data from the Illinois State Water Survey (station 118740; Urbana, IL) and summed precipitation for 7 days prior to each survey (Rain). Observer effects (Observer) were coded in relation to a reference observer (38: pp. 117-118). Thirteen observers conducted surveys from 2007–2012. To avoid overparameterization of models, I grouped observers based on survey effort and modeled six total observers. I visually estimated the percent of trackable surface along the stream edge (Sandbar) starting in 2008; I did not measure ‘Sandbar’ during 2007 surveys. Because ‘Sandbar’ is an important detection covariate for mink (36), I estimated values for 2007 *a posteriori* for each site using mean Sandbar values for each site from 2008-2012. Average Sandbar indices for each site were highly

correlated between years (mean Pearson correlation coefficient = 0.60, range = 0.49 – 0.80, $P < 0.0001$). I quantified the relative amount of debris within each site (Debris) on a scale of 0-5, with 0 = no debris and 5 = ≥ 1 piece of debris every 10 m. I used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank models within the candidate set for each species. Additionally, I used the Akaike weights (ω) to derive model-averaged estimates of annual site occupancy (38) for mink and muskrats using all models from each species candidate set.

Precipitation

I used generalized linear models (PROC GENMOD, distribution = normal, link = identity; 39) to assess the importance of summer precipitation to annual site occupancy of mink and muskrats. I summed the 3-month cumulative rainfall prior to occupancy surveys (May, June and July) for 2007-2012 (station 118740; Illinois State Water Survey) and used this value as a proxy for regional summer precipitation. The weather station was centrally located in my study area (Urbana, IL) and recorded daily precipitation representative of my sites. I used a logit transformation for my response variables (model-averaged estimates of annual site occupancy for mink and muskrats) to meet linear model assumptions (40) and calculated a pseudo R^2 (1-[deviance of fitted model/deviance of intercept-only model]) to assess each model's goodness-of-fit.

Tracking space use and survival

I radiomarked and tracked mink to assess the frequency of space use and mortality risk in terrestrial areas, and compare these results to my previous studies of muskrat space use and survival (15, 28). I captured mink using baited (salmon or sardines) Tomahawk live traps (Model 202) attached to floating raft platforms (41) from 2009 to 2013. Traps were checked

daily, refreshed with bait as needed, and closed during periods of inclement weather. I transported animals to a sterile surgical laboratory at the Veterinary Teaching Hospital at the University of Illinois (Urbana, Illinois, USA) immediately after capture. I surgically implanted radio transmitters into the peritoneal cavities of 34 mink using methods similar to those outlined in my previous studies (15, 28, 42). Prior to surgery, mink were premedicated with atropine (0.20 mg/kg), dexmedetomidine (0.25 mg/kg), and butorphanol (0.30 mg/kg). I induced surgical anesthesia via facemask with isoflurane (5% for induction and maintained between 1-3% throughout procedure) while simultaneously administering and maintaining oxygen (0.60-1.00 l/min). I fitted smaller mink (<500 g) with 14-g internal transmitters (Model 1215; Advanced Telemetry Systems[®], Insanti, Minnesota, USA) and larger mink (\geq 500 g) with 23-g internal transmitters (Model 1230). Transmitters were equipped with mortality sensors that increased pulse rate when inactive for \geq 8 hours allowing us to quickly retrieve the carcass and determine location and cause of mortality. After transmitters were implanted, I administered atipamazole (2.50 mg/kg) to reverse the sedative effects of dexmedetomidine and meloxicam (0.20 mg/kg; post-operative analgesic). Additionally, I administered penicillin (0.10 ml) to limit post-operative infections. I monitored recovering animals for approximately 2 hours (after gaining all righting reflexes) and returned them to the site of capture.

I relocated mink using a combination of triangulation (when mink were active) and homing (when mink were inactive). Prior to the study, I used hidden test transmitters ($n = 10$) and determined triangulation error was minimal ($\bar{x} = 16.6$ m; $SD = 14.3$). I attempted to relocate individual mink at least once per week. Detailed descriptions of muskrat capture, marking, and radiotracking methods are described in my previous studies along with a comprehensive analysis of muskrat space use and mortality (15, 28). I did not include endangered or threatened species

in any part of my study and all methods and procedures were approved by the University of Illinois Animal Care and Use Committee (Protocols 07105 and 12190) and met guidelines of the American Society of Mammalogists (43).

A detailed analysis of habitat selection and survival by mink and muskrats is beyond the scope of this paper. However, I present a coarse assessment of terrestrial habitat use based on the proportion of relocations for radiomarked mink at various distances away from the stream edge and compare this to previously published space-use patterns for muskrats (15). I only considered mink with ≥ 25 locations ($n = 20$) for this analysis. To determine the mortality risk for mink ($n = 34$) and muskrats ($n = 27; 28$) in terrestrial habitat, I determined the likelihood of mortality in relation to distance from the stream edge. For mink, I tested for differences in the distributions of mortality locations and telemetry locations in relation to distance from the stream edge with a two-sample Kolmogorov-Smirnov test. For muskrats, I could not statistically test for potential distribution differences because of the small number of observed mortalities in terrestrial areas and no observed movements in terrestrial habitat (see Results).

Results

Based on a 123-year record of precipitation, the average summer precipitation for this region was 32.3 cm (SD = 10.2; Figure 2.2a). During my study, summer precipitation (cm) was extremely variable among years (Figure 2.2a): 2007 = 27.3; 2008 = 51.7; 2009 = 41.7; 2010 = 39.3; 2011 = 27.2; 2012 = 15.2. Summer precipitation was high during a year of record-breaking floods (2008 = 51.8 cm) and low during a year with widespread drought (2012 = 15.2 cm).

My ability to detect muskrat sign was negatively affected by the amount of rain 7 days prior to surveys ($\beta = -0.0897$, SE = 0.05; Table 2.1). Models including 'Rain' had the most support

among all models of muskrat detectability ($\Sigma\omega = 0.67$). Although my other models were competitive, none had a substantially better model fit than the top-ranked model (Table 2.1). Thus, I considered the variables ‘Sandbar’, ‘Date’, and ‘Debris’ non-informative (44-45). The intercept-only model also was among the top-ranked models but it had a reduced model fit compared to my best model.

My models of mink detectability were competitive ($\Delta AIC_c \leq 2$; Table 2.1). Each model contained the variables ‘Observer’ and ‘Sandbar’. My second- and third-ranked models also included the effects of ‘Date’ and ‘Rain’, respectively, and the fourth-ranked model included the additive effects of ‘Observer’, ‘Sandbar’, ‘Date’, and ‘Rain’ (Table 2.1). In concordance with past research (36), my ability to detect mink sign was affected by observer variability (range of β s = -1.8288 – 0.8105), positively related to amount of trackable surface ($\beta = 0.0031$, SE = 0.0014) and survey date ($\beta = 0.0036$, SE = 0.0006), and negatively related to amount of rain 7 days prior to surveys ($\beta = -0.0417$, SE = 0.0466).

Model-averaged estimates of site occupancy by muskrats varied substantially among years (Figure 2.2b): 2007 = 0.58 (SE = 0.05), 2008 = 0.69 (SE = 0.05), 2009 = 0.88 (SE = 0.04), 2010 = 0.91 (SE = 0.04), 2011 = 0.36 (SE = 0.07), 2012 = 0.09 (SE = 0.04). Occupancy rates were higher in years when summer precipitation was above the 123-year mean (2008, 2009 and 2010), and occupancy rates were lower when summer precipitation was below the 123-year mean (2007, 2011 and 2012). The estimated proportion of sites occupied by muskrats each year was positively associated with summer precipitation ($\beta = 0.1045$; $P = 0.0016$; pseudo $R^2 = 0.62$; Figure 2.3a).

My model-averaged estimates of annual site occupancy by mink also varied among years (Figure 2.2b): 2007 = 0.44 (SE = 0.06), 2008 = 0.90 (SE = 0.03), 2009 = 0.89 (SE = 0.04), 2010

= 0.82 (SE = 0.05), 2011 = 0.67 (SE = 0.06), 2012 = 0.56 (SE = 0.06). Mink were widely distributed during years with above-average precipitation (2008, 2009 and 2010). Estimated occupancy rates were lower during years with below-average precipitation (2007, 2011 and 2012), but remained moderately high in 2011 following three relatively wet years and did not decline to the extent observed for muskrats during the extreme drought of 2012 (Figure 2.2). As predicted, the proportion of sites occupied by mink each year also was positively related to summer precipitation ($\beta = 0.0681$; $P < 0.0001$; pseudo $R^2 = 0.77$; Figure 2.3b).

For the 20 mink for which I had sufficient movement data to assess extent of habitat use in terrestrial areas, each individual was relocated an average of 102 times (SE = 10.27; range = 25 – 192) for a total of 2035 locations (MoveBank DOI: 10.5441/001/1.gd686078). The distribution of mink mortalities differed from the distribution of telemetry locations in relation to distance from the stream edge ($D = 0.62$; $P < 0.0002$). On average, mink were relocated >100 m from the stream edge only 14% of the time (Figure 2.4b). In contrast, of 17 known-fate mortalities (seven road kill, six predation, three poisoning and one disease), 76% ($n = 13$) occurred when mink were >100 m from the stream edge (Figure 4b). My previous studies of muskrat space use and survival found that muskrats rarely used upland habitat and were never relocated > 3 m from the stream edge (Figure 2.4a; 15). Of 15 known-fate mortalities, 80% ($n = 12$) occurred along the stream edge and were attributed to mink predation (Figure 2.4a; 28). I recovered the other 3 muskrat carcasses in or around coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) burrows > 50 m from the stream edge (28). One canid-related mortality occurred while the muskrat was displaced into a corn field during a flooding event. Because I did not detect muskrat movements > 3 m away from the water's edge, all mortalities attributed to canid mortality likely occurred along the stream edge and carcasses were transported back to active canid burrows (28).

Discussion

Annual occupancy of stream segments by mink and muskrats was strongly related to summer precipitation. Occupancy rates for both species were higher during years with above-average precipitation than years with below-average precipitation (Figure 2.2). This contrast was especially clear for muskrats; estimated annual occupancy rates were > 10 times lower (from 0.91 to 0.09) during the severe drought of 2012. Increased frequency of summer droughts is predicted by climate models for the Midwestern USA (29), and the patterns observed in 2012 may therefore be a harbinger for semiaquatic mammals.

Mink and muskrats were widely distributed during years with above-average precipitation. Higher water levels due to increased precipitation likely provided more suitable habitat and increased connectivity between areas of high-quality habitat for both species. Higher water levels also may have provided escape routes from terrestrial predators and lowered predation risk for both species. Previous research demonstrated that site occupancy for mink and muskrats is correlated positively with water depth (35-36, 46). Furthermore, the probability of vacant sites being recolonized by both species is positively related to water depth (35-36). Conversely, mink and muskrat occupancy rates were lower during years of below-average precipitation. Low water levels can limit available resources and reduce overall body condition of muskrats resulting in increased mortality (47). Muskrats also are susceptible to increased predation risk during drought because their locomotion is more limited on land than in water, and the openings of their burrow dens may be exposed as streams dry (17). Despite this deterioration in habitat quality during drought, muskrats are typically reluctant to leave their home ranges to find other suitable habitat (16), and this effect may be exacerbated in areas where habitat loss has reduced spatial connectivity.

Investigations of how mink respond behaviorally to drought are lacking. However, reduced occupancy rates during years of below-average precipitation suggest mink are foraging in terrestrial habitat away from the stream edge. I think the decline in occupancy for mink partly represents increased use of alternate habitats rather than just mortality because mink are not as constrained to aquatic habitats in my region as are muskrats. All telemetry locations of muskrats occurred within 3 m of stream banks (15). In contrast, 14% of telemetry locations of mink occurred >100 m from stream banks (Figure 2.4b), revealing more flexibility by mink in habitat use. The switch to terrestrial habitats may come with increased mortality costs, however, as mortality risk was disproportionately greater for mink when moving through terrestrial areas (Figure 2.4b). Thus, the greater mobility of mink may allow them to exploit secondary habitats during droughts, reducing their susceptibility to degradation of stream habitats relative to muskrats in the short term. However, if climate change increases the frequency of droughts (7), increased use of more risky habitats by mink should eventually reduce survival rates and affect population dynamics. Unfortunately, I have insufficient data on mortality by muskrats or mink during the drought year to evaluate this hypothesis directly.

Although the patterns are clear, I acknowledge a caveat associated with my interpretations. I cannot directly link discrete flooding and drought events during my study to changing climate. Nevertheless, these extreme events will be more common in the future (6-7, 29-30). Contemporary climate models suggest severe and widespread drought this century (7). Species obligately associated with drought-sensitive habitats will be most at risk. Thus, population patterns associated with observed climate-driven events should mimic those during future climate-change conditions.

In Canada, mink and muskrats represent a classic predator-prey system in which mink populations exhibit a lagged numerical response to changes in muskrat abundances (48-50). However, there is significant geographic variation in the strength of this predator-prey relationship (48, 50). Mink and muskrat population dynamics in Canada may be partially affected by the spatial variability in winter precipitation (51). Additionally, differences in predator-prey interaction strength may be partially attributed to spatial variability in prey richness across Canada (52). In my region, habitat occupancy for mink and muskrats was strongly related to summer precipitation (Figure 2.3). This correlation suggests environmental variability affects populations of both species similarly and possibly decouples any classic predator-prey relationship. Mink diet in this region is diverse and seasonal occurrence of mammals in mink scats were always <50% of the percentage volume of sampled scats (53). Increased diversity of mink prey in this region may release muskrats from the specialized predation pressure necessary for cyclic population dynamics (54). In my study, synchrony of mink and muskrat populations (without a time lag) and their sensitivity to summer precipitation suggest these populations are largely limited by external forcing.

Many semiaquatic species may be negatively affected by the synergistic effects of habitat loss and climate change. Interactions between these stressors can depress population densities and reduce species diversity (23). Moreover, increases in the frequency and intensity of regional flooding and drought can potentially synchronize population dynamics of species at large spatial scales—especially habitat specialists occurring in homogenous agricultural landscapes (22, 55). For instance, intensively farmed landscapes can function as habitat sinks for common frog (*Rana temporaria*) populations during extreme drought compared to landscapes retaining some heterogeneity (55). Additionally, populations of platypus (*Ornithorhynchus anatinus*), another

obligate wetland species, are threatened by both increasing thermal stress and habitat loss due to climate change and increased irrigation demands for agriculture (56).

In many ecosystems worldwide in which most wetland habitat has been converted to agriculture, the primary remaining habitats for semiaquatic species are small, flashy streams. Because habitat suitability for these species is generally linked with water availability, increased variability in precipitation should drive spatial and temporal variation in habitat quality. A more mechanistic understanding is urgently needed of how extreme weather events, like those observed in my study and predicted under climate-change models, will affect populations of semiaquatic species in human-modified environments.

Chapter 2 meets the formatting requirements of *PLoS One*

Literature Cited

1. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.
2. Root TL, Price JT, Hall KR, Schneiders SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
3. Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024-1026.
4. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37: 637-669.
5. Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature* 470: 479-485.
6. Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289: 2068-2074.
7. Dai A (2013) Increasing drought under global warming in observations and models. *Nature Clim Change* 3: 52-58.
8. Hof C, Brandle M, Dehling DM, Munguia M, Brandl R, Araujo MB, Rahbek C (2012) Habitat stability affects dispersal and the ability to track climate change. *Biol Letters* 8: 639-643.
9. Campbell RD, Nouvellet P, Newman C, MacDonald DW, Rosell F (2012) The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. *Global Change Biol* 18: 2730-2742.
10. Bellrose FC, Low JB (1943) The influence of flood and low water levels on the survival of muskrats. *J Mammal* 24: 173-188.

11. Andersen DC, Wilson KR, Miller MS, Flack M (2000) Movement patterns of riparian small mammals during predictable floodplain inundation. *J Mammal* 81: 1087-1099.
12. Kupferberg SJ, Palen WJ, Lind AJ, Bobzien S, Catenazzi A, Drennan J, Power ME (2012) Effects of flow regimes altered by dams on survival, population declines, and range-wide losses of California river-breeding frogs. *Conserv Biol* 26: 513-524.
13. Schooley RL, Branch LC (2009) Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecol Appl* 19: 1708-1722.
14. Cosentino BJ, Schooley RL, Phillips CA (2011) Connectivity of agroecosystems: dispersal costs can vary among crops. *Landscape Ecol* 26: 371-379.
15. Ahlers AA, Heske EJ, Schooley RL, Mitchell MA (2010) Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats. *Wildlife Biol* 16: 400-408.
16. Errington PL (1939) Reaction of muskrat populations to drought. *Ecology* 20: 168-186.
17. Errington PL (1943) An analysis of mink predation upon muskrats in north-central United States. *Iowa Agric Exp Stn Res Bull* 320: 798-924.
18. Kinler QJ, Chabreck RH, Kinler NW, Linscombe RG (1990) Effect of tidal flooding on mortality of juvenile muskrats. *Estuaries* 13: 337-340.
19. Larivière S (1999) *Mustela vison*. *Mamm Species* 608: 1-9.
20. Gerell R (1970) Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* 21: 160-173.
21. Suloway L, Hubbell M (1994) Wetland resources of Illinois: an analysis and atlas. Illinois Natural History Survey, Champaign, Illinois, U.S.A.

22. Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *P Roy Soc Lond B Bio* 270: 467-473.
23. Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biol* 18: 1239-1252.
24. MacKenzie DI, Nichols JD (2004) Occupancy as a surrogate for abundance estimation. *Animal Biodivers Conserv* 27: 461-467.
25. Noon BR, Bailey LL, Sisk TD, McKelvey KS (2012) Efficient species-level monitoring at the landscape scale. *Conserv Biol* 26: 432-441.
26. McCauley LA, Jenkins DG (2005) GIS-based estimates of former and current depressional wetlands in an agricultural landscape. *Ecol Appl* 15: 1199-1208.
27. Baker DB, Richards RP, Loftus TT, Kramer JW (2004) A new flashiness index: characteristics and applications to Midwestern rivers and streams. *J Am Water ResMy As* 40: 503-522.
28. Ahlers AA, Schooley RL, Heske EJ, Mitchell MA (2010) Effects of flooding and riparian buffers on survival of muskrats (*Ondatra zibethicus*) across a flashiness gradient. *Can J Zool* 88: 1011-1020.
29. Wuebbles DJ, Hayhoe K (2004) Climate change projections for the United States Midwest. *Mitig Adapt Strategies Glob Chang* 9: 335-363.
30. Trenberth KE (2011) Changes in precipitation with climate change. *Climate Res* 47: 123-138.
31. Changnon SA, Black A (2009) 2008: a record wet and stormy year in Illinois. Champaign: Illinois State Water Survey. 21 p.

32. Illinois State Water Survey. 2012. Drought Update. Champaign, Illinois.
<<http://www.isws.illinois.edu/hilites/drought/archive/2012/docs/DroughtUpdate20120723.pdf>>. Accessed 13 June 2013.
33. Yamaguchi N, Rushton S, Macdonald DW (2003) Habitat preferences of feral American mink in the Upper Thames. *J Mammal* 84: 1356-1373.
34. Melero Y, Palazón S, Revilla E, Martelo J, Gosálbez J (2008) Space use and habitat preferences of the invasive American mink (*Mustela vison*) in a Mediterranean area. *Eur J Wildl Res* 54: 609-617.
35. Cotner LA, Schooley RL (2011) Habitat occupancy by riparian muskrats reveals tolerance to urbanization and invasive vegetation. *J Wildlife Manage* 75: 1637-1645.
36. Schooley RL, Cotner LA, Ahlers AA, Heske EJ, Levensgood JM (2012) Monitoring site occupancy for American mink in its native range. *J Wildlife Manage* 76: 824-831.
37. MacKenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. *J Appl Ecol* 42: 1105-1114.
38. MacKenzie D, Nichols J, Royle JA, Pollock KH, Bailey LL, Hines J (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Massachusetts. Academic Press. 324 p.
39. SAS Institute Inc. 2009; SAS® 9.23 – SAS Institute Inc., Cary, North Carolina, USA.
40. Warton DI, Hui FK (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92: 3-10.
41. Reynolds JC, Short MJ, Leigh RJ (2004) Development of population control strategies for mink *Mustela vison*, using floating rafts as monitors and trap sites. *Biol Conserv* 120: 533-543.

42. Ahlers AA, Mitchell MA, Schooley RL, Heske EJ, Levenson JM (2011) Hematologic and blood chemistry reference values for free-ranging muskrats (*Ondatra zibethicus*). J Wildlife Dis 47: 685-689.
43. Sikes RS, Gannon WL, Animal Care and Use Committee of the American Society of Mammalogists (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal 92: 235-253.
44. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer-Verlag. 353 p.
45. Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. J Wildlife Manage 74: 1175-1178.
46. Messier F, Virgl JA, Marinelli L (1990) Density-dependent habitat selection in muskrats: a test of the ideal free distribution model. Oecologia 84: 380-385.
47. Virgl JA, Messier F (1997) Habitat suitability in muskrats: a test of the food limitation hypothesis. J Zool 243: 237-253.
48. Erb J, Boyce MS, Stenseth NC (2001) Spatial variation in mink and muskrat interactions in Canada. Oikos 93: 365-375.
49. Viljugrein H, Lingjærde OC, Stenseth NC, Boyce MS (2001) Spatio-temporal patterns of mink and muskrat in Canada during a quarter century. J Anim Ecol 70: 671-682.
50. Holmengen N, Lehre Seip K, Boyce M, Stenseth NC (2009) Predator-prey coupling: interaction between mink *Mustela vison* and muskrat *Ondatra zibethicus* across Canada. Oikos 118: 440-448.

51. Estay SA, Albornoz AA, Lima M, Boyce MS, Stenseth NC (2011) A simultaneous test of synchrony causal factors in muskrat and mink fur returns at different scales across Canada. PLOS ONE 6: e27766. Doi:10.1731/journal.pone.002776
52. Shier CJ, Boyce MS (2009) Mink prey diversity correlates with mink-muskrat dynamics. J Mammal 90: 897-905.
53. Wolff PJ, Taylor CA, Heske EJ, Schooley RL. Habitat selection by American mink during summer is driven by hotspots of crayfish prey. Wildlife Biol (*In Press*).
54. Hanski I, Henttonen H, Korpimäki E, Oksanen L, Turchin P (2001) Small-rodent dynamics and predation. Ecology 82: 1505-1520.
55. Piha H, Luoto M, Piha M, Merilä J (2007) Anuran abundance and persistence in agricultural landscapes during a climatic extreme. Global Change Biol 13: 300-311.
56. Klamt M, Thompson R, Davis J (2011) Early response of the platypus to climate warming. Global Change Biol 17: 3011-3018.

Tables and Figures

Table 2.1.—Ranking of multi-season models for detection (p) of riparian muskrats (*Ondatra zibethicus*) and American mink (*Neovison vison*) in Illinois, USA from 2007-2012. ΔAIC_c = difference between model AIC_c and lowest AIC_c . ω = Akaike weights. K = number of estimable parameters. -2LogLike = twice the negative log-likelihood. For both species, I present all models with $\Delta AIC_c \leq 2$, along with the base model. The base model includes parameters for initial occupancy in 2007 [$\Psi(\cdot)$], annual colonization [$\gamma(2008-2012)$], annual extinction [$\epsilon(2008-2012)$], and constant detection probability [$p(\cdot)$]. Detection covariates include rain 7 days prior to survey (Rain), percentage of trackable surface (Sandbar), day of year site was surveyed (Date), amount of debris (Debris), and observer conducting survey (Observer).

Model	ΔAIC_c	ω	K	-2LogLike
Muskrat				
$\Psi(\cdot), \gamma(2008-2012), \epsilon(2008-2012), p(\text{Rain})$	0.00	0.18	13	1046.77
$\Psi(\cdot), \gamma(2008-2012), \epsilon(2008-2012), p(\text{Rain} + \text{Sandbar})$	1.26	0.09	14	1046.03
$\Psi(\cdot), \gamma(2008-2012), \epsilon(2008-2012), p(\text{Rain} + \text{Date})$	1.49	0.08	14	1046.26
$\Psi(\cdot), \gamma(2008-2012), \epsilon(2008-2012), p(\text{Rain} + \text{Debris})$	1.55	0.08	14	1046.26
$\Psi(\cdot), \gamma(2008-2012), \epsilon(2008-2012), p(\cdot)$	1.93	0.07	12	1050.70
Mink				
$\Psi(\cdot), \gamma(2008-2012), \epsilon(2008-2012), p(\text{Observer} + \text{Sandbar})$	0.00	0.37	18	1230.99

Table 2.1 (cont.)

$\Psi(\cdot), \gamma(2008-2012), \varepsilon(2008-2012), p(\text{Observer} + \text{Sandbar} + \text{Date})$	0.77	0.25	19	1229.76
$\Psi(\cdot), \gamma(2008-2012), \varepsilon(2008-2012), p(\text{Observer} + \text{Sandbar} + \text{Rain})$	0.98	0.22	19	1229.97
$\Psi(\cdot), \gamma(2008-2012), \varepsilon(2008-2012), p(\text{Observer} + \text{Sandbar} + \text{Date} + \text{Rain})$	1.99	0.14	20	1228.98
$\Psi(\cdot), \gamma(2008-2012), \varepsilon(2008-2012), p(\cdot)$	42.03	0.00	12	1285.02

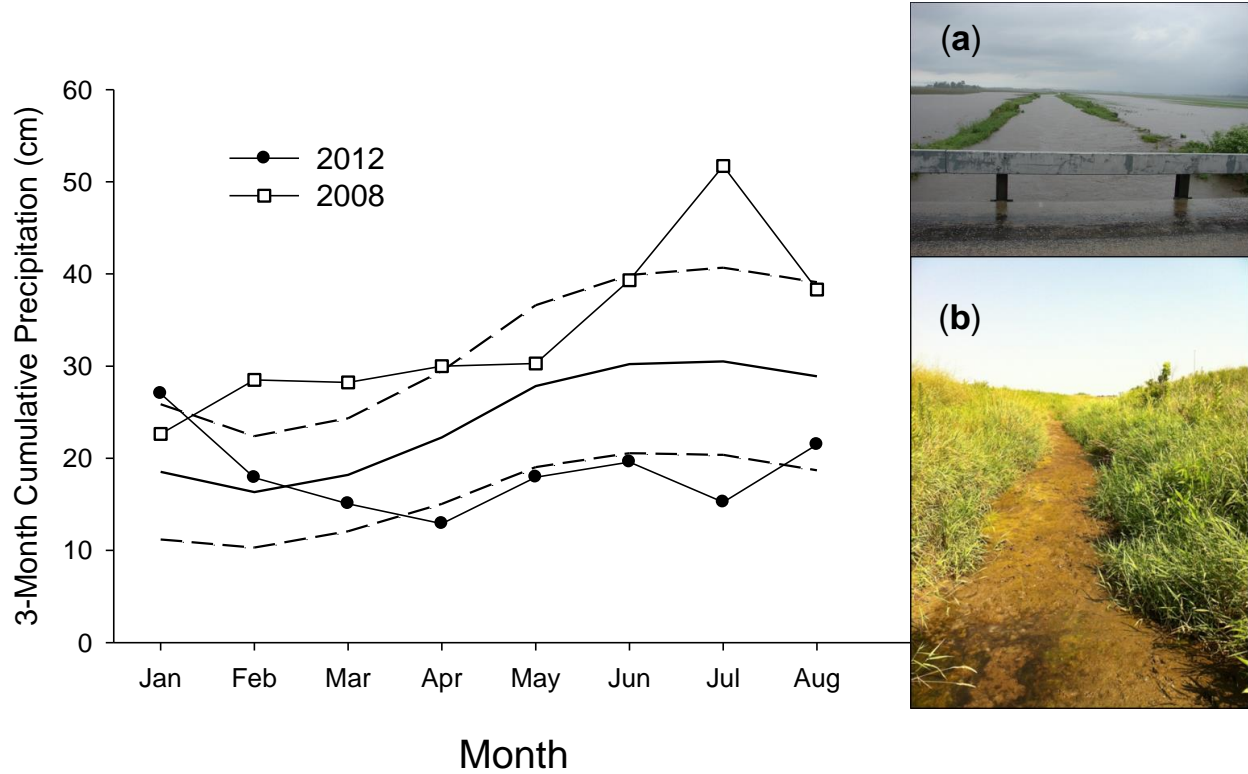


Figure 2.1. Three-month cumulative precipitation (sum of current month and the previous two months) in Urbana, Illinois prior to occupancy surveys for mink (*Neovison vison*) and muskrat (*Ondatra zibethicus*). Mean (solid line) ± 1 SD (dashed line) represent the historical 3-month cumulative precipitation (1889-2012). Photographs are from the same stream segment during (a) 2008 and (b) 2012.

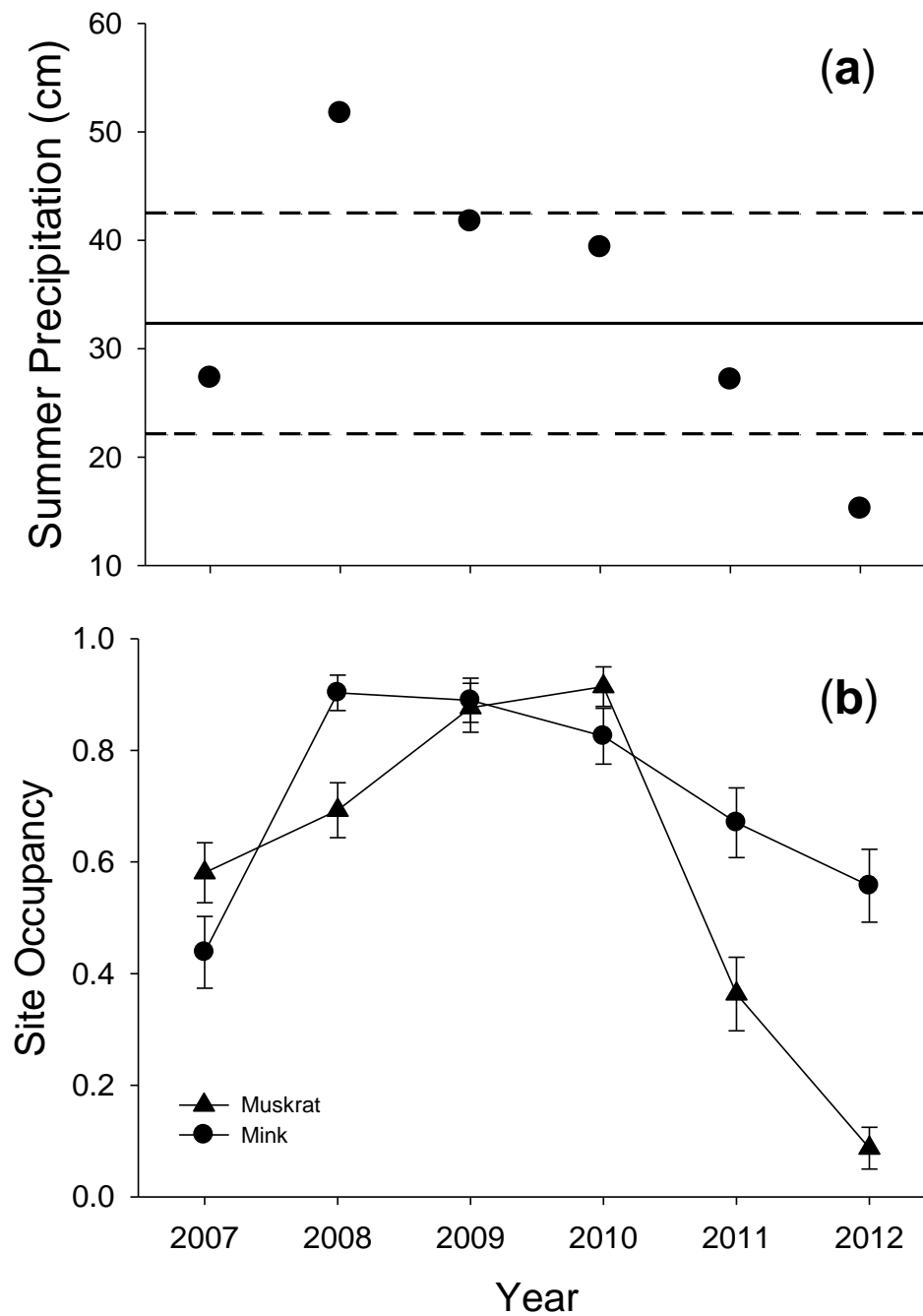


Figure 2.2. Trends in (a) summer precipitation and (b) site occupancy dynamics of mink (*Neovison vison*) and muskrats (*Ondatra zibethicus*) in Illinois, USA from 2007-2012. Summer precipitation (sum of May, June, and July) for each year is compared to the 123-year mean (solid line) ± 1 SD (dashed line) for the same period. Estimates of site occupancy (± 1 SE) are model-averaged and corrected for imperfect detection.

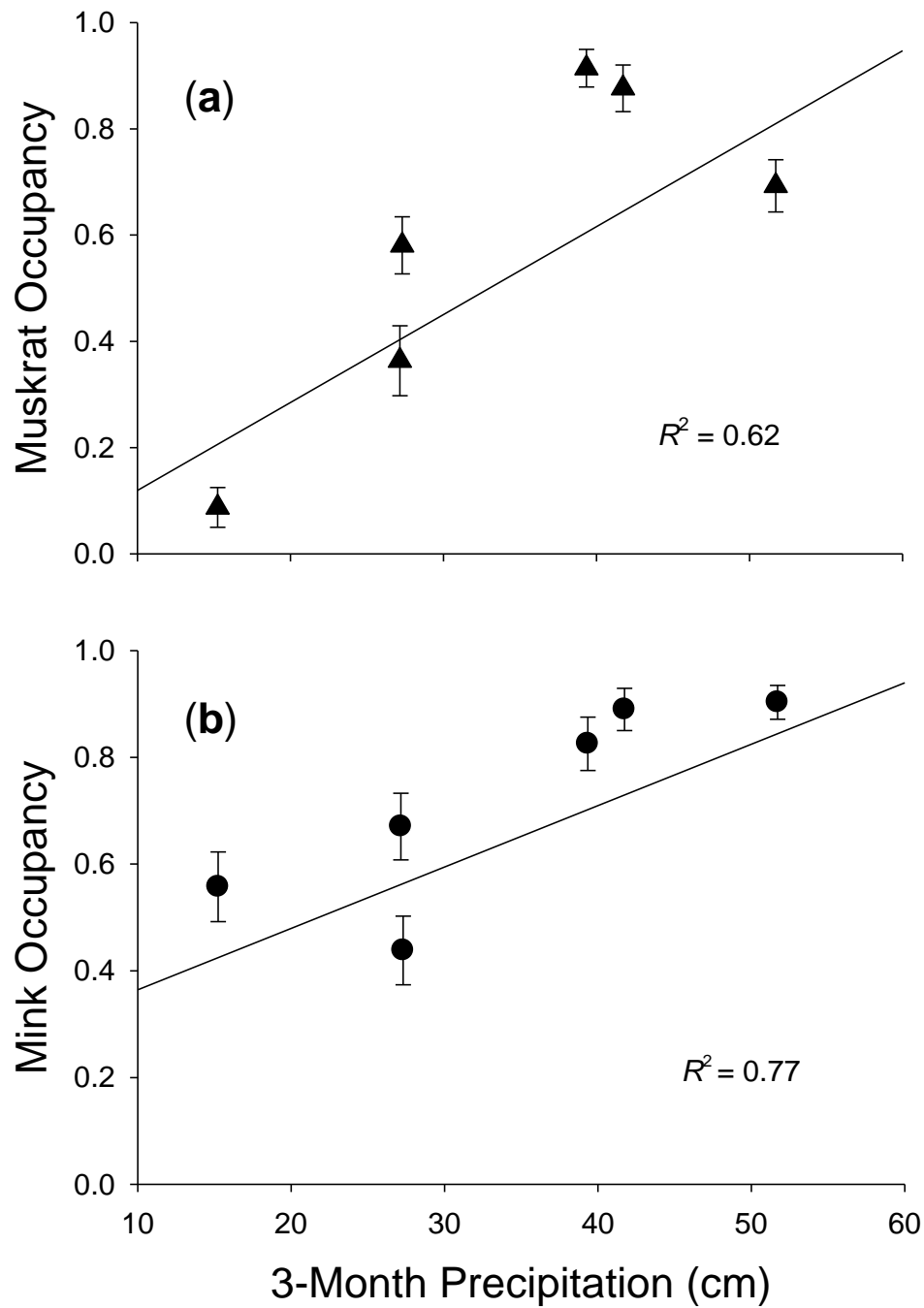


Figure 2.3. Relationship between site occupancy by (a) muskrat, and (b) mink and 3-month precipitation (May, June, and July) from 2007-2012 in Illinois, USA. Estimates of site occupancy (± 1 SE) are model-averaged and corrected for imperfect detection.

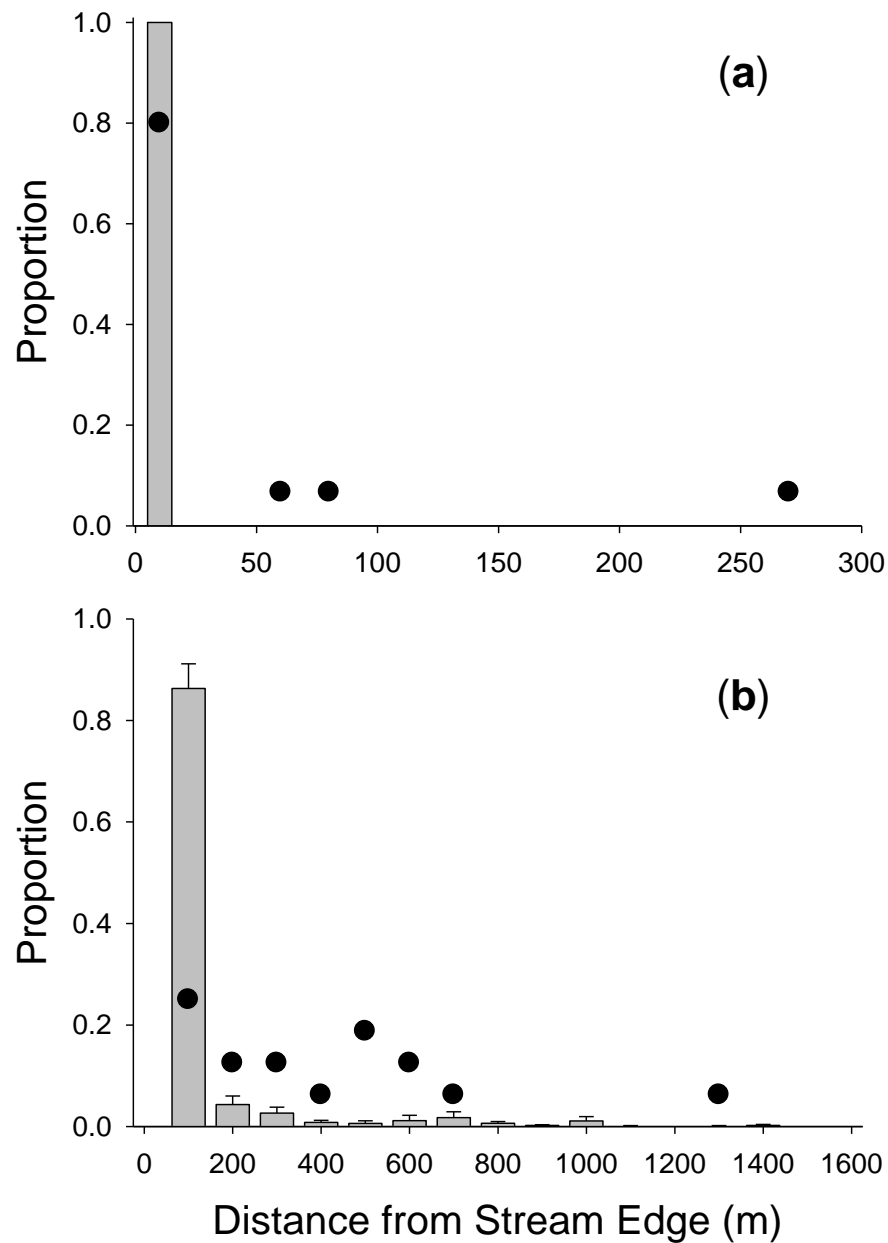


Figure 2.4. Bars indicate the proportion of locations (mean + 1 SE) of radiomarked (a) muskrat ($n = 26$) and (b) American mink ($n = 20$) in relation to distance from the stream edge. Locations are grouped into 10-m bins for muskrats and 100-m bins for mink. Dark circles represent the proportion of known-fate mortalities in relation to distance from the stream edge. I adapted space-use and mortality data from my previous studies (15, 28). Muskrat movements never exceeded > 3 m from the stream edge. Note differences in scale of x axis for (a) and (b)

CHAPTER 3

PREY DISTRIBUTION, CONTEXT, AND POTENTIAL LANDSCAPE

SUPPLEMENTATION AFFECT OCCUPANCY DYNAMICS OF AMERICAN MINK IN

STREAMS

Abstract

Land-use change can reduce and isolate suitable habitat generating spatial variation in resource availability. Improving species distribution models requires a multi-scale understanding of resource requirements and species' sensitivities to novel landscapes. I investigated how the spatial distribution of supplementary habitats (permanent wetlands), urban land cover, water depths, and distribution of a key prey species (muskrat; *Ondatra zibethicus*) influence occupancy dynamics of American mink (*Neovison vison*). Although mink are widespread across North America and a destructive invasive species in Europe, South America, and Asia, there is a limited understanding of factors affecting their spatial distribution. I used six years of presence-absence data (2007-2012) to evaluate occupancy dynamics of mink at 58-90 stream sites along an urbanization gradient in Illinois, USA. I predicted negative relationships between stream occupancy and urban land cover and distance from permanent wetlands, and positive associations with muskrat presence, water depth, and width of the riparian zone. Contrary to my hypothesis, stream sites closer to permanent wetlands had lower occupancy and colonization rates for mink. Occupancy and colonization rates were higher at sites with deeper water, and colonization rates were related negatively to urban land cover. Mink were more likely to leave stream habitat if muskrats were not present and permanent wetlands were nearby. Factors interplaying across multiple scales influenced occupancy dynamics of American mink in stream

habitat in a highly modified landscape. My results highlight the importance of considering both the spatial distribution of supplementary habitats and direct measures of prey availability to improve species distribution models.

Introduction

Urbanization and large-scale agricultural production are major contributors to habitat degradation and affect wildlife populations worldwide (Cardillo et al. 2004; Foley et al. 2005; Green et al. 2005). Carnivores are particularly sensitive to these landscape changes because their high trophic level requires large home ranges (Woodroffe and Ginsberg 1998; Crooks 2002; Crooks et al. 2011). Habitat loss and subsequent conflict with humans directly influence the distribution (Randa and Yunker 2006; Ordenana et al. 2010), space use (Gosselink et al. 2003; Gehrt et al. 2009; Šálek et al. 2015), and survival (Gosselink et al. 2007; Collins and Kays 2011) of carnivores, thus affecting their persistence (Cardillo et al. 2004) and community-level dynamics (Crooks and Soule 1999; Prange and Gehrt 2004; Prugh et al. 2009). In highly modified landscapes, landscape supplementation (Dunning et al. 1992) may enable persistence of species in human-modified or climate-sensitive landscapes (Asensio et al. 2009; Smith et al. 2013). However, the spatial distribution and accessibility of resources may ultimately affect the ability of individuals to exploit certain habitat patches, and thus be consequential for carnivore populations.

American mink (hereafter mink; *Neovison vison*) are small (0.5 – 3.0 kg), generalist carnivores that are facultatively associated with wetland habitats (Larivière 1999), native to North America, and an invasive species across Europe, South America, and Asia (Bonesi and Palazon 2007; Fasola et al. 2011). Although widespread throughout North America and one of

Europe's most destructive invasive species (European Environment Agency 2007; MacPherson and Bright 2011), our understanding of how mink respond to modified landscapes is surprisingly limited. In the Midwestern USA, widespread loss of wetland habitats (Suloway and Hubbell 1994; McCauley and Jenkins 2005; Urban 2005), primarily through conversion to agriculture, has constrained most available mink habitat to agricultural ditches and small streams. These habitats have dynamic flow regimes (Baker et al. 2004; Ahlers et al. 2010) with dramatic variability in habitat quality largely determined by precipitation events (Ahlers et al. 2010; Ahlers et al. 2015). Remaining permanent, two-dimensional, wetland habitat is often human-made (e.g., urban water-retention ponds, borrow pits for highway construction) and spatially isolated from streams.

Permanent wetlands may provide supplementary resources for mink (e.g., crayfish, fish, muskrats [*Ondatra zibethicus*], waterfowl) when prey become limited in less stable streams (Krapu et al. 2004). Mink will exploit wetlands when they are in close proximity to stream habitat (A. Ahlers unpublished data) and incorporate them into their home range (Gerell 1969; Gerell 1970). During periods of below-average precipitation, mink will likely forage in secondary habitats away from the stream edge (Ahlers et al. 2015). Mink movements between stream habitats and permanent wetlands may be costly in human-modified landscapes, however, as they are for other species (Schooley and Branch 2009; Cosentino et al. 2011a). For example, although mink used terrestrial habitat only 14% of the time, 76% of mortalities occurred there (Ahlers et al. 2015). Mink are territorial (Gerell 1970; Dunstone 1993), like most mustelid species (Powell 1979), making it unlikely that stream habitat within their home range will be occupied by another individual while they are temporarily exploiting secondary habitats.

Our understanding of how carnivores respond to urbanization remains limited and results are contradictory for mink. Studies report negative relationships between mink activity and exurban development (Racey and Euler 1983; Melero et al. 2008; Brzeziński et al. 2012) and urban land cover (Wolff et al. 2015). However, Brzeziński et al. (2012) caution that behavioral adaptability may allow mink to colonize human-developed areas. Additionally, anecdotal evidence suggests mink may frequently use highly urbanized areas (Mech 2003) or other human settlements (Gerell 1970). In my region, coyotes (*Canis latrans*), the main predator of mink, rarely occur in urban areas (Gosselink et al. 2003), whereas presence of muskrats, a major prey species (Errington 1943; Erb et al. 2001; Haydon et al. 2001; Holmengen et al. 2009), is related positively to urban land cover (Cotner and Schooley 2011). Thus, urban areas could provide mink with refuge from intraguild predation while also providing a key prey resource. However, vehicle-related mortality is high (Ahlers et al. 2015) and may preclude mink from effectively exploiting urban landscapes.

I used six years of presence-absence data to assess how landscape context and supplementation, presence of muskrats, and local habitat quality affect habitat occupancy and turnover of mink in their native range. If mortality risk from vehicles is greater than that posed by coyotes, and outweighs the benefit of higher occurrence of muskrats in urban areas, I expect habitat occupancy and colonization by mink should be negatively related to urban land cover, whereas local extinctions would be positively related to urban land cover. In contrast, if the potential benefits of urban landscapes (increased muskrat prey and reduced coyote predation) outweigh the mortality risks from vehicles, I expect the opposite associations with habitat occupancy, colonization, and extinction. I assume permanent wetlands are important supplementary habitats for mink (Arnold and Fritzell 1989; Arnold and Fritzell 1990; Krapu et

al. 2004; Ahlers et al. 2015), and spatial proximity to these wetlands should be a good predictor of site occupancy at less stable stream habitats. Thus, I predicted that stream sites closer to permanent wetlands would have higher initial occupancy and colonization probabilities, and lower extinction probabilities, than stream sites farther from permanent wetlands. Because muskrats are an important prey for mink, I predicted occupancy of stream sites by muskrats would have a positive effect on initial occupancy and colonization and a negative effect on local extinction of mink. Lastly, I considered the importance of local habitat quality on site occupancy by mink. I predicted that mink would select stream sites with deeper water (Schooley et al. 2012) and larger riparian zones as these habitats may support greater abundances of both aquatic and terrestrial prey (e.g., small mammals, ground-nesting birds). To my knowledge, this study represents the most comprehensive analysis of habitat selection of this semiaquatic carnivore in its native range.

Methods

Study area

I conducted my study in an intensively farmed region (785,400 ha) of east-central Illinois, USA, centered on the cities of Champaign, Urbana, and Savoy (40°12'N, 88°26'W; estimated human population in 2012: 231,891; Fig. 3.1). Eighty-five percent of the landscape is dedicated to agricultural production with maize (*Zea mays*, 45%) and soybeans (*Glycine max*, 40%) as the dominant crops. To accommodate agricultural production, most of the region is drained with subsurface tiles (52-82%; David et al. 2010), and wetlands represent only ~0.9% of the landscape (McCauley and Jenkins 2005). Remaining stream habitat is highly modified, and

water depths are largely determined by the frequency and intensity of precipitation events (Baker et al. 2004; Ahlers et al. 2010; Ahlers et al. 2015).

Sampling design

I selected 90 sites to survey for presence of mink and muskrat along an urban land cover gradient using a stratified-random sampling design. I randomly selected 45 sites within a 2-km radius of incorporated cities (population size >2500) and 45 sites outside of this buffer. I sampled all 90 sites in 2007 and 2008. Because of logistical constraints in 2009-2012, I randomly reduced the number of sites that I surveyed from 90 to 60. Each site represented a potential resource patch for mink and constituted a 200-m stretch of wadeable stream (Yamaguchi et al. 2003; Melero et al. 2008; Schooley et al. 2012). Investigating site occupancy at this scale allowed me to assess annual changes in resource patch use for mink (MacKenzie et al. 2006). Sites were within streams ranging from 1st to 5th order in size and separated by a mean nearest-neighbor Euclidian distance of 2.5 km (range = 0.5 – 22.8 km).

I sampled each site from July to October, 2007-2012 using a removal design framework (MacKenzie and Royle 2005) to obtain an unbiased estimate of site occupancy for mink and muskrat. Trained observers conducted walking surveys for mink sign (scat and tracks) and muskrat sign (scat, tracks, burrows, and clippings) located within 5 m of the stream edge (Cotner and Schooley 2011; Schooley et al. 2012). Initially (2007-2008), my survey effort was based on a removal design framework focused on muskrat habitat occupancy (Cotner and Schooley 2011). Sites were surveyed twice (two independent observers during 1st site visit) for both species and not revisited if I detected muskrat sign. I conducted two additional surveys (two independent observers during 2nd site visit) for both species if muskrat sign was not found during the 1st visit.

Thus, I conducted a maximum of four surveys per site. I based my removal sampling design on presence of mink sign at each site from 2009-2012. If mink sign was not found during the first site visit, I returned for a 2nd site visit yielding a maximum of four surveys per site (Ahlers et al. 2015). In all years, if sites experienced rain events with ≥ 1 cm of precipitation, I postponed surveys by >2 days to reduce the risk of visible sign being washed away. I was unable to survey two sites in 2009 and 2011 because of flooding and access limitations. My mixed removal design and reduction of sampling sites resulted in missing observations that were efficiently handled by my occupancy modeling approach (MacKenzie et al. 2006). My total sampling effort included 1196 surveys (2007 = 276; 2008 = 282; 2009 = 130; 2010 = 160; 2011 = 162; 2012 = 186) across ~239 km of wadeable streams.

Detection and occupancy covariates

I estimated detection probability, initial site occupancy, colonization, and extinction rates of mink from stream sites using the multi-season model structure in Program PRESENCE 6.9. I obtained unbiased estimates of mink presence at each site using survey-specific covariates for detection informed by my previous studies in this region (Schooley et al. 2012; Ahlers et al. 2015). Covariates potentially influencing detection included survey date, recent rainfall, observer, and amount of substrate adjacent to the stream that could potentially hold recognizable mink tracks. Survey date (Date) was a continuous variable (1-365) coded for the day of each independent survey. I summed total precipitation (Rain) for the 7 days prior to each survey (Illinois State Water Survey station #118740; Urbana, IL). Multiple observers (Observer) were coded following recommendations by MacKenzie et al. (2006; pp. 117-118). In total, thirteen observers conducted surveys from 2007–2012. To avoid overparameterization of models, I

modeled six total observers by grouping observers based on survey year and survey effort. In 2008, I identified the amount of trackable surface (Sandbar) at each site as an important covariate for mink detection (Schooley et al. 2012). Thus, I visually estimated the percent ‘Sandbar’ at each site from 2008-2012. Because sandbar indices were highly correlated between years for each site (mean Pearson correlation coefficient = 0.60, range = 0.49 – 0.80, $p < 0.0001$), missing ‘Sandbar’ values from 2007 were estimated *a posteriori* using mean ‘Sandbar’ values from each site collected from 2008-2012.

I considered both local (muskrat occupancy, water depth, riparian-zone width) and landscape (proportion of urban land cover within 500-m buffer, distance to permanent wetland) factors in my analysis of initial occupancy, colonization, and extinction for mink. I used single-season occupancy models (MacKenzie et al. 2006) to determine the probability of a site being occupied by muskrat prey (Muskrat) during a particular year. I chose to include ‘Muskrat’ as a covariate in my analysis, and not use the multiseason, two-species model structure in PRESENCE, to avoid overparameterization of models (see also Cosentino et al. 2011b). I constructed occupancy models for muskrats using covariates previously determined important for detection and site occupancy (Cotner and Schooley 2011; APPENDIX A). To obtain robust measures of muskrat occupancy at each site, I derived model-averaged estimates of site occupancy for each year using all models from the candidate set (Burnham and Anderson 2002; APPENDIX A). For sites where muskrats were detected at least once, the conditional occupancy probability was 1. The occupancy probability of sites where muskrats were not detected was < 1 .

I measured water depth (Depth) at sites each year at the deepest location every 50 m (0, 50, 100, 150 and 200 m) then averaged measurements (mean Depth across years = 0.31 m, SE = 0.01, range = 0 - 1.50 m). I also measured the width of the riparian zone (RipWidth) every 50 m

within each site then averaged measures (mean RipWidth = 43 m, SE = 7, range = 0 – 466 m). I quantified urban land cover (Urban) as the proportion of area devoted to buildings, parking lots, roads, maintained lawns and railroads within a 500-m buffer surrounding the center of each site (Cotner and Schooley 2011; Wolff et al. 2015). Urban land cover was remotely delineated using ArcMap v. 9.2 (Environmental Systems Research Institute 2006) and digital ortho-quadrangles (Illinois National Aerial Photography Program 2005) and confirmed with on-site visits.

Although site selection was stratified by urban and non-urban areas, my survey sites occurred along a continuous gradient of urbanization (mean urban cover = 0.17, SD = 0.25, range = 0.00 - 0.99). I defined permanent wetlands as non-ephemeral, two-dimensional water basins. In my study area, permanent wetlands are generally isolated and embedded in an agricultural matrix. These habitats were mostly human-made borrow pits ($n = 30$), retention ponds and lakes ($n = 59$), and one natural wetland. The surface area of these wetlands varied (mean surface area = 223 ha, SD = 2090). I measured the Euclidian distance (m) from the center of each stream site to the nearest permanent wetland (DistPerm) using aerial photographs and measuring tools in ArcMap (mean DistPerm = 1346 m, SD = 1590, range = 15 - 7094 m). Because my sampling regime was focused solely in stream habitat, I did not assess mink or muskrat occupancy in permanent wetlands.

Occupancy models

I initially conducted my analysis to select the model best explaining variation in detection while all other rate parameters remained constant. I then sequentially fit models to initial occupancy, colonization, and extinction by retaining the best model for each rate parameter to fit remaining parameters (Cosentino et al. 2010; Duggan et al. 2011; Cosentino et al. 2011b). For

my analysis of detectability, I fit models representing the single main effects of my detection covariates (Date, Rain, Observer, Sandbar), 12 models representing all possible combinations of additive main effects, and an intercept-only model that held all rate parameters constant. I constructed 15 models that were the same for each rate parameter to fit models of initial occupancy, colonization, and extinction. Because of multicollinearity between some covariates ($r > |0.35|$), I did not include the variable ‘Muskrat’ in models that also included ‘Urban’, ‘RipWidth’, or ‘Depth’, and I did not fit models that contained both ‘RipWidth’ and ‘Depth’. I considered five models with only single main effects (DistPerm, Muskrat, Depth, Urban, RipWidth) and seven models representing the additive effects of My covariates (DistPerm + Depth; Depth + Urban; DistPerm + Urban; DistPerm + Muskrat; DistPerm + RipWidth; Urban + RipWidth; DistPerm + Depth + Urban). Because the relative importance of landscape supplementation may vary depending upon the availability of prey at stream sites, I also examined models representing interactions between distance to nearest wetland and muskrat presence at stream sites (DistPerm + Muskrat + DistPerm x Muskrat) and water depth and distance to permanent wetlands (DistPerm + Depth + DistPerm x Depth). Lastly, I considered one model that constrained the rate parameter to be constant across sites (Intercept Only).

I used an information-theoretic approach to select the most parsimonious model for each rate parameter (Burnham and Anderson 2002). Models were ranked according to AIC_c (Akaike’s information criterion corrected for small sample sizes), and I considered models with ΔAIC_c values ≤ 2 to have substantial support. I evaluated the importance of each parameter’s inclusion into competitive models of interest by assessing relative changes in model fit (Burnham and Anderson 2002; Arnold 2010).

Results

Site occupancy, colonization, and extinction by mink from 2007 to 2012 were dynamic (Table 3.1). In 2008, a year with record-breaking summer precipitation (Ahlers et al. 2015), 49 sites were colonized (Table 3.1). Additionally, 14 sites in 2011 and 13 sites in 2012 (years with below average summer precipitation; Ahlers et al. 2015) experienced local extinction events (Table 3.1). During the six years of the study, four sites were never occupied and 21 sites were always occupied; all other sites experienced at least one colonization or extinction event. After accounting for imperfect detection within a multi-season model structure, colonization probability was 0.615 (SE = 0.055) and extinction probability was 0.159 (SE = 0.025) while holding initial site occupancy, colonization, and extinction constant.

A constant model of detection revealed that per-survey detection probability for mink was typically high ($\rho = 0.69$, SE = 0.02). Similar to previous research (Schooley et al. 2012, Ahlers et al. 2015), my competitive models of detection indicated that Rain, Sandbar, Date, and Observer were important covariates affecting my ability to detect mink sign (Table 3.2). Rain ($\beta = -0.0470$, SE = 0.0464) negatively affected detection probability, whereas Sandbar ($\beta = 0.0029$, SE = 0.0014) and Date ($\beta = 0.0036$, SE = 0.0006) positively affected detection. There was strong observer bias during surveys (range of β s = -1.9292 – 0.7835 relative to baseline observer). Based on differences in model fit, I used my 4th ranked competitive model (Table 3.2) that contained the additive effects of all my detection covariates to subsequently fit models of initial occupancy, colonization, and extinction.

The top-ranked model of initial occupancy included the additive effects of water depth ($\beta = 3.1429$, SE = 1.6595) and proximity to a permanent wetland ($\beta = 0.0002$, SE = 0.0006; Table 3.2). All models with substantial support included water depth. Mink were more likely to occur

at stream segments with deeper water and that were farther from permanent wetlands (Fig. 3.2). The negative effect of urbanization also was included in competitive models; however, inclusion of ‘Urban’ did little to improve model fit. Models that incorporated ‘Muskrat’ ($\Sigma\omega_i = 0.03$) and ‘RipWidth’ ($\Sigma\omega_i = 0.02$) were not well supported (all $\Delta AIC_c \geq 5.04$). Thus, I used my top-ranked model (DistPerm + Depth) to fit subsequent models of colonization and extinction.

Competing models of colonization probability included distance to permanent wetland, muskrat presence, water depth, and urban land cover (Table 3.2). My top-ranked model indicated that colonization was more likely at stream sites farther from permanent wetlands ($\beta = 0.0009$, $SE = 0.0009$) and with high probabilities of muskrat occupancy ($\beta = 2.8584$, $SE = 0.7114$). The second-best model had similar support and indicated that water depths ($\beta = 6.5499$, $SE = 2.2617$), in addition to spatial proximity to permanent wetlands, influenced colonization probability. Based on relative differences in model fit ($\Delta -2l = 1.84$, Table 3.2), the most supported model of colonization included the positive effects of water depth ($\beta = 6.1968$, $SE = 2.1271$) and distance to a permanent wetland ($\beta = 0.0007$, $SE = 0.0009$), and also the negative effect of urban land cover ($\beta = -1.4289$, $SE = 1.1140$; Table 3.2). Sites with deeper water (Fig. 3.3A) or a high probability of muskrat occurrence (Fig. 3.3B) were more likely to be colonized. Additionally, mink were less likely to colonize stream sites that were close to permanent wetlands (Fig. 3.3C) or surrounded by urban land cover (Fig. 3.3D).

Extinction probabilities for mink were moderated by the positive interaction ($\beta = 0.00003$, $SE = 0.0002$) between muskrat occupancy probability ($\beta = -1.6601$, $SE = 0.4840$) and distance to permanent wetland ($\beta = -0.0002$, $SE = 0.0002$; Table 3.2). No other models were competitive. Mink were more likely to abandon streams when muskrats were unlikely to be present if stream sites were closer to permanent wetlands (Fig. 3.4). My second-ranked model, including the

interaction between water depth and distance to permanent wetland (DistPerm + Depth + DistPerm x Depth), had no support ($\Delta AIC_c = 12.66$, $\omega_i = 0.00$).

Discussion

In many regions, landscape conversions to agriculture and urbanization have eliminated many natural wetlands (Brady and Flather 1994; Gutzwiller and Flather 2011), isolated remaining wetlands (McCauley and Jenkins 2005), and altered riparian ecosystems (Snyder et al. 2003; Riseng et al. 2011). Water depths in stream habitats are temporally dynamic (Baker et al. 2004) and persistence of semiaquatic species in these areas may depend on accessibility of non-ephemeral wetlands. My results demonstrate that occupancy dynamics of American mink in stream habitats is influenced by the spatial distribution of permanent wetlands. Contrary to my prediction, however, mink were less likely to occupy and colonize stream sites closer to permanent wetlands. This outcome suggests that rather than supplementing stream habitats, permanent wetlands may be attractive alternative habitats for mink, drawing them away from streams. An alternate interpretation, however, is that effects of landscape supplementation are occurring at larger spatial scales (mink home range) than my sampling unit. As expected, mink more frequently occurred in and colonized stream sites with deeper water and avoided stream habitat surrounded by urban land cover. Local site extinctions were mediated by an interaction between the distribution of an important prey species (muskrats) and spatial proximity to permanent wetlands, demonstrating the interplay of local and landscape factors. Mink were more likely to abandon a stream site if the probability of occupancy by muskrats was low, especially if an attractive alternative habitat, a permanent wetland, was nearby.

Mink were more likely to occur in and colonize stream habitats that were spatially isolated from permanent wetlands. These results imply that mink may be choosing stable wetland habitats over unstable and less predictable stream habitats when both are in close spatial proximity. Stable water levels would buffer mink from dynamic water depths common in stream habitats and provide aquatic and semiaquatic prey resources regardless of changes in local precipitation (Arnold and Fritzell 1987; Arnold and Fritzell 1990; Krapu et al. 2004). Krapu et al. (2004) posited that construction of permanent freshwater bodies posed substantial risks to waterfowl production because these wetlands supported ample prey that buffered mink (a key waterfowl predator) populations from regional droughts. Colonization of stream sites was more likely when they were isolated from permanent wetlands by >2 km (Fig. 3.3C), revealing a potential isolation-by-distance threshold. I documented maximum movements by radiomarked mink of ~1.4 km away from the water's edge, which are within this critical distance (Ahlers et al. 2015).

Another interpretation regarding distance to permanent wetlands and distribution of mink is that my sampling scale was too fine to reveal the effects of landscape supplementation. Average mink home ranges in stream habitats are much larger (male = 3.34 km, female = 2.06; Melero et al. 2014) than the resource patches that I sampled (200-m stream segments). Mink may be supplementing stream habitat with permanent wetlands at the home-range scale. That is, occupancy and colonization of home ranges could be more likely when wetlands are nearby, even though an individual could be absent more often from a particular stream segment in that situation. Unfortunately, my survey design was limited to stream habitat and I do not have information on mink occupancy status or habitat quality of the permanent wetlands. My patterns

are clear, however, and demonstrate that permanent wetlands strongly affect mink occupancy dynamics in nearby stream habitat.

Prey distribution and abundances are often dynamic, and simple measures of prey habitat (used as surrogates) may not always represent prey availability (Keim et al. 2011; Wolff et al. 2015). Muskrats are an important resource for mink (Errington 1943; Erb et al. 2001; Haydon et al. 2001; Holmengen et al. 2009) and their distribution is dependent, among other factors, on water depths (Errington 1963; Dannell 1978; Cotner and Schooley 2011). Muskrat occurrence was included in a well-supported colonization model and also in my only supported model of site extinctions (Table 3.2). Thus, spatial variation in muskrat availability seems to partially drive patterns of mink habitat selection. My models incorporating water depth also indicated that mink readily occur in and colonize sites with deeper water levels (Figs. 3.2 & 3.3A). Crayfish also are important prey for mink (Melero et al. 2014), and mink select stream segments with hotspots of high crayfish density during drought conditions (Wolff et al. 2015). Deeper water may provide a source of aquatic and semiaquatic prey in addition to muskrats in dynamic stream habitats.

The relationship between occupancy dynamics for mink and wetland isolation was complex as I documented an interaction between muskrat occupancy and distance to permanent wetlands affecting local site extinction for mink. Mink were more likely to leave streams without muskrats if they were closer to permanent wetlands (Fig. 3.4). Extinction models including water depth had little support indicating mink were cueing directly on muskrat presence rather than water depths, a potential surrogate for prey availability, when considering whether to leave a site. Movements in terrestrial areas can be costly, however, which may reduce the likelihood of mink making long-distance movements to permanent wetlands even when muskrats are not

present in stream habitat. My previous research revealed that 76% of mink mortalities occur in terrestrial habitat although mink use these areas only ~14% of the time (Ahlers et al. 2015). Such costs should deter individuals from frequent forays between habitats and may constrain landscape supplementation processes to limited scales (~2 km). My data suggest prey availability and distance interact to influence motivation for movements between patches by carnivores, and estimates of connectivity based on the spatial arrangement of habitats should consider such interactions.

Increased frequencies of extreme weather events (e.g., prolonged droughts and flooding) are predicted by current climate change models (Easterling et al. 2000; Dai 2013) and will likely compound the effects of land use on species occurring in heavily modified environments (Piha et al. 2007; Klamt et al. 2011). Landscape supplementation may buffer populations during these extreme events if supplementary wetland habitats retain relatively stable water depths. Smith et al. (2013) found that landscape supplementation influenced the distribution of koalas (*Phascolarctos cinereus*) in a semiarid landscape. Koalas were more likely to occur in landscapes with large amounts of both woodland and riverine habitat. Distance from the nearest water source was an important predictor of koala presence, and Smith et al. (2013) hypothesized that these areas may provide refugia during drought and prolonged extreme heat. Occupancy rates for mink in stream habitat are reduced during drought conditions—presumably because mink are foraging in supplementary habitats (Ahlers et al. 2015). Permanent wetlands may provide refugia for mink during extreme weather events if they are in close proximity (< 2 km) to climate-sensitive stream habitat.

My hypothesis that urbanization imposes distribution constraints on mink populations was supported. Because most of my highly urban sites were located in small-to-moderate sized urban

areas, this avoidance pattern will likely hold for larger cities with higher levels of traffic and habitat disturbance. Mink were less likely to colonize sites surrounded by urban land cover, especially when the proportion of urban land cover exceeded 80% (Fig. 3.3D). In contrast, colonization probability was highest when the proportion of urban land cover surrounding a site was <10% (Fig. 3.3D). Wolff et al. (2015) documented a negative effect of urban land cover on mink habitat occupancy using a single-season modeling approach during a severe drought, and other studies have reported similar sensitivities to human-developed areas (Racey and Euler 1983; Melero et al. 2008; Brzeziński et al. 2012). Urban streams can support prey resources used by mink; muskrat habitat occupancy is positively related to urban land cover (Cotner and Schooley 2011), and crayfish densities are similar across my urban land cover gradient (Wolff et al. 2015). However, mink movements are not restricted to the stream edge as they will also move in terrestrial areas. Vehicle-related mortality is considerable (Ahlers et al. 2015), and mink may not be able to persist in highly urbanized areas because movements outside of the stream can result in increased risk of mortality from automobile traffic. Human-related mortality is common among carnivores occurring in or around urban areas (Riley et al. 2003; Grilo et al. 2009; Bateman and Fleming 2012) and may preclude some species from exploiting urban landscapes.

My study highlights the importance of considering the spatio-temporal distribution of key local resources, such as primary prey, along with landscape context and accessibility of supplementary habitats, to enhance species distribution models. Future studies should focus on elucidating factors that affect the functional connectivity of secondary habitats and how key demographic parameters are affected by landscape supplementation.

Chapter 3 meets the formatting requirements of *Landscape Ecology*

Literature Cited

- Ahlers AA, Schooley RL, Heske EJ, Mitchell MA (2010) Effects of flooding and riparian buffers on survival of muskrats (*Ondatra zibethicus*) across a flashiness gradient. *Can J Zool* 88:1011-1020
- Ahlers AA, Cotner LA, Wolff PW, Mitchell MA, Schooley RL, Heske EJ (2015) Summer precipitation predicts spatial distribution of semiaquatic mammals. *PLoS One* (in press)
- Arnold TW, Fritzell EK (1989) Spring and summer prey remains collected from male mink dens in southwestern Manitoba. *Prairie Nat* 21:189-192
- Arnold TW, Fritzell EK (1990) Habitat use by male mink in relation to wetland characteristics and avian prey abundances. *Can J Zool* 68:2199-2208
- Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. *J Wildl Manage* 74:1175-1178
- Asensio N, Arroyo-Rodríguez V, Dunn JC, Cristóbal-Azkarate J (2009) Conservation value of landscape supplementation for howler monkeys living in forest patches. *Biotropica* 41:768-773
- Baker DB, Richards RP, Loftus TT, Kramer JW (2004) A new flashiness index: characteristics and applications to Midwestern rivers and streams. *J Am Water Resour My Assoc* 40:503-522
- Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. *J Zool* 287:1-23
- Bonesi L, Palazon S (2007) The American mink in Europe: Status, impacts, and control. *Biol Conserv* 134:470-483

- Brady SJ, Flather CH (1994) Changes in wetlands on nonfederal rural land of the conterminous United States from 1982-1987. *Environ Manage* 18:693-705
- Brzeziński M, Natorff M, Zalewski A, Żmihorski M (2012) Numerical and behavioral responses of waterfowl to the invasive American mink: a conservation paradox. *Biol Conserv* 147:68-78
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York
- Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biol* 2:909-914
- Collins C, Kays R (2011) Causes of mortality in North American populations of large and medium-sized mammals. *Anim Conserv* 14:474-483
- Cosentino BJ, Schooley RL, Phillips CA (2010) Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*. *Landsc Ecol* 25:1589-1600
- Cosentino BJ, Schooley RL, Phillips CA (2011a) Connectivity of agroecosystems: dispersal costs can vary among crops. *Landsc Ecol* 26:371-379
- Cosentino BJ, Schooley RL, Phillips CA (2011b) Spatial connectivity moderates the effect of predatory fish on salamander metapopulation dynamics. *Ecosphere* 2:1-14
- Cotner LA, Schooley RL (2011) Habitat occupancy by riparian muskrats reveals tolerance to urbanization and invasive vegetation. *J Wildl Manage* 75:1637-1645
- Crooks KR, Soule ME (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563-566

- Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv Biol* 16:488-502
- Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philos Trans R Soc B* 366:2642-2651
- Dai A (2013) Increasing drought under global warming in observations and models. *Nature Clim Change* 3:52-58
- Dannell, K (1978) Intraannual and interannual changes in habitat selection by muskrat. *J Wildl Manage* 42:540-549
- David MB, Drindwater, LE, McIsacc GF (2010) Sources of nitrate yield in the Mississippi river basin. *J Environ Qual* 39:1657-1667
- Duggan JM, Schooley RL, Heske EJ (2011) Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? *Landsc Ecol* 26:1477-1490
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-175
- Dunstone N (1993) *The mink*. T & AD Poyser, London, United Kingdom
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068-2074
- Environmental Systems Research Institute, Inc. (2006) ArcGIS. Version 9.2. Environmental Systems Research Institute, Inc., Redlands, California
- Erb J, Boyce MS, Stenseth NC (2001) Spatial variation in mink and muskrat interactions in Canada. *Oikos* 93:365-375

- European Environment Agency (2007) Europe's environment. The fourth assessment. European Environment Agency. Copenhagen, Denmark
- Errington PL (1943) An analysis of mink predation upon muskrats in north-central United States. Bulletin No. 320, Iowa State College of Agricultural Research, Ames
- Errington PL (1963) Muskrat Populations. Iowa State University Press, Iowa City, Iowa
- Ewers RW, Didham RK (2006) Confounding factor in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117-142
- Farhig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Sys* 34:487-515
- Fasola L, Muzio J, Chehebar C, Cassini M, Macdonald DW (2011) Range expansion and prey use of American mink in Argentinean Patagonia: dilemmas for conservation. *Eur J Wildl Res* 57:283-294
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. *Science* 309:570-574
- Gehrt SD, Anchor C, White LA (2009) Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *J Mammal* 90:1045-1057
- Gerell R (1969) Activity patterns of the mink *Mustela vison* Schreber in Southern Sweden. *Oikos* 20:451-460
- Gerell R (1970) Home ranges and movements of the mink *Mustela vison* Shreber in southern Sweden. *Oikos* 21:160-173

- Gosselink TE, Van Deelen TR, Warner RE, Joselyn MG (2003) Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. *J Wildl Manage* 67:90-103
- Gosselink TE, Van Deelen TR, Warner RE, Mankin PC (2007) Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. *J Wildl Manage* 71:1862-1873
- Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. *Science* 307:550-555
- Grilo C, Bissonette JA, Santos-Reis M (2009) Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. *Biol Conserv* 142:301-313
- Gutzwiller KJ, Flather CH (2011) Wetland features and landscape context predict the risk of wetland habitat loss. *Ecol Appl* 21:968-982
- Haydon DT, Stenseth NC, Boyce MS, Greenwood PE (2001) Phase coupling and synchrony in the spatiotemporal dynamics of muskrat and mink populations across Canada. *Proc Natl Acad Sci USA* 98:13149-13154
- Holmengen N, Lehre Seip K, Boyce M, Stenseth NC (2009) Predator-prey coupling: interaction between mink *Mustela vison* and muskrat *Ondatra zibethicus* across Canada. *Oikos* 118:440-448
- Illinois National Aerial Photography Program (2005) Illinois digital ortho-photography quarter quadrangle data. Champaign, Illinois,
<<http://www.isgs.illinois.edu/nsdihome/webdocs/doq05/download.html>>
- Keim JL, DeWitt PD, Lele SR (2011) Predators choose prey over prey habitats: evidence from a lynx-hare system. *Ecol Appl* 21:1011-1016

- Klamt M, Thompson R, Davis J (2011) Early response of platypus to climate warming. *Global Change Biol* 17:3011-3018
- Krapu GL, Pietz PJ, Brandt DA, Cox PR (2004) Does presence of permanent fresh water affect recruitment in prairie-nesting dabbling ducks? *J Wildl Manage* 68:332-341
- Larivière S (1999) *Mustela vison*. *Mamm Species* 608:1-9
- Mackenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. *J Appl Ecol* 42:1105-1114
- MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, Burlington, Massachusetts
- MacPherson, JL, Bright PW (2011) Metapopulation dynamics and a landscape approach to conservation of lowland water voles (*Arvicola amphibius*). *Landsc Ecol* 26:1395-1404.
- McCauley LA, Jenkins DG (2005) GIS-based estimates of former and current depressional wetlands in an agricultural landscape. *Ecol Appl* 15:1199-1208
- Mech LD (2003) Incidence of mink, *Mustela vison*, and river otter, *Lutra canadensis*, in a highly urbanized area. *Can Field Nat* 117:115-116
- Melero Y, Palazón S, Revilla E, Martelo J, Gosàlbez J (2008) Space use and habitat preferences of the invasive American mink (*Mustela vison*) in a Mediterranean area. *Eur J Wildl Res* 54:609-617
- Melero Y, Palazón S, Lambin X (2014) Invasive crayfish reduce food limitation of alien American mink and increase their resilience to control. *Oecologia* 174:427-434

- Ordenana MA, Crooks KR, Boydston EE, Fisher RN, Lyren LM, Siudyla S, Haas CD, Harris S, Hathaway SA, Turschak GM, Miles AK, Van Vuren DH (2010) Effects of urbanization on carnivore species distribution and richness. *J Mammal* 91:1322-1331
- Piha H, Luoto M, Miha M, Merilä J (2007) Annuran abundance and persistence in agricultural landscapes during a climatic extreme. *Global Change Biol* 13:300-311
- Powell RA (1979) Mustelid spacing patterns: variations on a theme by *Mustela*. *Z Tierpsychol* 50:153-165
- Prange S, Gehrt SD (2004) Changes in mesopredator-community structure in response to urbanization. *Can J Zool* 82:1804-1817
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The Rise of the Mesopredator. *BioScience* 59:779-791
- Racey GD, Euler DL (1983) Changes in mink habitat and food selection as influenced by cottage development in central Ontario. *J Appl Ecol* 20:387-402
- Randa LA, Yunker JA (2006) Carnivore occurrence along an urban-rural gradient: A landscape-level analysis. *J Mammal* 87:1154-1164
- Reigada C, Schreiber SJ, Altermatt F, Holyoak M (2015) Metapopulation dynamics on ephemeral patches. *Am Nat* 185:183-195
- Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C, Wayne RK (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv Biol* 17:566-576
- Riseng CM, Wiley MJ, Black RW, Munn MD (2011) Impacts of agricultural land use on biological integrity: a causal analysis. *Ecol Appl* 21:3128-3146

- Šálek M, Drahníková L, Tkadlec E (2015) Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Rev* 45:1-14
- Schooley RL, Branch LC (2009) Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecol Appl* 19:1708-1722
- Schooley RL, Cotner LA, Ahlers AA, Heske EJ, Levensgood JM (2012) Monitoring site occupancy for American mink in its native range. *J Wildl Manage* 76:824-831
- Smith AG, McAlpine CA, Rhodes JR, Lunney D, Seabrook L, Baxter G (2013) Out on a limb: habitat use of a specialist folivore, the koala, at the edge of its range in a modified semi-arid landscape. *Landsc Ecol* 28:415-426
- Snyder CD, Yound JA, Vilella R, Lemarié DP (2003) Influences of upland and riparian land use patterns on stream biotic integrity. *Landsc Ecol* 18:647-664
- Suloway L, Hubbell M (1994) Wetland resources of Illinois: an analysis and atlas. Illinois Natural History Survey, Champaign, Illinois, U.S.A.
- Urban MA (2005) An uninhabited waste: transforming the Grand Prairie in nineteenth century Illinois, USA. *J Hist Geogr* 31:647-665
- Wassens S, Watts RJ, Jansen A, Roshier D (2008) Movement patterns of southern bell frogs (*Litoria raniformis*) in response to flooding. *Wildl Res* 35:50-58
- Wolff PJ, Taylor CA, Heske EJ, Schooley RL (2015) Habitat selection by American mink during summer is related to hotspots of crayfish prey. *Wildlife Biol* 21:9-17
- Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. *Science* 280:2126-2128
- Yamaguchi N, Rushton S, MacDonald DW (2003) Habitat preferences of feral American mink in the Upper Thames. *J Mammal* 84:1356-1373

Tables and Figures

Table 3.1 Habitat occupancy, colonization, and extinction dynamics of American mink (*Neovison vison*) in stream habitat in Illinois, USA, 2007-2012.

Year	No. sites	Naïve Ψ	Adjusted Ψ (SE)	Local γ	Local ε
2007	90	0.3556	0.4382 (0.0643)	-	-
2008	90	0.8889	0.9029 (0.0317)	49	1
2009	58	0.8772	0.8897 (0.0396)	3	3
2010	60	0.8167	0.8253 (0.0499)	6	7
2011	58	0.6552	0.6703 (0.0624)	3	14
2012	60	0.5500	0.5574 (0.0652)	8	13

Naïve Ψ = raw estimate of site occupancy by mink (number of sites where sign detected/total number of sites surveyed); Adjusted Ψ = estimate of site occupancy by mink after controlling for detection probability; Local γ = number of sites colonized; Local ε = number of sites that went locally extinct.

Table 3.2 Model selection statistics for detection, initial occupancy, colonization and extinction of American mink (*Neovison vison*) at stream sites in Illinois, USA, 2007-2012.

Rate Parameter	Model	ΔAIC_c	ω	$-2l$	K
Detection ₂₀₀₇₋₂₀₁₂	Observer + Sandbar	0.00	0.22	1278.79	10
	Observer + Sandbar + Date	0.14	0.21	1276.93	11
	Observer + Sandbar + Rain	0.26	0.20	1277.05	11
	Observer + Sandbar + Rain + Date	0.75	0.15	1275.54	12
	<i>Intercept Only</i>	40.80	0.00	1331.59	4
Occupancy ₂₀₀₇	Dist + Depth	0.00	0.32	1265.37	14
	Depth	0.38	0.26	1267.75	13
	Depth + Urban	1.09	0.18	1266.46	14
	Dist + Depth + Urban	1.39	0.16	1264.76	15
	<i>Intercept Only</i>	6.17	0.01	1275.54	12
Colonization ₂₀₀₈₋₂₀₁₂	Dist + Muskrat	0.00	0.23	1237.47	16
	Dist + Depth	0.02	0.23	1237.49	16
	Dist + Depth + Urban	0.16	0.21	1235.63	17
	Depth + Urban	1.11	0.13	1238.58	16
	Dist + Muskrat + Dist x Muskrat	1.71	0.10	1237.18	17
	<i>Intercept Only</i>	23.90	0.00	1275.54	14
Extinction ₂₀₀₈₋₂₀₁₂	Dist + Muskrat + Dist x Muskrat	0.00	0.99	1215.32	20
	<i>Intercept Only</i>	14.31	0.00	1235.63	17

I present only models with $\Delta AIC_c < 2$ for each rate parameter along with the *Intercept Only* model. Covariates include: Observer = individual conducting survey; Sandbar = amount of trackable surface at stream site; Date = day of the year survey was conducted; Rain = amount

Table 3.2 (cont.)

of rain 7-days prior to survey; Dist = Euclidian distance to permanent wetland; Depth = average water depth at site; Urban = proportion of urban area surrounding site; Muskrat = model-averaged muskrat occupancy probability at site. ΔAIC_c = Difference in Akaike's information criterion values (corrected for small sample sizes) between model of interest and the model with lowest AIC_c value; ω = model weight; $-2l = -2(\text{Log Likelihood})$ of model; K = number of model parameters.

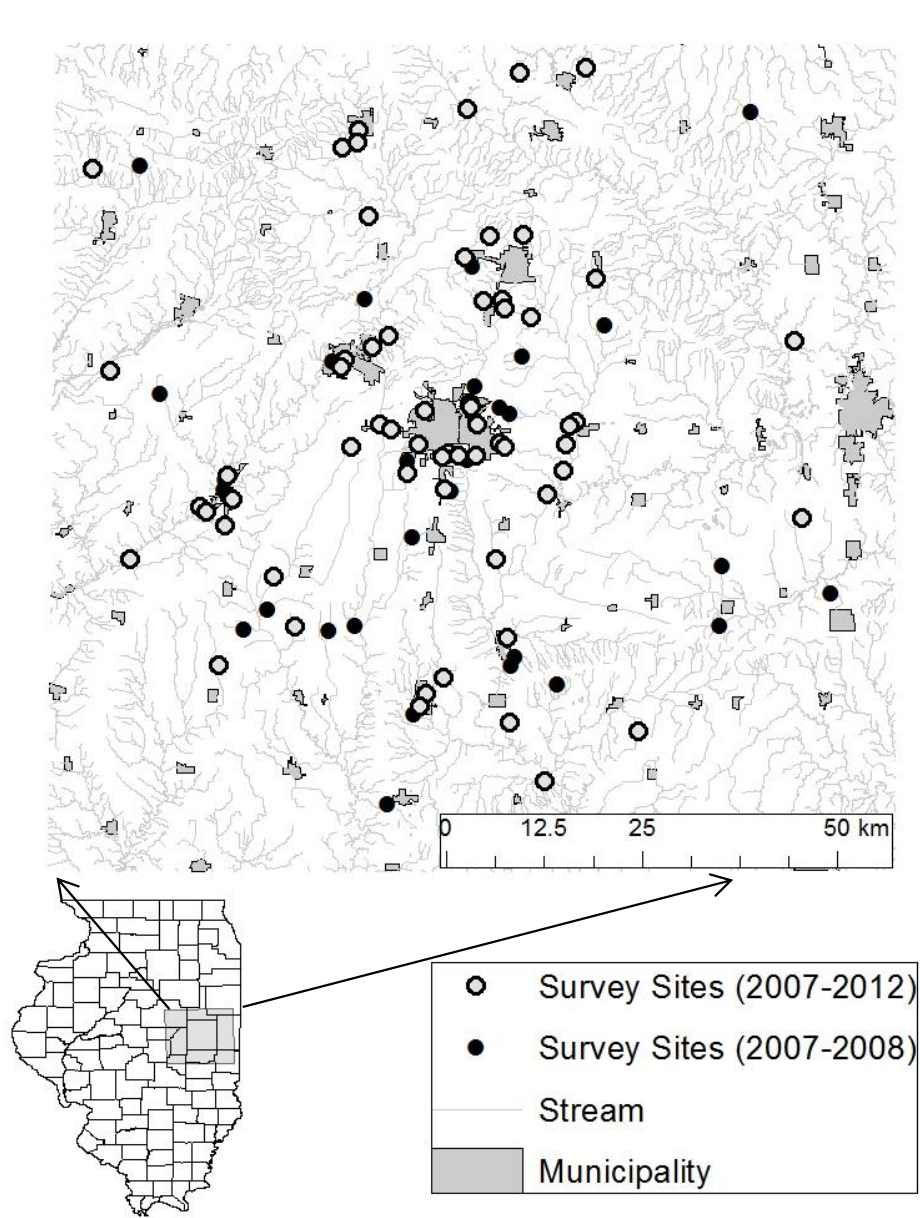


Fig. 3.1 Locations of stream survey sites ($n = 90$) for American mink (*Neovison vison*) and muskrat (*Ondatra zibethicus*) in Illinois, U.S.A. Sites represented 200-m stretches of stream that were sampled by using multiple walking surveys to determine mink and muskrat occupancy from 2007-2012.

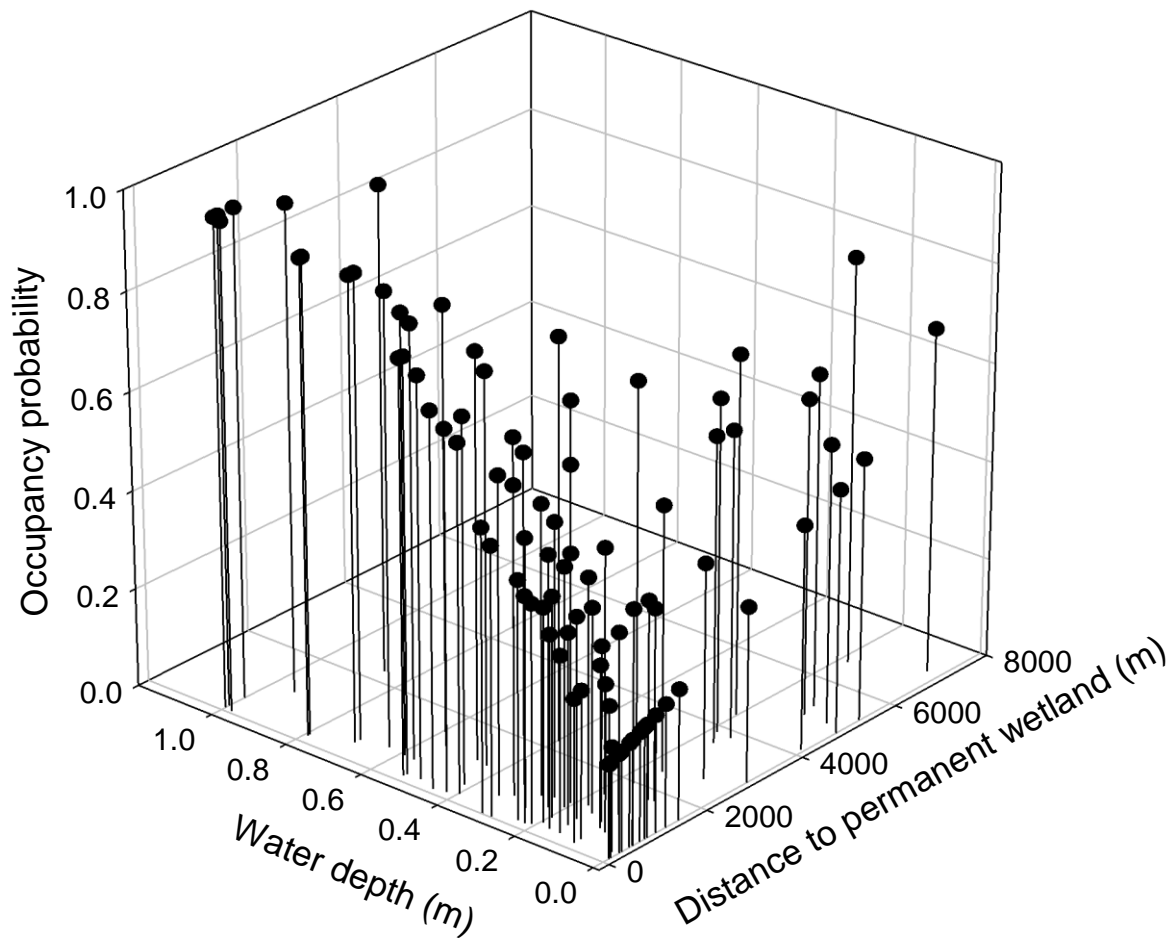


Fig. 3.2 Relationships between initial site occupancy by American mink (*Neovison vison*) and covariates from my most supported model (see Table 2). Initial occupancy was best explained by the positive effects of water depth and distance to a permanent wetland.

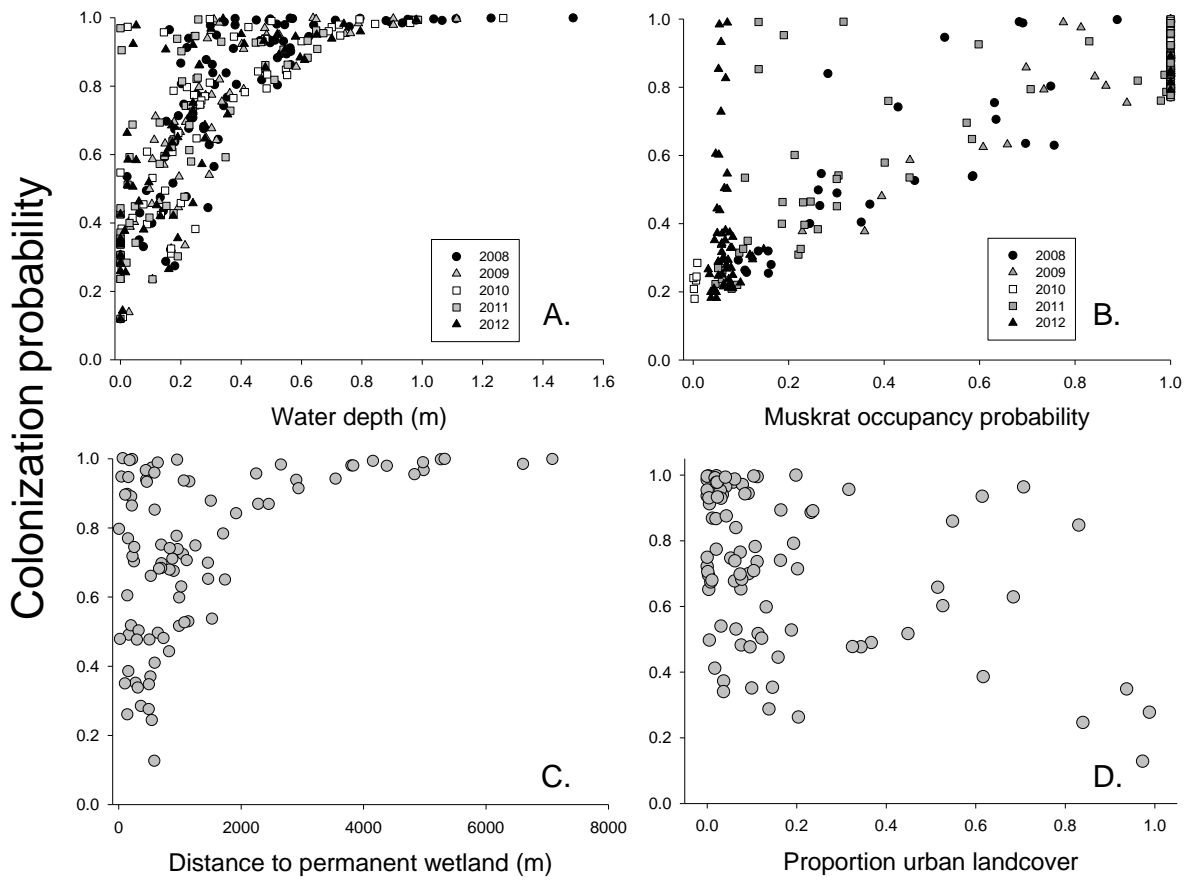


Fig. 3.3 Relationships between probability of site colonization by American mink (*Neovision vison*) and covariates from my most supported models (see Table 2). Site colonization was best explained by the positive effects of (A) water depth, (B) muskrat (*Ondatra zibethicus*) occupancy probability, and (C) distance to a permanent wetland; and the negative effects of (D) urbanization.

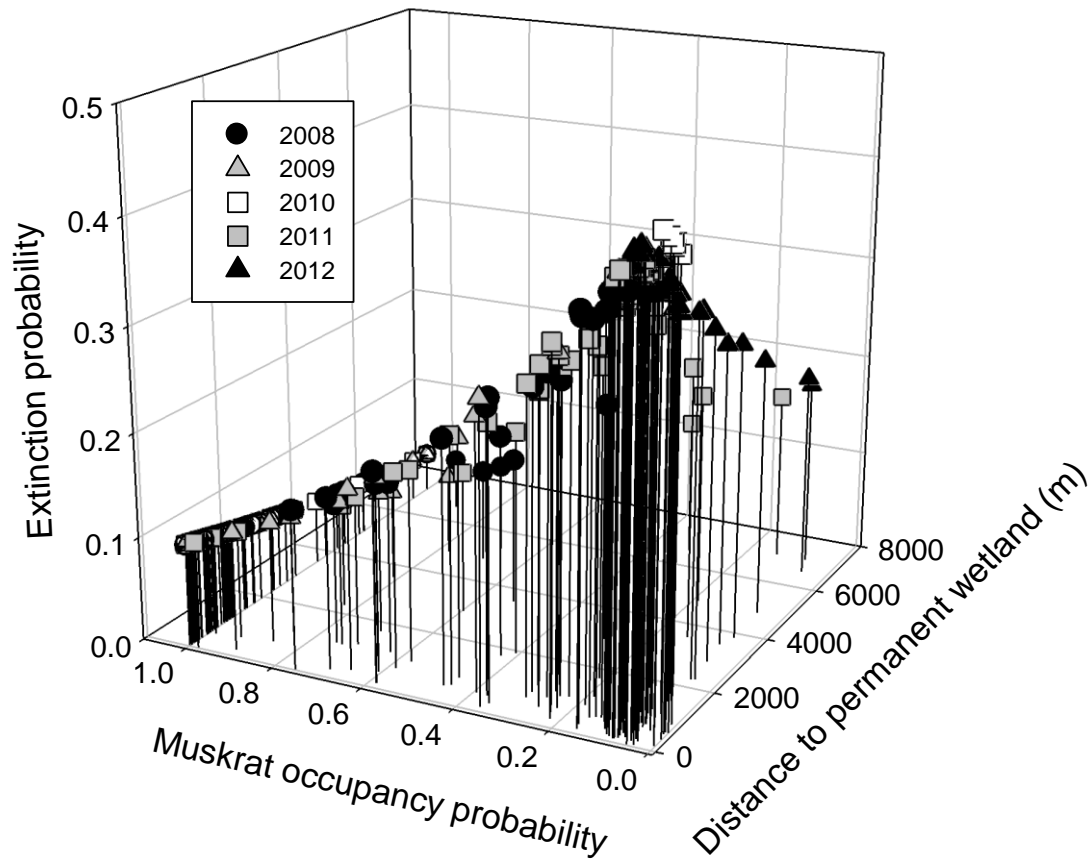


Fig. 3.4 Effects of muskrat (*Ondatra zibethicus*) occupancy and distance to permanent wetlands on extinction probability of American mink (*Neovison vison*) from stream sites in Illinois. Mink were less likely to abandon stream sites with a high probability of muskrat presence and sites farther from permanent wetlands.

CHAPTER 4

TERRESTRIAL HABITAT USE IS RISKY FOR AMERICAN MINK (*NEOVISON VISON*) IN A HIGHLY MODIFIED LANDSCAPE

Abstract

Anthropogenic landscape changes in the Midwest, USA have generated a novel set of mortality risks for species occurring there. Semiaquatic mammals in this region may have to move through terrestrial habitat to find supplementary resources or to increase mating opportunities. However, movements in terrestrial areas may expose individuals to increased predation risks or negative human interactions. I used habitat use and known-fate survival information to evaluate factors that could explain the degree of terrestrial habitat use for American mink (*Neovison vison*) in east-central Illinois, and determine mortality risk factors including the relative risk of using stream versus upland habitats. My results indicate that male mink are more likely to use terrestrial habitat than females. Male mink also had lower weekly survival rates than females. Weekly survival rates were lower during the mating season (February, March, and April) than in non-mating season and adult mink had higher weekly survival rates than subadult mink. By incorporating data on habitat use and known-fate mortality information, I show that mink using terrestrial habitat away from the stream edge are exposed to increased mortality risks in human-dominated landscapes. To my knowledge, this study is the first to empirically assess the relative mortality risk of a semiaquatic mammal using terrestrial habitat. Future studies should focus on elucidating the mechanistic understanding of maladaptive habitat selection by semiaquatic species in highly altered landscapes.

Introduction

Agricultural production and urbanization are important drivers of habitat loss and fragmentation and strongly contribute to biodiversity declines (McKinney 2002; Green et al. 2005; Hoffman et al. 2011). These landscape conversions are occurring at unprecedented rates predicted to outpace current conservation efforts (Seto et al. 2012; Wright and Wimberly 2013; Lark et al. 2015). Movements (Atwood et al. 2004; Prange et al. 2004; Šálek et al. 2015), densities (Prange et al. 2003), and survival (Gosselink et al. 2007; McCleery et al. 2008) of mammalian species may be affected by these anthropogenic alterations of the landscape. Carnivores are particularly sensitive to these habitat alterations due to their large area requirements. Crooks et al. (2011) found that for terrestrial carnivores, only ~54% of each species' geographic range included high-quality habitat.

Anthropogenic landscape changes can generate a novel set of mortality risks for species. For instance, increased road densities are linked with reduced survival of many carnivore species (Grilo et al. 2009; Snow et al. 2012). Vehicle collisions account for 9% of all mammal mortalities but 59% of all mortalities in areas of increasing human development (Collins and Kays 2011). Road-kill mortalities of most carnivores show seasonal patterns correlated with species' life-history traits (e.g., dispersal, mate searching; Grilo et al. 2009).

From an evolutionary perspective, habitat selection by individuals should infer maximum fitness benefits (Morris 2003). In rapidly changing landscapes, however, imperfect perceptual cues may result in maladaptive habitat selection generating ecological traps (Battin 2004; Robertson and Hutto 2006) or perceptual traps (Gilroy and Sutherland 2007, Patten and Kelly 2010). Additionally, imperfect spatial awareness of remaining high-quality habitats may prevent individuals from freely selecting habitats that maximize fitness benefits (Lima and Zollner

1996). Thus, detailed information on habitat selection and resulting fitness consequences are needed to inform efforts to conserve biodiversity in changing landscapes (Gilroy and Sutherland 2007; Fischer et al. 2015).

Integrating space-use patterns with mortality risk information may provide insight into how resource selection scales up to the abundance or persistence of species (McLoughlin et al. 2005; DeCesare et al. 2014). In particular, researchers have identified risky habitats by using resource selection and habitat-specific mortality data in concert (Falcucci et al. 2009; DeCesare et al. 2014). For instance, McLoughlin et al. (2005) demonstrated that habitat-specific predation mortalities were different than habitat selection for woodland caribou (*Rangifer tarandus caribou*). Likewise, Falcucci et al. (2009) found high-quality habitat for Apennine brown bears (*Ursus arctos marsicanus*) could only be identified effectively when integrating habitat use and mortality data.

The Grand Prairie ecoregion (Omernik 1987) is one of the most highly altered landscapes in the United States (Urban 2005). For instance, in Champaign County, Illinois, 85% of the landscape is converted to row-crop agriculture and ~98% of historical wetlands have been drained (Suloway and Hubbell 1994; McCauley and Jenkins 2005). Prior to this widespread drainage, wetland-dependent species had a high probability (>50%) of encountering another wetland within 260 m of their focal wetland (McCauley and Jenkins 2005). At present, however, most available habitat for semiaquatic species is located along small streams and agricultural ditches. Crops are typically planted close to the stream edges reducing the extent of the natural riparian zones (Ahlers et al. 2010). Increased human presence (e.g., roads, farms, urban sprawl) also has enhanced the likelihood of negative wildlife-human interactions.

American mink (*Neovison vison*) are semiaquatic carnivores that occur along riparian areas in the Midwest, USA (Schooley et al. 2012; Wolff et al. 2015; Ahlers et al. In Press). Mink are native to and widespread across North America (Larivière 1999) and considered a destructive invasive species in Europe, South America, and Asia (Bonesi and Palazon 2007; Fasola et al. 2011). We have a surprisingly limited understanding of how landscape change affects mink populations in their native range. In this region, mink occurring in riparian habitat must make habitat selection decisions including whether to use supplementary resources (e.g., permanent wetlands) in terrestrial areas that often are isolated by agriculture and urban development. Moreover, coyote (*Canis latrans*) populations have rapidly expanded (Gosselink et al. 2007), increasing the potential for intraguild predation when mink move through terrestrial areas. Thus, mortality risk may be disproportionate for mink when using terrestrial habitat due to heightened risk factors (Ahlers et al. In Press).

My objectives were to assess factors that could explain the degree of terrestrial habitat use by mink, and to distinguish the relative risk of using stream versus upland habitats. Regarding terrestrial habitat use, because male mink have larger home ranges than females (Zschille et al. 2012; Melero et al. 2014), and larger home ranges of males may reflect searching for mates as well as foraging, I expected males to use proportionally more upland habitat than females. I also predicted greater use of upland habitat during the mating season. Because larger streams typically have deeper water that should support greater prey resources for mink (Ahlers et al. In Press), I predicted individuals occurring in larger streams would use terrestrial habitat less often. I also assessed the effects of access to supplementary habitats (permanent wetlands) on the extent of terrestrial habitat use by mink. I predicted a negative relationship between terrestrial habitat use and distance from home ranges within streams to permanent wetlands.

Regarding survival, if use of upland habitat imposes greater exposure of mink to mortality factors such as intraguild predation, vehicular collisions, and negative interactions with humans, survival rates should be lower for mink when using these areas. Intraspecific competition and extended range use are common for mink during the mating season (Zschille et al. 2012), so I expected lower survival rates during this time. I expected that males would experience greater costs associated with maintaining territories and competing for mates, and predicted that males would have lower survival rates than females. Information regarding age-specific survival of mink is lacking. However, I expected younger mink would experience greater costs associated with establishing territories (e.g., inferior competitors and imperfect spatial awareness of resources) and predicted subadult mink would have lower survival rates than adult mink. I evaluated these predictions by integrating location and mortality data from radiomarked mink occurring primarily in stream habitats in a highly altered ecosystem.

Methods

Study Area. – My study area (~72,000 ha) was embedded in Champaign County, Illinois, USA (Fig. 4.1), which is relatively flat (~70 m elevation relief), and dominated by row-crop agriculture (85%) and urban development (6%). Champaign County has a humid continental climate with wide-ranging seasonal temperatures (-8.5°C – 30.0°C) and moderate annual rainfall (\bar{x} = 104 cm) and snowfall (\bar{x} = 67 cm). Prior to human settlement, wetlands covered 40-61% of the landscape (McCauley and Jenkins 2005). Extensive tile drainage and agricultural expansion, however, have reduced wetland coverage to ~0.9% (Suloway and Hubbell 1994; McCauley and Jenkins 2005). Subsurface tiles drain most of the landscape (52-82%; David et al. 2010) to support corn (*Zea mays*; 45%) and soybean (*Glycine max*; 40%) production. Consequently,

small streams and agricultural ditches represented the majority of available habitat for mink. Riparian zone widths along streams were relatively narrow (mean = 43 m, Cotner and Schooley 2011). This region had a 23.2% growth in the human population from 1970-2010 (163,281 to 201,081), with most growth occurring in urban areas. Additionally, there were 4452 km of road systems in my study area (interstate = 125 km, state highway systems = 340 km, local highway systems = 3987 km). To my knowledge, there were no commercial mink farms within my study area. Additionally, recreational mink trapping was rare.

Capture and radiomarking. – I focused my trapping effort in streams and ditches ranging from 1st – 5th order in size. Mink were live-trapped using collapsible single- and double-door Tomahawk traps (models 200 and 202; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) from November 2009 to May 2012. Traps were affixed to floating platforms constructed of a 25-mm polystyrene filling (122 cm x 610 mm) sandwiched between two pieces of 6-mm plywood (Reynolds et al. 2004; Schooley et al. 2012). I covered traps with a 3-panel plywood tunnel (each panel = 6 mm x 610 mm x 239 mm) or natural vegetation from the stream edge. Platforms were tethered in place by a 5-m rope attached to a stake, tree, or fencepost along the stream edge. I baited traps with sardines or canned salmon and checked traps daily. Trap success was low for this elusive carnivore, so I focused trapping effort in areas with abundant mink sign to increase capture probability.

I immediately transported captured mink to a sterile surgical suite at the University of Illinois College Of Veterinary Medicine. Mink were weighed and then premedicated with atropine (0.20 mg/kg), dexmedetomidine (0.25 mg/kg), and butorphanol (0.30 mg/kg) prior to surgery. I administered isoflurane (5% for induction and maintained between 1-3% throughout procedure)

while simultaneously maintaining oxygen (0.60-1.00 l/min) via facemask to induce surgical anesthesia. Once individuals were anesthetized, I conducted a thorough physical examination and determined sex and age class (subadult or adult). I aseptically prepared healthy mink for surgery and implanted either a sterile 14-g (for mink weighing < 500g) or 23-g (for mink \geq 500 g) internal radio transmitter (Models 1215 and 1230; Advanced Telemetry Systems, Insanti, Minnesota, USA) into the peritoneal cavity. Transmitters were equipped with a mortality sensor that increased pulse rates when inactive for \geq 8 hrs. Prior to recovery, I subcutaneously implanted a unique passive integrated transponder (PIT) tag between the scapulae (Schooley et al. 1993). I then administered atipamazole (2.50 mg/kg; reverse sedative effects) and meloxicam (0.20 mg/kg; post-operative analgesic). Additionally, I administered penicillin (0.10 ml) to limit post-operative infections. I monitored recovering animals for approximately 2 hours after they gained all righting reflexes and returned them to the site of capture. All capture and handling techniques were approved by the Illinois Animal Care and Use Committee (protocol # 12190) and covered under the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Tracking habitat use and survival. – I initially determined an individual's general location with a vehicle-mounted unidirectional antennae and receiver (model R410; Advanced Telemetry Systems). Generally, because of steep bank slopes and deep burrows along the stream edge, signal detection was difficult when mink were >500 m from the receiver. Once the signal was located, I used a three-element Yagi antenna to determine mink locations by using combinations of triangulation (when mink were active) and homing (when mink were inactive). A pre-study experiment using above- and below-ground transmitters ($n = 10$) revealed triangulation error was small (mean = 16.6 m; SD = 14.3). I recorded locations (Universal Transverse Mercator

coordinates) with a hand-held global positioning system unit (model GPS 76; Garmin International, Olathe, Kansas, USA) once satellite error was < 6 m. I distributed my radotracking efforts across diurnal, crepuscular, and nocturnal hours and attempted to relocate mink at least once per week.

Predicting terrestrial habitat use. – I used generalized linear models (PROC GENMOD; SAS Institute Inc. 2013), and an information-theoretic approach (Burnham and Anderson 2002; Arnold 2010), to investigate several hypotheses regarding the extent to which mink use terrestrial habitat away from the stream edge. I only included individuals with ≥ 25 locations for this analysis. The extent of terrestrial habitat use for each individual was measured as the proportion of total locations occurring >50 m from the stream edge. This is a plausible distance threshold as the average width of riparian zones (area of vegetation between the stream edge and adjacent human-modified area) was 43 m.

Most mink movements were restricted to the stream edge (Ahlers et al. 2015) and commonly used home-range estimators can be inappropriate measures of space use for species occurring in these linear areas (Blundell et al. 2011; Downs and Horner 2008). Instead, measuring the linear extent of animal locations is a widely accepted way to quantify space use within these linear habitats (Melero et al. 2008; Ahlers et al. 2010; Melero et al. 2014). I measured the extent of each individual's linear home range as the meandering stream length between the most upstream and downstream locations. I tested for differences in home range size between sexes using a Kruskal-Wallis Test.

I assessed the importance of sex, age (subadult or adult), stream order (StrmOrder; Strahler 1957), distance to nearest permanent wetland (DistWetland), and proportion of individual mink

locations occurring within the breeding season (Season) for predicting terrestrial habitat use by mink. The distance to permanent wetlands is an important predictor of site occupancy for mink occurring in riparian habitat as these areas can provide supplementary prey resources (Ahlers et al. unpublished data). For each individual, I measured DistWetland as the shortest Euclidian distance from the stream edge within the extent of their home range to the nearest permanent wetland (mean = 407 m, range = 15 – 1717 m). Mink can extend their space use during the breeding season (Zschille et al. 2012) and may use terrestrial habitat more often during this time. I calculated the proportion of radiolocations recorded during the breeding season (February - April) for each individual (Season).

Prior to analysis, I used a logit transformation of my response variable, proportion of locations occurring >50 m from the stream edge, to meet linear model assumptions (Warton and Hui 2011). I considered 14 models that reflected combinations of the single or additive effects of my measured covariates along with the null model. I estimated the goodness-of-fit for my top model using a pseudo R^2 ($1 - [\text{deviance of model of interest} / \text{deviance of null model}]$).

Survival and mortality risk analysis. – I used known-fate models in Program MARK (White and Burnham 1999) to derive weekly survival estimates of mink. Survival was estimated over the study duration (4 November 2009 – 30 July 2014) and included 250 weekly encounter intervals. Mink were added to the study when they were marked (staggered entry) and monitored until mortality or signal failure. Individuals were right-censored if I could not relocate the transmitter signal (e.g., transmitter failure, emigration). I used a logit-link function to express survival probabilities as a linear function of my modeled covariates (Cooch and White 2008).

I developed a candidate set of 13 models to test hypotheses that related variation in mink survival to season (breeding or non-breeding; Season), sex, age, and degree of terrestrial habitat use (THU). My two seasons were based on when males are actively searching for females (February - April; Mitchell 1961; Larivière 1999). To assess the effects of terrestrial habitat use on survival, I developed an individual time-varying covariate (Cooch and White 2008) that represented if a mink was located (1) or not located (0) more than 50 m from the stream edge at least once during each weekly interval. I considered models that contained single effects and various additive combinations of my measured covariates and compared these to a null model. I ranked models by descending ΔAIC_c scores and used an information-theoretic approach to inform model selection (Burnham and Anderson 2002; Arnold 2010).

To assess how terrestrial habitat use may impact mortality risk of mink at a finer spatial resolution, I developed a metric of relative mortality risk that relates the spatial distribution of mink mortality events, relative to mink habitat use, to distance away from the stream edge (similar to Ford et al. 2014). This approach is analogous to resource selection methods that focus on habitat use-availability ratios. I established 6 classes representing Euclidian distances from the stream edge (0 – 50 m; 51 – 100 m; 101 – 200 m; 201 – 300 m; 301 – 400 m; 401 – 500+ m). I estimated the relative mortality risk in each distance class as the ratio of the proportion of mortality events ($n = 17$) and proportion of live encounters ($n = 2035$). For any given distance, a ratio of 1.00 implies that the proportion of observed mortality events is that expected given the level of habitat use at that distance. Ratios > 1.00 indicate relatively risky habitats because the proportion of mortality events is greater than expected given habitat use. Conversely, ratios < 1.00 imply less risky habitat as mortality events are less than expected.

Results

I live-captured 37 mink from November 2009 to April 2013. However, I did not fit transmitters on three mink (one lactating female and two deemed unfit for surgery). Thus, I surgically implanted transmitters in and monitored 34 mink (26 males, 8 females; 22 adults, 12 subadults). Sixty five percent of males ($n = 17$) and 63% of females ($n = 5$) were adults. Seventeen mink were right-censored as they outlasted the battery life of their transmitters or were never relocated.

Of 34 radiomarked mink, 20 were relocated ≥ 25 times (13 males, 7 females) and included in my analyses of space use. I recorded 2035 locations with an average of 102 locations (SE = 10.27) per individual. Male home ranges (mean = 4.36 km, SE = 0.86) were longer than female home ranges (mean = 1.35 km, SE = 0.16; $\chi^2 = 10.30$, DF = 1, $P = 0.001$). Average linear home range of both sexes combined was 3.30 km (SE = 0.64).

Mink were mostly relocated within 50 m of the stream edge (mean proportion of locations = 0.85, SE = 0.05), but they also used terrestrial habitat further away (mean proportion of locations = 0.15, SE = 0.05). My top model (Table 4.1; $R^2 = 0.31$) indicated that male mink were much more likely than females to use terrestrial habitat (Fig. 4.2). The proportion of locations occurring > 50 m from the stream edge was higher for males (mean = 0.22, SE = 0.07) than for females (mean = 0.02, SE = 0.01). The only other competitive model (Sex + StrmOrder; Table 4.1) also indicated that mink occurring in larger streams were less likely to use terrestrial habitat. However, the addition of StrmOrder did little to improve model fit and is likely uninformative (Arnold 2010).

My two most competitive models ($\Delta AIC_c < 2.00$) for explaining variation in mink survival indicated that THU, Season, Age, and Sex were all important risk factors (Table 4.2). Survival of

mink was related negatively to terrestrial habitat use. Weekly survival rates were 0.0053 higher (95% CI = 0.0009 – 0.0327) for mink that remained within 50 m of the stream edge compared to those who used habitat > 50 m away from the stream. Additionally, estimated weekly survival rates were 0.1843 higher (95% CI = 0.0404 – 0.8408) for mink during the non-breeding season compared to the breeding season. Weekly survival rates also were higher for females (0.9861, SE = 0.0098) than for males (0.9573, SE = 0.0108), and higher for adults (0.9992, SE = 0.0011) than for subadults (0.9934, SE = 0.0059). Relative mortality risk increased with distance from the stream edge, and was greater than expected when using habitat > 50 m from the stream edge (Fig. 4.3).

Discussion

Species occurring in highly modified environments are faced with novel and changing mortality risks. Biodiversity conservation in these areas requires knowledge of how factors associated with altered landscapes affect fitness of individuals and population persistence (Gilroy and Sutherland 2007; Fischer et al. 2015). I show that incorporating data on habitat use and known-fate mortality is a powerful approach for identifying risky habitats, which is consistent with other studies (McLoughlin et al. 2005; Falcucci et al. 2009; DeCesare et al. 2014; Ford et al. 2014). My results demonstrate that semiaquatic mink that use terrestrial habitat away from the stream edge are exposed to elevated mortality risks. Moreover, I documented reduced survival during the breeding season, and significant age- and sex-specific variation in mink survival rates. Male mink were more likely to use terrestrial habitat than females, which is likely due to establishment and maintenance of larger territories and greater movements during the breeding season.

My results strongly demonstrate that terrestrial habitat exposes mink to higher-than-expected levels of mortality risk (Fig. 4.3). Increased mortality risks in these areas are likely related to widespread agricultural production and urban development in the region. Ahlers et al. (In Press) attributed 58% of known mink mortalities ($n = 17$) to negative interactions with humans (roadkill = 41%, poisoning = 17%) and 35% to depredation by coyotes. Increased road densities in human-modified areas have been linked with reduced survival of many carnivores (Grilo et al. 2009). For instance, vehicle collisions account for 49% of mortalities of Eurasian badgers (*Meles meles*; Clarke et al. 1998) and are a significant source of mortality for Iberian lynx (*Felis pardina*; Ferreras et al. 1992) and Florida panthers (*Puma concolor coryi*; Taylor et al. 2002). Secondary poisoning of carnivores also is common in agricultural and urban landscapes (Fournier-Chambrillon et al. 2004; Cypher et al. 2014). For instance, an extensive survey of semiaquatic carnivores in France found anticoagulant rodenticides in 13% of all mustelids sampled (Fournier-Chambrillon et al. 2004).

Widespread wetland-drainage practices have drastically changed the environment for semiaquatic species. Historically, the terrestrial matrix in my study area likely consisted of tallgrass prairie and wetland habitats were abundant and less isolated (McCauley and Jenkins 2005; Urban 2005). Mink were less likely to encounter roads, urban areas, row-crop agriculture, or farmsteads when moving among wetland habitats. Coyotes also have become abundant only in recent decades. Thus, the negative effect of terrestrial habitat use on mink survival was probably not as strong in these unaltered landscapes. The rapid rate of landscape change in the Grand Prairie region may have created an evolutionary lag so that mink have yet to recognize these terrestrial areas have become risky habitats (Remeš 2000). Alternatively, mink may knowingly assume the high mortality risk because movements in these habitats are necessary

when prey is limited in stream habitat, territorial behavior prohibits free habitat selection, or to increase mating opportunities. In either case, climate change is likely to increase precipitation variability (including floods and droughts) and force mink to leave stream habitats and use risky terrestrial habitat more often in the future (Ahlers et al. In Press).

Survival rates of mink were lower during the breeding season and varied with sex and age. Male mink substantially increase their range during the breeding season (Zschihlle et al. 2012) to search for mates and are likely encountering roads and predators in unfamiliar areas. Coyotes are the apex predator in this region (Gosselink et al. 2007) and a substantial mortality risk for mink (Ahlers et al. In Press). During the breeding season (February - April), crop fields are fallow leaving virtually no cover in upland areas. Mink moving through these areas are likely visible to coyotes and at increased risk of intraguild predation. While searching for mates, males may allocate less time to antipredator vigilance and foraging to maximize reproductive success (Wolff and Van Horn 2003) resulting in increased mortality risk. Subadult mink likely encounter unfamiliar areas while trying to establish a new home range. It is likely subadult mink have imperfect knowledge of available resources within these areas and are engaging in behavioral trade-offs that reduce anti-predator vigilance to maximize prey searching. These trade-offs may result in reduced survival rates for younger mink.

I acknowledge there is one large caveat associated with my interpretation of how risky terrestrial habitats are to mink. My study was conducted in one of the most highly altered agricultural regions within the geographic distribution of American mink. Thus, in more heterogeneous landscapes, the negative effects of terrestrial habitat use on survival of mink (and other semiaquatic mammals) may not be as strong.

As expected, my results revealed that male mink have larger linear home ranges than females and are more likely to use terrestrial habitat away from the stream edge. Nearly all studies of mink space use report males have larger home ranges than females (Yamaguchi and Macdonald 2003; Zschihlle et al. 2012; Melero et al. 2014), which likely reflects the increased metabolic demands of larger body size or the distribution of female mink (Powell 1994). Increased population densities and territorial defense in restricted linear habitats may drive despotic distributions resulting in non-free habitat selection (Fretwell 1972) as larger males outcompete smaller males for territories along the stream edge. Conversely, limited prey resources in variable stream habitats may force trade-offs between the greater metabolic needs of male mink and use of riskier terrestrial habitats (Lima and Dill 1990). Unfortunately, I do not have information on relative mink abundances or availability of prey resources in my study area and cannot directly address these questions.

To my knowledge, this is the first study to empirically assess the relative mortality risk for use of terrestrial habitats by semiaquatic mammals. Moreover, this research represents the most extensive study of movements and survival of American mink in their native range. Future research should evaluate whether use of risky terrestrial habitat by semiaquatic mammals is maladaptive habitat selection resulting from imperfect spatial knowledge, or a necessary consequence of limited local resources, mating strategies, and natal dispersal in these patchy and highly altered landscapes.

Chapter 4 meets the formatting requirements of *Journal of Mammalogy*

Literature Cited

- AHLERS, A.A., E.J. HESKE, AND R.L. SCHOOLEY. Prey distribution, context, and potential landscape supplementation affect occupancy dynamics of American mink in streams. *Landscape Ecology (In Review)*.
- AHLERS, A.A., E.J. HESKE, R.L. SCHOOLEY, AND M.A. MITCHELL. 2010. Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats. *Wildlife Biology* 16: 400-408.
- AHLERS, A.A., M.A. MITCHEL, J.P. DUBEY, R.L. SCHOOLEY, AND E.J. HESKE. 2015. Risk factors for *Toxoplasma gondii* exposure in semiaquatic mammals in a freshwater ecosystem. *Journal of Wildlife Diseases* 51: 488-492.
- AHLERS, A.A., L.A. COTNER, P.J. WOLFF, M.A. MITCHELL, E.J. HESKE, AND R.L. SCHOOLEY. 2015. Summer precipitation predicts spatial distributions of semiaquatic mammals. *PLoS One*: In Press.
- ARNOLD, T.A. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74: 1175-1178.
- ATWOOD, T.C., H.P. WEEKS, AND T.M. GEHRING. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. *Journal of Wildlife Management* 68: 1000-1009.
- BATTIN, J. 2004. When good animals love bad habitats: ecological traps and conservation of animal populations. *Conservation Biology* 18: 1482-1491.
- BLUNDELL, G.M., J.A.K. MAIER, AND E.M. DEBEVEC. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71: 469-489.

- BONESI, L., AND S. PALAZON. 2007. The American mink in Europe: Status, impacts, and control. *Biological Conservation* 134: 470-483.
- BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Ed. Springer-Verlag, New York, New York, USA.
- CLARKE, G.P., P.C.L. WHITE, AND S. HARRIS. 1998. Effects of roads on badger *Meles* populations in south-west England. *Biological Conservation* 86: 117-124.
- COLLINS, C., AND R. KAYS. 2011. Causes of mortality in North American populations of large and medium-sized mammals. *Animal Conservation* 14: 474-483.
- COOCH E, AND G. WHITE. 2008. Program MARK: a gentle introduction. 6th ed. Available from <http://www.phidot.org/software/mark/docs/book/> [Accessed 19 May 2015]
- COTNER, L.A., AND R.L. SCHOOLEY. 2011. Habitat occupancy by riparian muskrats reveals tolerance to urbanization and invasive vegetation. *Journal of Wildlife Management* 75: 1637-1645.
- CROOKS, K.R., C.L. BURDETT, D.M. THEOBALD, C. RONDINNI, AND L. BOITANI. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B – Biological Sciences* 366: 2642-2651.
- CYPHER, B.L., S.C. McMILLIN, T.L. WESTALL, C. VAN HORN JOB, R.C. HOSEA, B.J. FINLAYSON, AND E.C. KELLY. 2014. Rodenticide exposure among endangered kit foxes relative to habitat use in an urban landscape. *Cities and the Environment* 17: Article 8.
- DAVID, M.B., L.E. DRINKWATER, AND G.F. MCISAAC. 2010. Sources of nitrate yield in the Mississippi river basin. *Journal of Environmental Quality* 39: 1657-1667.

- DECESARE, N.J., M. HEBBLEWHITE, M. BRADLEY, D. HERVIEUX, L. NEUFELD, AND M. MUSIANI. 2014. Linking habitat selection and predation risk to spatial variation in survival. *Journal of Applied Ecology* 83: 343-352.
- DOWNS, J.A., AND M.W. HORNER. 2008. Effects of point pattern shape on home-range estimates. *Journal of Wildlife Management* 72: 1813-1818.
- FALCUCCI, A., P. CIUCCI, L. MAIORANO, L. GENTILE, AND L. BOITANI. 2009. Assessing habitat quality for conservation using an integrated occurrence-mortality model. *Journal of Applied Ecology* 46: 600-609.
- FASOLA, L., J. MUZIO, C. CHEHEBAR, M. CASSINI, AND D.W. MACDONALD. 2011. Range expansion and prey use of American mink in Argentinean Patagonia: dilemmas for conservation. *European Journal of Wildlife Research* 57: 283-294.
- FERRARAS, P., J.J. ALDAMA, J.F. BELTRÁN, AND M. DELIBES. 1992. Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck 1824. *Biological Conservation* 61: 197-202.
- FISCHER, J.D., S.C. SCHNEIDER, A.A. AHLERS, AND J.R. MILLER. 2015. Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*. In Press.
- FORD, A.T., J.R. GOHEEN, T.O.O. OTIENO, L. BINDER, L.A. ISBELL, T.M. PALMER, D. WARD, R. WOODROFFE, AND R.M. PRINGLE. 2014. Large carnivores make savanna tree communities less thorny. *Science* 346: 346-349.
- FOURNIER-CHAMBRILLON, C., P.J. BERNY, O. COIFFIER, P. BARBEDIENNE, B. DASSE, G. DELAS, H. GALINEAU, A. MARZET, P. POUZENC, R. ROSOUX, AND P. FOURNIER. 2004. Evidence of secondary poisoning of free ranging riparian mustelids by anticoagulant rodenticides in

- France: implications for conservation of European mink (*Mustela lutreola*). *Journal of Wildlife Diseases* 40: 688-695.
- FRETWELL, S.D. 1972. *Populations in seasonal environments*. Princeton University Press, Princeton, NJ.
- GILROY, J.J., AND W.J. SUTHERLAND. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology and Evolution* 22: 351-356.
- GREEN, R.E., S.J. CORNELL, J.P.W. SCHARLEMANN, AND A. BALMFORD. 2005. Farming and the fate of wild nature. *Science* 307: 550-555.
- GOSSELINK, T.E., T.R. VAN DEELEN, R.E. WARNER, AND P.C. MANKIN. 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. *Journal of Wildlife Management* 71: 1862-1873.
- GRILO, C., J.A. BISSONETTE, AND M. SANTOS-REIS. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. *Biological Conservation* 142: 301-313.
- HOFFMAN, M., ET AL. 2011. The changing fates of the world's mammals. *Philosophical Transactions of the Royal Society B – Biological Sciences* 366: 2598-2610.
- LARIVIÈRE, S. 1999. *Mustela vison*. *Mammalian Species* 608: 1-9.
- LARK, T.J., J.M. SALMON, AND H.K. GIBBS. 2015. Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environmental Research Letters* 10: doi:10.1088/1748-9326/10/4/044003.
- LIMA, S.L., AND L.M. DILL. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.

- LIMA, S.L., AND P.A. ZOLLNER. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11: 131-135.
- MCCAULEY, L.A., AND D.G. JENKINS. 2005. GIS-Based estimates of former and current depressional wetlands in an agricultural landscape. *Ecological Applications* 15: 1199-1208.
- McKINNEY, M.L. 2002. Urbanization, biodiversity, and conservation. *Bioscience* 52: 883-890.
- MCCLEERY, R.A., R.R. LOPEZ, N.J. SILVY, AND D.L. GALLANT. 2008. Fox squirrel survival in urban and rural environments. *Journal of Wildlife Management* 72: 133-137.
- McLOUGHLIN, P.D., J.S. DUNFORD, AND S. BOUTIN. 2005. Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology* 74: 701-707.
- MELERO, Y., S. PALAZÓN, E. REVILLA, J. MARTELO, AND J. GOSÁLBEZ. 2008. Space use and habitat preferences of the invasive American mink (*Mustela vison*) in a Mediterranean area. *European Journal of Wildlife Research* 54: 609-617.
- MELERO, Y., S. PALAZÓN, AND X. LAMBIN. 2014. Invasive crayfish reduce food limitation of alien American mink and increase their resilience to control. *Oecologia* 174:427-434.
- MORRIS, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136: 1-13.
- OMERNIK, J.M. 1987. Ecoregions of the conterminous united states. *Annals of the Association of American Geographers* 77: 118-125.
- PATTEN, M.A., AND J.F. KELLY. 2010. Habitat selection and the perceptual trap. *Ecological Applications* 20: 2148-2156.
- POWELL, R.A. 1994. Structure and spacing of *Martes* populations. In: Martens, sables and fishers, biology and conservation. Cornell University Press, London, UK.

- PRANGE, S., S.D. GEHRT, AND E.P. WIGGERS. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. *Journal of Wildlife Management* 67: 324-333.
- PRANGE, S., S.D. GEHRT, AND E.P. WIGGERS. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *Journal of Mammalogy* 85: 483-490.
- REMEŠ, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? *Oikos* 91: 579-582.
- REYNOLDS, J.C., M.J. SHORT, AND R.J. LEIGH. 2004. Development of population control strategies for mink *Mustela vison*, using floating rafts as monitors and trap sites. *Biological Conservation*. 120: 533-543.
- ROBERTSON, B.A., AND R.L. HUTTO. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87: 1075-1085.
- ŠÁLEK, M., L. DRAHNÍKOVÁ, AND E. TKADLEC. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Review* 45:1-14.
- SAS INSTITUTE INC. 2013. SAS® 9.4 – SAS Institute Inc., Cary, North Carolina, USA.
- SCHTICKZELLE, N., G. MENNECHEZ, AND M. BAGUETTE. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87: 1057-1065.
- SCHOOLEY, R.L., B. VAN HORNE, AND K.P. BURNHAM. 1993. Passive integrated transponders for marking free-ranging Townsend's ground squirrels. *Journal of Mammalogy* 74: 480-484.
- SCHOOLEY, R. L., L.A. COTNER, A.A. AHLERS, E.J. HESKE, AND J.M. LEVENGOOD. 2012. Monitoring site occupancy for American mink in its native range. *Journal of Wildlife Management* 76: 824-831.

- SETO, K.C., B. GÜNERALP, AND L.R. HUTYRA. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences* 109: 16083-16088.
- SIKES, R.S., W.L. GANNON, AND ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of mammalogist for the use of wild mammals in research. *Journal of Mammalogy* 92: 235-253.
- SNOW, N.P., W.F. ANDELT, T.R. STANLEY, J.R. RESNIK, AND L. MUNSON. 2012. Effects of roads on survival of San Clemente Island foxes. *Journal of Wildlife Management* 76: 243-252.
- STRAHLER, A.N. 1957. Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union* 38: 913-920.
- SULOWAY, L., AND M. HUBBELL. 1994. Wetland resources of Illinois: an analysis and atlas. Special publication 15. Illinois Natural History Survey, Champaign, Illinois, USA.
- TAYLOR, S.K., C.D. BURGELT, M.E. ROELKE-PARKER, B.L. HOMER, AND D.S. ROTSTEIN. 2002. Causes of mortality of free-ranging Florida panthers. *Journal of Wildlife Diseases* 38: 107-114.
- URBAN, M.A. 2005. An uninhabited waste: transforming the Grand Prairie in nineteenth century Illinois, USA. *Journal of Historical Geography* 31: 647-665.
- WARTON, D.I., AND F.K. HUI. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92: 3-10.
- WHITE, G.C., AND K.P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement, 120-138.
- WOLFF, J.O., AND T. VAN HORN. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* 81: 266-271.

- WOLFF, P.J., C.A. TAYLOR, E.J. HESKE, AND R.L. SCHOOLEY. 2015. Habitat selection by American mink during summer is related to hotspots of crayfish prey. *Wildlife Biology* 21: 9-17.
- WRIGHT, C.K., AND M.C. WIMBERLY. 2013. Recent land use change in the western corn belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences* 110: 4134-4139.
- YAMAGUCHI, N., AND D.W. MACDONALD. 2003. The burden of co-occupancy: intraspecific resource competition and spacing patterns in American mink, *Mustela vison*. *Journal of Mammalogy* 84: 1341-1355.
- ZSCHILLE, J., N. STIER, AND M. ROTH. 2012. Dynamics in space use of American mink (*Neovison vison*) in a fishpond area in Northern Germany. *European Journal of Wildlife Research* 58: 955-968.

Tables and Figures

Table 4.1. – Ranking of models used to predict the extent of terrestrial habitat use by American mink (*Neovison vison*) in Illinois, USA, 2009 – 2014. ΔAIC_c = difference between model AIC_c and lowest AIC_c in the model set. ω = Akaike model weight. k = number of estimable parameters. *LogLike* = Log Likelihood. Model covariates include Sex, Age (subadult or adult), stream order (StrmOrder), distance to permanent wetland (DistWetland), and proportion of locations recorded during mating season (February - April; Season). I only present the models within $\Sigma\omega \leq 0.95$.

Model	ΔAIC_c	ω	k	<i>LogLike</i>
Sex	0.00	0.40	3	-29.33
Sex + StrmOrder	1.92	0.15	4	-28.71
Sex + DistWetland	2.48	0.11	4	-28.99
Sex + Age	2.57	0.11	3	-29.03
Sex + Season	2.60	0.11	4	-29.05
Null	4.53	0.04	2	-32.99
Season	5.51	0.03	3	-32.08

Table 4.2. – Ranking of known-fate models for survival of American mink (*Neovison vison*) in Illinois, USA, 2009-2014. ΔAIC_c = difference between model AIC_c and lowest AIC_c in the model set. ω = Akaike model weight. k = number of estimable parameters. Deviance = measure of model fit. Model covariates include terrestrial habitat use (THU), mating season (Season; February - April), Sex, and Age (subadult or adult). I only present the models within $\Sigma \omega \leq 0.95$ along with the Null model.

Model	ΔAIC_c	ω	k	Deviance
THU + Season + Age	0.00	0.53	4	68.23
THU + Season + Age + Sex	1.10	0.30	5	67.28
THU + Age + Sex	4.72	0.05	4	72.95
THU + Season	4.88	0.05	3	75.14
THU + Age	5.51	0.03	3	75.67
Null	150.04	0.00	1	148.04

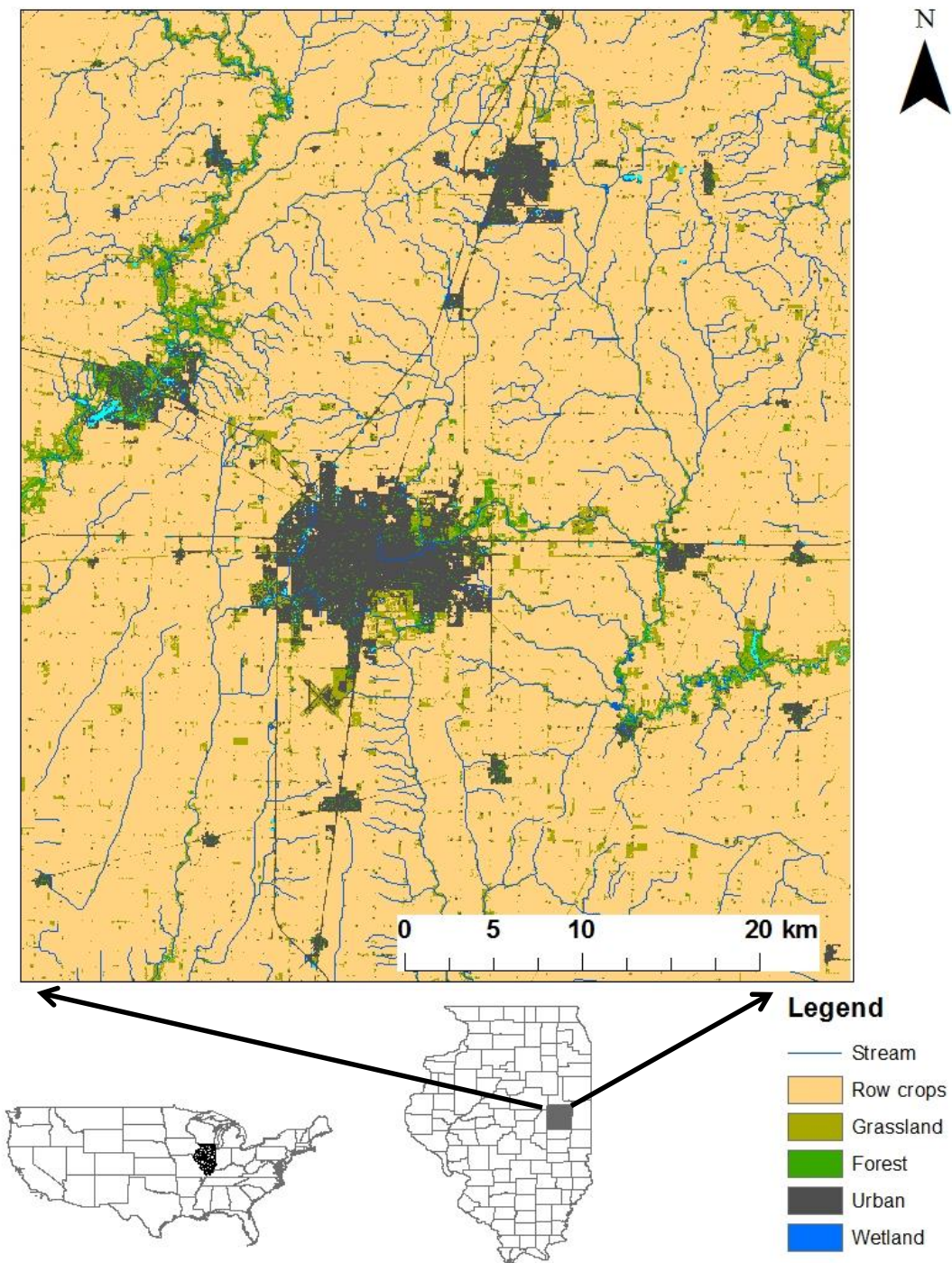


Fig. 4.1. - Map of My study area in Champaign County, Illinois, USA. Row-crop agriculture is the dominate land use (85% of landscape). Remaining wetlands occur on < 1% of the landscape, and small streams and agricultural ditches represent most suitable habitat for American mink (*Neovison vison*).

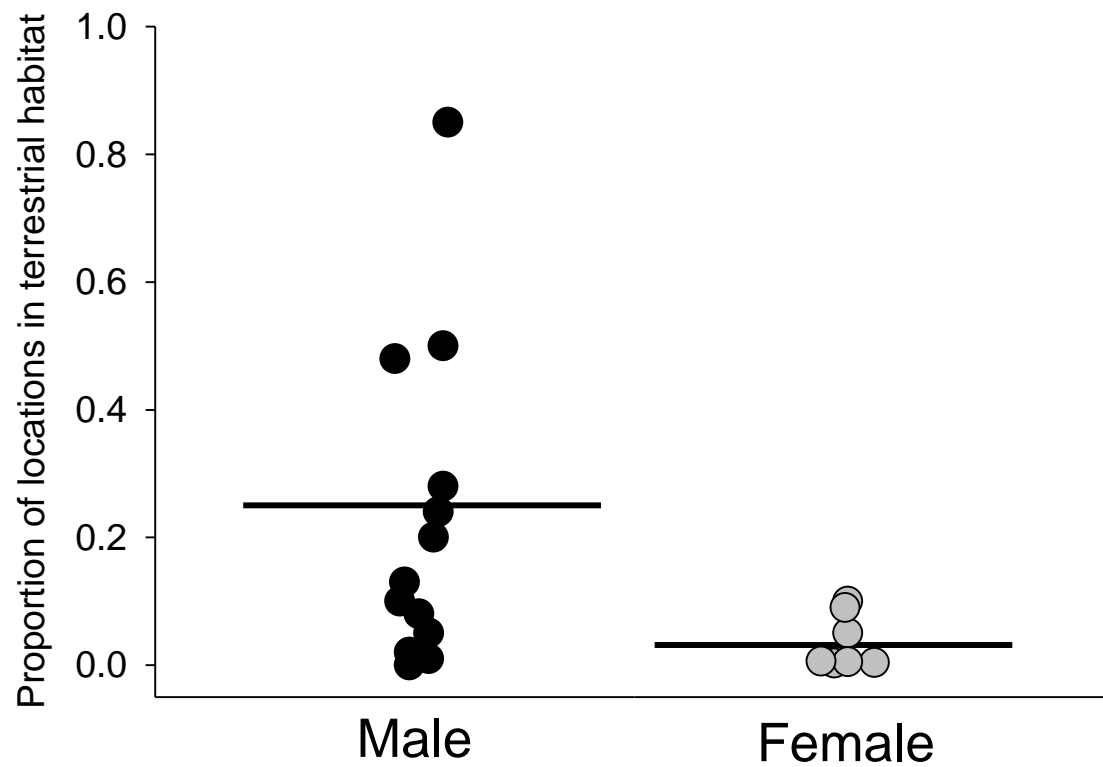


Fig. 4.2. – Proportion of locations located >50 m from the stream edge for radiomarked male (n = 13) and female (n = 7) American mink (*Neovison vison*) in Illinois, USA. Solid lines represent the mean proportion of locations occurring in terrestrial habitat for both male and female mink.

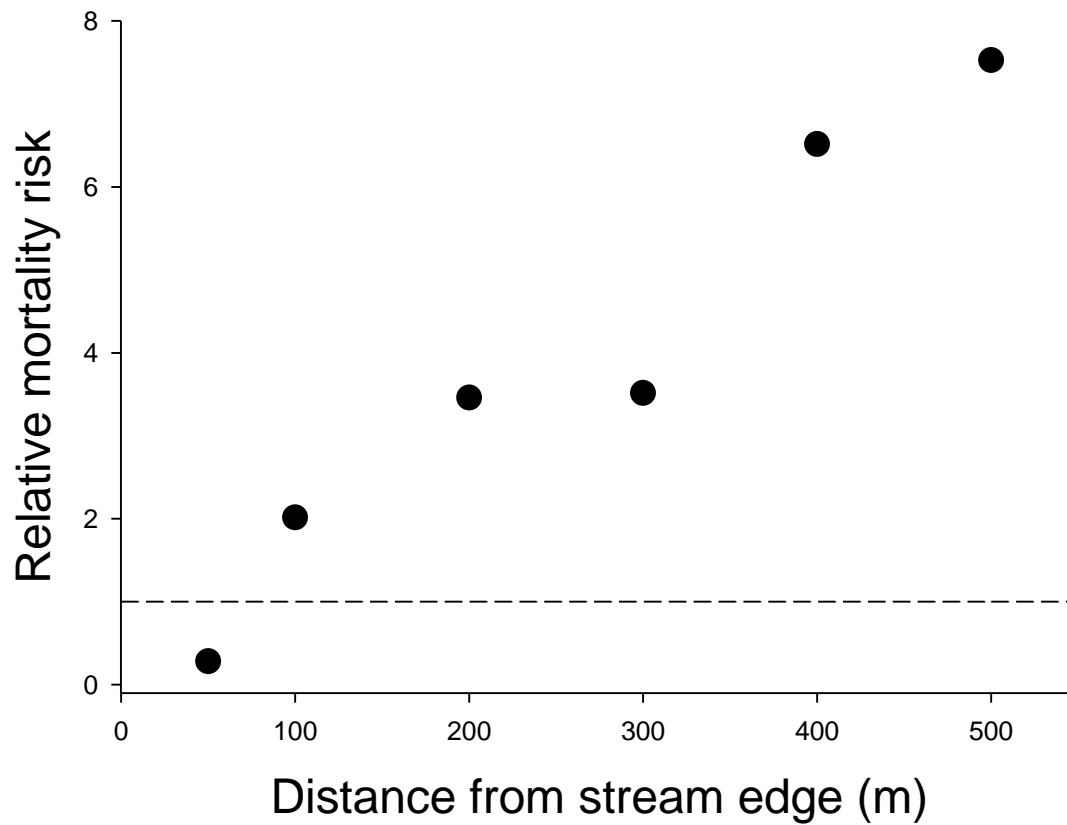


Fig. 4.3. – Relative mortality risk for American mink (*Neovison vison*) in relation to movements away from the stream edge in Illinois, USA, 2009 - 2014. Mortality risk was calculated as the proportion of mortalities recorded in a distance class /proportion of live locations in a distance class. Estimates < 1 (below dashed line) indicate relatively safe habitat in which mortality is less than expected given habitat use patterns. Estimates >1 (above dashed line) indicate relatively risky habitat.

CHAPTER 5

RISK FACTORS FOR *TOXOPLASMA GONDII* EXPOSURE IN SEMIAQUATIC MAMMALS IN A FRESHWATER ECOSYSTEM¹

Abstract

I assessed risk factors for *Toxoplasma gondii* exposure in semiaquatic mammals in east-central Illinois, USA. This agricultural region has extensive drainage systems that could potentially transport *T. gondii* oocysts into the watershed. I used muskrats (*Ondatra zibethicus*) and American mink (*Neovison vison*) as sentinels of watershed contamination. I predicted individuals from larger sub-watersheds would more likely be antibody-positive for *T. gondii* as they were exposed to drainage from larger areas. I also evaluated amount of urban land cover within the sub-watershed, proximity to farmsteads, and age of individuals in competing models of *T. gondii* infection. Antibodies to *T. gondii* were assayed in animal sera by modified agglutination tests (titer 25 or higher) and detected in 18 (60%) of 30 muskrats and 20 (77%) of 26 mink. Infection rates were ≥ 1.7 times higher than those typical for mammals in upland habitats in this region. Sub-watershed size and age class were important predictors of *T. gondii* infection in muskrats ($R^2=0.35$). Models incorporating urban land cover and proximity to farmsteads had little support. None of my models of antibody prevalence in mink were well supported, possibly because mink are less strictly associated with riparian habitats. Because ~91% of my study area is devoted to agricultural production and urbanization, transport of *T. gondii* into freshwater ecosystems is likely facilitated by modified drainage practices common in these areas.

¹ This chapter appeared in its entirety in the *Journal of Wildlife Diseases* as Ahlers, A.A., M.A. Mitchell, J.P. Dubey, R.L. Schooley, and E.J. Heske. 2015. Risk factors for *Toxoplasma gondii* exposure in semiaquatic mammals in a freshwater ecosystem. 51: 488-492.

Toxoplasma gondii is a protozoal parasite of endothermic vertebrates and a significant risk to human and wildlife health (Dubey 2010; Torey and Yolken 2013). Felids are the definitive host and are required to complete the parasite's sexual cycle. Infected felids shed *T. gondii* oocysts in feces, which have variable persistence times depending on environment and temperature (Dubey, 1998). Infection occurs via ingestion of oocysts or ingestion of bradyzoites in tissues of terminal hosts.

Waterborne transmission of *T. gondii* is a growing concern. Contaminated runoff has been implicated in outbreaks in humans (Jones and Dubey, 2010) and may negatively affect the survival of southern sea otters (*Enhydra lutris nereis*; Conrad et al. 2005). Direct testing for *T. gondii* in aquatic ecosystems is technically difficult (Jones and Dubey, 2010) and often requires sampling sentinel species (Conrad et al. 2005).

High densities of domestic and free-ranging cats are associated with farmsteads (Wiegel et al. 1999) and urban areas (VanWormer et al. 2013) and contribute *T. gondii* oocysts to the environment. In east-central Illinois, most of the land is modified for row-crop agriculture, including extensive subsurface tile drainage and ditches. These drainage systems could potentially collect and transport *T. gondii* oocysts, although the viability of this transport mechanism has not been assessed. Similarly, run-off from urban areas could transport *T. gondii* into riparian systems (Miller et al. 2002).

I used muskrat (*Ondatra zibethicus*) and American mink (*Neovison vison*) as sentinels for *T. gondii* in a freshwater ecosystem. Both species are semiaquatic and associated with riparian habitats. I evaluated five predictors of prevalence: watershed, sub-watershed size, proximity to farmsteads, area of urbanized landscape within the sub-watershed, and age class. If runoff from surrounding landscape transports *T. gondii* oocysts, *T. gondii* antibody-prevalence should be

related positively to sub-watershed size. Urbanized areas and farmsteads may contribute *T. gondii* from domestic and feral cats (Weigel et al. 1999; VanWormer et al. 2013), but their relative contribution to riparian habitats is unknown. I predicted antibody-prevalence would be higher in older individuals because of longer life-time exposure to *T. gondii*.

I conducted this study in Champaign County, Illinois, USA (40°12'N, 88°26'W; 258,337 ha). Eighty-five percent of the landscape is developed for corn-soybean production, and 6% is urbanized. Most of the landscape (52–82%) is drained via subsurface tiles (David et al. 2010). Consequently, precipitation runoff is channeled by subsurface conduits into nearby streams and agricultural ditches. Bobcats (*Lynx rufus*) are rare and mountain lions (*Puma concolor*) were extirpated by 1870. Thus, domestic and feral cats are the primary definitive host of *T. gondii*. On average, there are six antibody-positive cats per farm in Illinois (Weigel et al. 1999).

I sampled mink and muskrats for *T. gondii* antibody prevalence in three watersheds (Kaskaskia, 4,064 km²; Vermillion, 3,726 km²; Embarras, 6,324 km²) from 2007–2012. Individuals were live-trapped in streams and ditches using baited traps affixed to floating platforms. I transported animals to a sterile surgical laboratory immediately after capture, placed them under surgical anesthesia (see Ahlers et al. 2010), determined age class (subadult or adult), and collected blood samples (1.5 mL) via cranial vena cavae. I used a modified agglutination test (MAT) to measure specific *T. gondii* antibodies. Sera were diluted 1:25 before evaluation and reactive sera were considered antibody-positive. Although MAT has not been evaluated specifically for muskrats and mink, extensive testing across taxa indicates that a titer of 25 indicates *T. gondii* exposure (Dubey 2010). All procedures were approved by the Animal Care and Use Committee at the University of Illinois.

I assessed differences in antibody-prevalence among watersheds for both species. Although sampling occurred within the three large watersheds, sub-watershed size for each mink or muskrat sample was the total surface area drained (km^2) from the head of the watershed downstream to the capture site. Thus, a unique sub-watershed size was calculated for each individual. I calculated sub-watershed sizes using watershed and raster elevation layers in ArcMap v9.2 (Environmental Systems Research Institute, Inc. Redlands California, USA). I quantified the percentage land cover by urban areas (high, medium, and low density urbanization combined) within individual sub-watersheds, and measured the Euclidian distance (m) from capture sites to the nearest farmstead.

I used logistic regression to model *T. gondii* antibody-prevalence as a function of landscape factors (watershed, sub-watershed area, urbanization, distance to nearest farmstead) and age class. I used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank 31 models for each species that represented single and additive effects of all combinations of my variables plus an intercept-only model. I considered models with $\Delta AIC_c \leq 2$ competitive and evaluated the goodness-of-fit of my most supported model with a Hosmer-Lemeshow test (Lemeshow and Hosmer 1982).

I tested serum samples from 30 muskrats (6 adults, 24 subadults) in the Kaskaskia ($n=17$) and Embarras ($n=13$) watersheds, and 26 mink (15 adults, 11 subadults) in the Kaskaskia ($n=11$), Vermillion ($n=5$) and Embarras ($n=10$) watersheds. Sixty percent of muskrats (18/30; 95% CI: 43–78%) and 77% of mink (20/26; 95% CI: 61–93%) were antibody-positive. In the Kaskaskia watershed, 65% (11/17) of muskrats and 81% (9/11) of mink were antibody-positive. In the Embarras watershed, 54% (7/13) of muskrats and 60% (6/10) of mink were antibody-positive. All five mink sampled in the Vermillion watershed were antibody-positive.

Sub-watershed area and age class were the only factors included in the two most supported models explaining *T. gondii* antibody-prevalence in muskrats (model-fit statistics for my second-ranked model: Hosmer-Lemeshow test, $\chi^2=3.82$, $df=7$, $P=0.80$; $R^2=0.35$; Table 5.1). Muskrats captured in larger sub-watersheds had a higher probability of being antibody-positive ($\beta=0.0387$, $SE=0.0144$; odds ratio (OR)=1.039, 95% CI=1.010–1.069; Fig. 5.1). Antibody-prevalence in muskrats was higher among adults (67%; 4/6) than subadults (58%; 14/24), however, this effect was weak (OR=1.172, 95% CI=0.112–12.237). In contrast, none of my models of mink antibody-prevalence were well supported; the intercept-only model was my top-ranked model ($\omega_i=0.15$, Table 5.1).

Infection rates of *T. gondii* in mink and muskrats were 1.7 times greater than those reported for terrestrial mammals in this region (Lehrer et al. 2010; Fredebaugh et al. 2011; range 0–35%). Contaminated runoff has been implicated in high *T. gondii* infection rates for some marine mammals (Conrad et al. 2005; Dubey 2010) and likely contributes *T. gondii* oocysts into freshwater watersheds. Rates of *T. gondii* infection in mink in my study were similar to those reported by Smith and Frenkel (1995) (66%, $n=29$, 1:8 titer, Sabin-Feldman dye test) and Sepúlveda et al. (2011) (70%, $n=30$, 1:32 titer, latex agglutination test). Infection rates in muskrats were much higher than those reported by Nezval and Literak (1994) (47.3%, $n=146$; 9.1%, $n=110$, 1:4 titer, Sabin-Feldman dye test), Hejliček et al. (1997) (24%, $n=437$, 1:4 titer, Sabin-Feldman dye test), and Smith and Frenkel (1995) (17%, $n=42$, 1:8 titer, Sabin-Feldman dye test).

As predicted, muskrats captured in larger sub-watersheds were more likely to be antibody-positive than those in smaller sub-watersheds. This effect is likely a result of contaminated runoff from the surrounding landscape increasing risk of exposure to *T. gondii* oocysts in

riparian areas. Oocyst concentration in larger sub-watersheds may occur if land-derived oocysts attach to organic aggregates (Shapiro et al. 2012) or biofilms found on submergent vegetation (Mazzillo et al. 2013) within the stream. My inability to detect a similar effect in mink may be a result of interspecific differences in trophic and spatial ecologies or that few mink were negative for *T. gondii* antibodies. Mink are predators of aquatic and terrestrial prey, including muskrats, and use upland habitats more than do muskrats. Mink exposure to *T. gondii* may be enhanced by consuming infected vertebrates (Smith and Frenkel, 1995). Thus, exposure to *T. gondii* for mink may be less tightly linked to sub-watershed area. Muskrats, however, are mostly herbivorous and rarely leave the stream edge (Ahlers et al. 2010). Their exposure likely occurs through ingestion of oocysts while drinking, grooming, or foraging on submergent vegetation.

The weak difference in *T. gondii* antibody-prevalence between adult and subadult muskrats is likely due to adults having longer life-time exposure. However, a more robust sample may be required to confirm this effect. Unlike Sepúlveda et al. (2011), I did not detect an age effect on *T. gondii* seropositivity in mink. Few mink in my study were antibody negative, and my sample might not have been large enough to detect an age effect.

Proximity to farmsteads and amount of urbanized land cover within the sub-watersheds did not predict antibody prevalence for muskrat or mink. However, because ~91% of my study area is dedicated to urbanization and agricultural production, drainage practices associated with these land-use types are likely transporting *T. gondii* oocysts into freshwater habitats. Although I could not distinguish the relative contribution of oocysts from agricultural and urban areas, both have drainage systems that bypass natural wetlands and riparian zones that historically have impeded transport of *T. gondii* oocysts into watersheds (Shapiro et al. 2010). This study represents an important first step in understanding spatial patterns of waterborne transmission of *T. gondii*.

This work was supported by the Illinois Department of Natural Resources, Illinois Department of Transportation and the Illinois Trappers Association. I thank G. Batzli, M. Samuel, and two anonymous reviewers for helpful comments.

Literature Cited

- Ahlers AA, Heske EJ, Schooley RL, Mitchell MA. 2010. Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats. *Wild Biol* 16:400-408.
- Conrad PA, Miller MA, Kreuder C, James ER, Mazet J, Dabritz H, Jessup DA, Gulland F, Grigg ME. 2005. Transmission of *Toxoplasma*: Clues from the study of sea otters as sentinels of *Toxoplasma gondii* flow into the marine environment. *Int J Parasitol* 35:1155-1168.
- David MB, Drinkwater LE, McIsaac GF. 2010. Sources of nitrate yield in the Mississippi River basin. *J Environ Qual* 39:1657-1667.
- Dubey JP. 1998. *Toxoplasma gondii* oocyst survival under defined temperatures. *J Parasitol* 84:862-865.
- Dubey JP. 2010. *Toxoplasmosis of animals and humans*. 2nd ed. CRC Press, Boca Raton, Florida, 313 pp.
- Fredebaugh SL, Mateus-Pinilla NE, McAllister M, Warner RE, Weng H. 2011. Prevalence of antibody to *Toxoplasma gondii* in terrestrial wildlife in a natural area. *J Wildlife Dis* 47:381-392.
- Hejliček K, Literák I, Nerval J. 1997. Toxoplasmosis in wild mammals from the Czech Republic. *J Wildlife Dis* 33:480-485.
- Jones JL, Dubey JP. 2010. Waterborne toxoplasmosis – recent developments. *Exp Parasitol* 124:10-25.
- Lehrer EW, Fredebaugh SL, Schooley RL, Mateus-Pinilla NE. 2010. Prevalence of antibodies to *Toxoplasma gondii* in woodchucks across an urban-rural gradient. *J Wildlife Dis* 46:977-980.
- Lemeshow S, Hosmer DW. 1982. A review of goodness of fit statistics for use in the development of logistic regression models. *Am J Epidemiol* 115: 92-106.

- Mazzillo FFM, Shapiro K, Silver MW. 2013. A new pathogen transmission mechanism in the ocean: The case of sea otter exposure to the land-parasite *Toxoplasma gondii*. *PLoS One* 8: e82477.
- Miller MA, Gardner IA, Kreuder C, Paradies DM, Worcester KR, Jessup DA, Dodd E, Harris MD, Ames JA, Packham AE, Conrad PA. 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). *Int J Parasitol* 32: 997-1006.
- Nezval J, Literák I. 1994. *Toxoplasma gondii* in muskrat (*Ondatra zibethicus*). *Vet Med Czech* 39:743-746.
- Sepúlveda MA, Muñoz-Zani C, Rosenfeld C, Jara R, Pelican KM, Hill D. 2011. *Toxoplasma gondii* in feral American minks at the Maullín River, Chile. *Vet Parasitol* 175:60-65.
- Shapiro K, Conrad PA, Mazet JAK, Wallender WW, Miller WA, Largier JL. 2010. Effect of estuarine wetland degradation on transport of *Toxoplasma gondii* surrogates from land to sea. *Appl Environ Microbiol* 76:6821-6828.
- Shapiro K, Silver MW, Largier JL, Conrad PA, Mazet JAK. 2012. Association of *Toxoplasma gondii* oocysts with fresh, estuarine, and marine macroaggregates. *Limnol Oceanogr* 57:499-456.
- Smith DD, Frenkel JK. 1995. Prevalence of antibodies to *Toxoplasma gondii* in wild mammals of Missouri and east central Kansas: Biologic and ecologic considerations of transmission. *J Wildlife Dis* 31:15-21.
- Torrey EF, Yolken RH. 2013. *Toxoplasma* oocysts as a public health problem. *Trends Parasitol* 29:380-384.

- VanWormer E, Conrad PA, Miller MA, Melli AC, Carpenter TE, Mazet JAK. 2013. *Toxoplasma gondii*, source to sea: Higher contribution of domestic felids to terrestrial parasite loading despite lower infection prevalence. *Ecohealth* 10:277-289.
- Weigel RM, Dubey JP, Dyer D, Siegel AM. 1999. Risk factors for infection with *Toxoplasma gondii* for residents and workers on swine farms in Illinois. *Am J Trop Med Hyg* 60:793-798.

Tables and Figures

Table 5.1. Ranking of models predicting *Toxoplasma gondii* antibody-prevalence in muskrats (*Ondatra zibethicus*) and American mink (*Neovison vison*) in a freshwater ecosystem. I examined the support of 31 models for each species that included the effects of landscape-level factors and age. Only models with $\Delta AIC_c \leq 2$ are presented along with the *Intercept Only* model for both species.

<i>Muskrats</i>		Parameter ^a		
Model ^b	<i>K</i>	ΔAIC_c	$-2LogLike$	ω_i
SubWatershed	2	0.00	29.13	0.25
SubWatershed + Age	3	0.63	26.73	0.18
<i>Intercept Only</i>	1	8.95	40.38	0.00
<i>Mink</i>				
<i>Intercept Only</i>	1	0.00	28.09	0.15
WatershedID	2	0.73	23.89	0.11
SubWatershed + WatershedID	3	0.99	21.35	0.09
SubWatershed	2	1.21	26.94	0.08
DistFarm	2	1.67	27.41	0.07

^a *K* = number of parameters including the intercept term; ΔAIC_c = difference in model AIC_c and the lowest model AIC_c of the candidate set; $-2LogLike$ is used for assessing model fit; ω_i = model weight.

^b Covariates include: WatershedID=Kaskaskia, Embarras, or Vermillion watershed; SubWatershed=sub-watershed drainage area; DistFarm=Euclidian distance between sampling point and nearest farmstead; Age=subadult or adult.

CHAPTER 6

SUMMARY

Landscape conversions to urban areas and agriculture have resulted in drainage of natural wetlands (Brady and Flather 1994; Gutzwiller and Flather 2011; McCauley and Jenkins 2005). Additionally, these land-use changes have also altered the remaining riparian ecosystems (Reiseng et al. 2011). These landscape conversions are happening at unprecedented rates and are predicted to outpace conservation efforts (Seto et al. 2012; Wright and Wimberly 2013; Larke et al. 2015). Semiaquatic species occurring in these highly altered landscapes have mostly shifted their distributions to remaining riparian ecosystems. These climate-sensitive habitats exhibit dramatic changes in flow regimes (Baker et al. 2004) that are tied to local precipitation event (Ahlers et al. 2010). To persist in these habitats species must adapt to novel landscapes and mortality risks. My research was directed at understanding factors that affect American mink (*Neovison vison*) and muskrat (*Ondatra zibethicus*) distributions, survival, and disease risk in these human-dominated landscapes.

Future climate change is expected to increase variability in precipitation and frequency of extreme flooding and summer drought events (Easterling et al. 2000; Dai 2013). Mink and muskrats occurring in climate-sensitive riparian habitats are particularly at risk as they must cope with and outlast extreme fluctuations in water levels (Ahlers et al. 2010). I demonstrated that annual occupancy of stream sites by mink and muskrats was strongly correlated with summer precipitation. Higher water levels likely provided ample resources and escape routes from terrestrial predators. Conversely, during drought conditions, muskrats likely suffered high mortality as their burrows were exposed to predators and they are generally reluctant to leave established home ranges (Errington 1939). Reduced habitat occupancy rates by mink during

drought conditions suggest mink shifted their foraging to upland habitats as aquatic prey resources became limited in stream habitat. Mortality risk for semiaquatic species is greater when using terrestrial habitat, however, and mink were likely exposed to increased predation risk and negative human interactions during drought conditions. Increased frequency and intensity of summer droughts is predicted for the Grand Prairie region (Wuebbles and Hayhoe 2004), and the patterns observed during drought may be common for semiaquatic mammals under future climate change scenarios.

I demonstrated that permanent wetlands are important resources for stream-dwelling mink in agroecosystems. Mink were more likely to occur and colonize stream sites that were spatially isolated from permanent wetland habitat. These patterns suggest that mink may be choosing stable wetland habitat over less predictable stream habitats when both are in close spatial proximity (< 2 km). Occupancy and colonization rates were higher at stream sites with deeper water levels, and colonization rates were related negatively to the amount of urban land cover surrounding stream sites. Additionally, mink were more likely to leave stream sites if muskrats were not present and if a permanent wetland was near. My results confirm that factors interplaying across multiple scales influence occupancy dynamics of mink in stream habitat in highly modified landscapes. My results also highlight the importance of considering both the spatial distribution of supplementary habitats and direct measures of prey availability to improve species distribution models.

Individuals should select habitats that infer maximum fitness benefits (Morris 2003). However, in regions undergoing rapid land-use changes, imperfect perceptual cues may drive maladaptive habitat selection resulting in ecological traps (Battin 2004; Robertson and Hutto 2006) or perceptual traps (Gilroy and Sutherland 2007, Patten and Kelly 2010). I demonstrated

that mink incur increased mortality risks when using habitat in terrestrial areas away from the stream edge. Most known mortalities were attributed to negative human interactions (roadkill and poisoning; 58%) and intraguild predation (coyote [*Canis latrans*]; 35%). I also documented sex- and age-specific variation in mink survival rates, and decreased survival during the mating season. Male mink were more likely to use terrestrial habitat than females. This effect is likely a result of males establishing and maintaining larger territories and searching larger areas for females during the mating season. My results suggest that mink have yet to recognize the changing mortality risks associated with the rapid rate of landscape change in the Grand Prairie region. An alternative hypothesis suggests that, although mink may realize the costs, movements in these areas are still necessary as prey become limiting in riparian habitat, to increase mating opportunities, or as territorial behavior excludes them from less-riskier habitats.

My results also demonstrate that semiaquatic mammals have increased exposure to the parasite *Toxoplasma gondii* in highly altered landscapes. In our region, most of the landscape is tile drained (52-82%; David et al. 2010) and less than 1% of historic wetlands remain. Degradation of wetlands and natural riparian zones may increase waterborne transmission of *T. gondii* oocysts into the watershed (Shapiro et al. 2010). I found mink and muskrat populations had infection rates much higher than those of terrestrial mammals in the region, consistent with my watershed contamination hypothesis. Additionally, I found that muskrats positioned in larger watersheds were at an increased risk of exposure to *T. gondii*. This effect is likely because muskrats in larger watersheds were exposed to runoff from relatively more hectares (and more land-derived *T. gondii* oocysts) than those positioned in smaller watersheds. I did not detect a similar watershed-effect in mink, likely because they are less tightly linked to the watershed than muskrats, and enhancing *T. gondii* exposure while foraging in upland areas. Muskrat exposure

to *T. gondii* is likely occurring while drinking, grooming, or foraging on emergent vegetation. This particular study was important because it represents an important first step in understanding the spatial epidemiology *T. gondii*. This study also provides additional evidence that wetland and riparian-zone loss and degradation can negatively affect biodiversity and watershed health in human-modified landscapes.

Widespread environmental change is rapidly altering the landscape. Biodiversity conservation in human-modified landscapes requires detailed knowledge of factors affecting the distribution, survival, and fitness of individuals and populations. My research was focused on understanding how American mink and muskrat populations responded to environmental change. Future research should investigate how key demographic traits (e.g., reproduction, population growth) of semiaquatic species are influenced by stressors commonly associated with agricultural and urban landscapes.

Chapter 6 meets the formatting requirements of *Journal of Mammalogy*

Literature Cited

- AHLERS A.A., R.L. SCHOOLEY, E.J. HESKE, AND M.A. MITCHELL. 2010. Effects of flooding and riparian buffers on survival of muskrats (*Ondatra zibethicus*) across a flashiness gradient. *Canadian Journal of Zoology* 88:1011-1020.
- BAKER, D.B., R.P. RICHARDS, T.T. LOFTUS, AND J.W. KRAMER. 2004. A new flashiness index: characteristics and applications to Midwestern rivers and streams. *Journal of American Water Resources Association* 40:503-522.
- BATTIN, J. 2004. When good animals love bad habitats: ecological traps and conservation of animal populations. *Conservation Biology* 18: 1482-1491.
- BRADY, S.J., AND C.H. FLATHER. 1994. Changes in wetlands on nonfederal rural land of the conterminous United States from 1982-1987. *Environmental Management* 18:693-705.
- COSENTINO B.J., R.L. SCHOOLEY, AND C.A. PHILLIPS. 2011. Connectivity of agroecosystems: dispersal costs can vary among crops. *Landscape Ecology* 26: 371-379.
- DAI, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* 3: 52-58.
- DAVID M.B., L.E. DRINKWATER, AND G.F. MCISAAC. 2010. Sources of nitrate yield in the Mississippi River basin. *Journal of Environmental Quality* 39:1657-1667.
- EASTERLING, D.R., G.A. MEEHL, C. PARMESAN, S.A. CHANGNON, T.R. KARL, AND L.O. MEARNES. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289: 2068-2074.
- ERRINGTON, P.L. 1939. Reaction of muskrat populations to drought. *Ecology* 20: 168-186.
- GILROY, J.J., AND W.J. SUTHERLAND. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology and Evolution* 22: 351-356.

- GUTZWILLER, K.J., AND C.H. FLATHER. 2011. Wetland features and landscape context predict the risk of wetland habitat loss. *Ecological Applications* 21:968-982.
- LARK, T.J., J.M. SALMON, AND H.K. GIBBS. 2015. Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environmental Research Letters* 10: doi:10.1088/1748-9326/10/4/044003.
- MCCAULEY, L.A., AND D.G. JENKINS. 2005. GIS-based estimates of former and current depressional wetlands in an agricultural landscape. *Ecological Applications* 15:1199-1208.
- MORRIS, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136: 1-13.
- PATTEN, M.A., AND J.F. KELLY. 2010. Habitat selection and the perceptual trap. *Ecological Applications* 20: 2148-2156.
- RISENG, C.M., M.J. WILEY, R.W. BLACK, AND M.D. MUNN. 2011. Impacts of agricultural land use on biological integrity: a causal analysis. *Ecological Applications* 21:3128-3146.
- ROBERTSON, B.A., AND R.L. HUTTO. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87: 1075-1085.
- SETO, K.C., B. GÜNERALP, AND L.R. HUTYRA. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences* 109: 16083-16088.
- SHAPIRO, K., P.A. CONRAD, J.A.K. MAZET, W.W. WALLENDER, W.A. MILLER, AND J.L. LARGIER. 2010. Effect of estuarine wetland degradation on transport of *Toxoplasma gondii* surrogates from land to sea. *Applied and Environmental Microbiology* 76:6821-6828.

WRIGHT, C.K., AND M.C. WIMBERLY. 2013. Recent land use change in the western corn belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences* 110: 4134-4139.

WUEBBLES, D.J., AND K. HAYHOE. 2004. Climate change projections for the United States Midwest. *Mitigation and Adaption Strategies for Global Change* 9: 335-363.

APPENDIX A: MUSKRAT OCCUPANCY METHODS

I used 6 years (2007-2012) of presence-absence survey data to assess muskrat occupancy at 58-90 riparian sites in my study area. Muskrat surveys were conducted in conjunction with mink surveys (see Methods). I used single-season occupancy models, corrected for detectability (p), to determine the model-averaged estimate of muskrat occupancy (Ψ) at each stream site for each year (2007-2012). I used variables already found important for detection and site occupancy of riparian muskrats in my region to build single-season models (Table A.1.). For an in-depth description of the methods used to derive these covariates, see Cotner and Schooley (2011). I assessed 31 models of p including a constant model for each year. I fit models including the single effects of each covariate (Observer; Date; Debris; Rain; Sandbar) and the additive effects of all combinations of each covariate. I used the most-supported model for p for a given year to fit subsequent models of Ψ for the same year. For each year, I included 16 models in my candidate set of Ψ (including a constant model of Ψ). I fit models including the single effects of each covariate (Size; Bank; Sand; Urban) and the additive effects of all combinations of each covariate. Thus, I constructed six total candidate sets of models (one for every year). The goal of this analysis was to derive robust estimates of occupancy probability for muskrats at each site for a given year. As such, I used Akaike weights (ω) to derive model-averaged estimates of Ψ for each site for a given year using all the models (16) in each candidate set (Burnham and Anderson 2002). Conditional Ψ of sites where muskrat sign was detected at least once during all surveys was 1. Occupancy probability was < 1 at sites where muskrat sign was not detected during any survey by an observer.

Tables and Figures

Table A.1. Description of covariates used to build single-season occupancy models for riparian muskrats (*Ondatra zibethicus*) from 2007-2012 in east-central, Illinois USA.

Covariate	Description
<i>Detection (ρ)</i>	
Observer	Person conducting the walking survey
Date	Day of the year (1-365)
Debris	Relative abundance of emergent debris (e.g., logs, rocks) within site on a scale from 0-5
Rain	Sum of rainfall 7-days prior to survey
Sandbar	Amount of trackable surface adjacent to stream edge
<i>Occupancy (Ψ)</i>	
Size	PCA containing wetted width and depth of stream site and subwatershed area
Bank	Linear distance (m) from bankfull to wetted edge
Sand	Percent sand in bank soil
Urban	Proportion of developed land cover within 500-m buffer around site