HABITAT, LANDSCAPE, AND CLIMATE EFFECTS ON RIPARIAN PREDATOR-PREY
INTERACTIONS IN A HUMAN-DOMINATED ECOSYSTEM

BY

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THESIS

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ABSTRACT

Predator-prey interactions form ecologically significant links between terrestrial and aquatic ecosystems, and may be particularly important in riparian ecosystems with highly variable habitat features in human-dominated landscapes. Climate models predict an increased frequency of summer drought and spring flooding events in the Midwestern United States. This variability in precipitation will alter within-stream habitat structure, and will affect predator-prey interactions in riparian ecosystems. I studied (1) habitat selection of a semiaquatic predator as it relates to the spatial distribution of a main prey, and (2) predation risk for an aquatic prey from a variety of aquatic and riparian predators.

I examined the seasonal diet of American mink and determined if a primary prey, crayfish, was an important driver of habitat selection during the summer of a severe drought year. I collected mink scats in three seasons. In summer 2012, I performed occupancy surveys for mink and concurrently measured crayfish densities and habitat features in 59 stream segments in east-central Illinois. Occupancy modeling showed that mink selected locations based directly on high prey concentrations instead of habitat characteristics that might indicate high prey densities. Mink shifted strongly to feeding mainly on crayfish during summer, and mink were more likely to occupy stream segments that contained crayfish hotspots. Mink were also negatively associated with both urbanization and stream size.

I also compared predation risk for crayfish in a year of severe drought (2012) to a non-drought year (2013). I evaluated the effects of crayfish size, within-stream characteristics, and landscape context on crayfish mortality between years. I conducted an experiment in which tethered crayfish were exposed to aquatic and riparian predators for 3 nights in 45 stream segments in east-central Illinois. Different stream conditions caused the factors most influential

on predation risk to differ between years. Crayfish mortality was lower (43%) during the drought than in the wet year (52.0%). Aquatic predators were predominant, but there was a shift to increased predation by terrestrial predators during the drought. During the drought, submerged vegetation cover had the greatest effect on predation risk; crayfish survival was higher where crayfish could find refuge in submerged vegetation. In the non-drought year, crayfish size was the most influential variable affecting predation risk; larger crayfish suffered higher mortality than smaller crayfish. Crayfish mortality was related positively to stream size, and negatively to urbanization in both years. My research demonstrates that habitat selection and predation risk are spatially and temporally dynamic, but patterns exist that help explain predator behavior and prey vulnerability.

ACKNOWLEDGMENTS

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CHAPTER 1: GENERAL INTRODUCTION

Predator-prey interactions form ecologically significant links between terrestrial and aquatic ecosystems (Polis et al. 1997). Studies across multiple taxa have documented the importance of predator-prey dynamics in riparian habitats (e.g., Schlosser 1995; Berger et al. 2001). Terrestrial and semiaquatic predators may depend on aquatic prey (Jędrzejewska et al. 2001; Marchand and Litvaitis 2004), and predators influence ecosystem productivity by facilitating the transfer of nutrients across ecosystem boundaries (Schmitz et al. 2010). Predation is also important for structuring prey communities, and can affect the abundance, behavior, and distribution of aquatic prey species (Stein and Magnuson 1976; Sih et al. 1985; Kershner and Lodge 1995).

The American Midwest is highly-modified region in which land conversions for agricultural production and urban expansion have severely reduced the amount of natural habitat for wildlife (Mattingly et al. 1993). These land-use changes are also associated with decreased species diversity (McKinney 2002, 2006). My research was conducted in the agroecosystem of east-central Illinois – a state that has lost over 90% of its original pre-settlement wetlands (Suloway and Hubbell 1994). Predators in this area are often restricted to linear riparian habitats along small streams and agricultural ditches, which provide movement corridors for terrestrial and aquatic wildlife (Naiman and Decamps 1997). Land-use changes for agriculture and urbanization result in stream channelization (Mattingly et al. 1993) and habitat degradation (Paul and Meyer 2001), which alter predator-prey interactions in these highly-modified landscapes (Shapira et al. 2008; Rodewald et al. 2011; Francis et al. 2009). Data collection for this project occurred from fall 2011 to summer 2013. This region experienced a severe drought in 2012 (Illinois Department of Natural Resources 2013), which allowed me to compare predator-prey

interactions between drought and non-drought years and to consider implications for future climate change.

In Chapter 2, I focus on the American mink (*Neovison vison*), a mammalian carnivore that inhabits riparian zones in east-central Illinois. This species is an economically important furbearer that is native to North America and invasive in Europe, Asia, and South America (Macdonald and Harrington 2003). Much research has focused on the impacts of American mink where it is invasive (Bonesi and Palazon 2007), but a better understanding of the behavior of mink in its native range is needed. In Chapter 2, I attempt to identify the mechanism by which American mink select habitat in this portion of its native range. I paired diet data with occupancy modeling to determine if the abundance of a primary prey item, crayfish, drove habitat selection behavior of mink. I also tested the influences of habitat and landscape characteristics on mink occupancy. My results have implications for the efficacy of habitat models for management, and indicate the factors that influence habitat selection by mink may vary spatially and temporally.

In Chapter 3, I examine predator-prey interactions from the perspective of an aquatic prey, crayfish. Crayfish are significant components of aquatic food webs (Momot 1995), and their behavior and distributions are influenced by predation risk from aquatic and terrestrial predators (Stein and Magnuson 1976; Kershner and Lodge 1995). I compared predation risk for crayfish in a year of severe drought to a non-drought year. My results reveal differences in predation risk between years, and illustrate the relative importance of aquatic and riparian predators under different environmental conditions. I also demonstrate that different stream conditions caused the biotic and abiotic factors most influential on predation risk to differ between years.

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CHAPTER 2: HABITAT SELECTION BY AMERICAN MINK DURING SUMMER IS DRIVEN BY HOTSPOTS OF CRAYFISH PREY

INTRODUCTION

Predators should select resource patches that maximize the probability of encountering prey. However, the mechanisms by which carnivores select habitat are often unclear. Predators may choose locations for hunting based on habitat characteristics that should indicate high prey abundance (Irwin et al. 2007; Slauson et al. 2007), or based directly on prey abundance (O'Donoghue et al. 1998, Fukui et al. 2006). Habitat surrogates for prey abundance could perform poorly when prey abundances are low or variable (Keim et al. 2011). Because prey habitat does not necessarily reflect actual habitat use by prey at any given time, direct measures of prey abundance are preferable (Keim et al. 2011). Moreover, habitat selection studies should be paired with mechanistic data such as diet metrics (Keim et al. 2011) to understand predator behavior more fully.

One such carnivore that may select habitat based on prey abundance is the American mink (*Neovison vison*). The species is an opportunistic, generalist carnivore native to North America and invasive in Europe and South America (Macdonald and Harrington 2003). Mink have seasonally variable diets due to changes in relative availabilities of prey at different times of the year (Gerell 1967; Dunstone and Birks 1987; Brzeziński 2008). Within its native range, mink are important predators of muskrats (*Ondatra zibethicus*) in western Canada (Proulx et al. 1987). Specialization by mink on muskrat decreases in eastern and south-central Canada where species richness of mink prey increases (Shier and Boyce 2009). In the Midwestern United States, diversity of potential mink prey is also high (Hoffmeister 1989; Osborne and Wiley 1992; Havera 1999). The diet of mink has been examined within its native range (Ben-David et al. 1997; Arnold and Fritzell 1987; Dearborn 1932; Sealander 1943; Korschgen 1958; Hoffman et

al. 2009; Racey and Euler 1983), and some studies have examined habitat use by mink in its native range (Burgess and Bider 1980; Arnold and Fritzell 1990; Ben-David et al. 1995; Stevens et al. 1997; Loukmas and Halbrook 2001). However, there has been little effort to link diet with habitat selection behavior of mink. Crayfish often occur in the diet of American mink where crayfish are available both in the native (Dearborn 1932; Burgess and Bider 1980) and invasive range (Gerell 1967; Day and Linn 1972; Ward et al. 1986; Melero et al. 2008; Fischer et al. 2009). Spatial variability in abundance of this aquatic food source could explain habitat selection by mink during seasons when crayfish are plentiful.

Mink may select habitat in relation to crayfish abundance in two ways. Mink could use habitat cues to decide where to hunt for crayfish, or they could respond directly to relative crayfish densities. More specifically, because crayfish are patchily distributed within streams (DiStefano et al. 2003), mink may respond either to average prey densities in a given area or to the presence of prey hotspots. Studies across multiple taxa have shown that prey hotspots can be important determinants of predator space use and foraging behavior (e.g., López-Bao et al. 2011; Gende and Sigler 2006; Davoren et al. 2003; Thompson et al. 2001). Mink use some parts of their home range more intensively than others (Yamaguchi et al. 2003), which could reflect prey distributions and suitable hunting places (Gerell 1970).

In addition to prey abundance, local habitat and landscape characteristics may be important drivers of habitat selection by mink. In the Midwestern United States, agricultural intensification and urbanization have reduced the amount of suitable habitat for semiaquatic wildlife. Land conversions and drainage for row-crop agriculture have reduced the amount of natural habitat (Zucker and Brown 1998), and mink in this region are often restricted to linear riparian habitats along small streams and agricultural ditches. These riparian buffers vary

considerably in characteristics such as width and vegetation structure (Ahlers et al. 2010). Larger riparian buffers provide mink with increased foraging space and terrestrial alternatives to the aquatic prey located within the stream channel. Large streams have a greater diversity of aquatic prey than do small streams (Sheldon 1968; Osborne and Wiley 1992), and mink are associated positively with water depth of streams (Schooley et al. 2012). Although little information exists regarding effects of urbanization on mink (Gehrt et al. 2010), mink might avoid areas of human development (Racey and Euler 1983; Brzeziński et al. 2012). Urban areas are generally associated with habitat loss and reduced species diversity (McKinney 2002).

I examined the seasonal diet of American mink and determined if a primary prey, crayfish, was an important driver of habitat selection during summer in a human-dominated landscape. I hypothesized that diet of mink would reflect seasonal availability of prey. I predicted crayfish would be most important in the diet during summer when they are most available, whereas consumption of crayfish would decrease during winter when mink shift to prey such as mammals and fish. I also hypothesized that habitat selection by mink during summer would be related directly to prey abundance. Hence, I expected a higher probability of mink occupancy at locations with crayfish hotspots or higher mean densities. I also hypothesized that stream and landscape characteristics would influence habitat selection by mink. I predicted mink occupancy would be related positively to water depth and stream size because larger streams contain more aquatic resources. I also predicted a positive association between mink occupancy and riparian buffer width because wider buffers provide more foraging opportunities, and a negative association with degree of urbanization.

METHODS

Study area

My study was conducted in east-central Illinois, U.S.A. and was centered on Champaign-Urbana (40°12'N, 88°26'W). Most sampling (diet, crayfish density, site occupancy by mink) occurred at 59 study sites. Each site was a 200-m stretch of wadeable stream, ranging from 1st to 5th order in size. Sites represented potential resource patches for mink so my measure of site occupancy corresponded to habitat use (Schooley et al. 2012). Sites had a median nearest-neighbor distance of 3.4 km (range = 0.5 – 13.5 km), were distributed across an urbanization gradient (proportion of impervious surface within a 500-m buffer around each site—Cotner and Schooley 2011), and included a wide range of riparian buffer widths (0 – 466 m). My 59 sites were randomly selected from a previous stratified random sample of 90 sites, 50% of which were located within a 2-km radius of incorporated towns (>2,500 people), and 50% of which were located outside of this urban buffer (Cotner and Schooley 2011). I also collected mink scats at an additional 60 locations. Crayfish sampling and occupancy surveys were conducted during the core months of the severe drought of 2012 (2nd driest January to July period on record in Illinois—Illinois State Water Survey 2012a; Illinois Department of Natural Resources 2013).

Scat collection

To evaluate seasonal variation in composition of mink diets, I collected scats during fall, winter, and summer. In fall 2011 (21 September – 10 November), 59 study sites were surveyed for mink scat by two trained searchers; scat was found at 18 sites. Mink scat was identified by its unique twisted appearance, with tapered ends. Mink scat is distinguishable from other mammal scat in the area based on size and appearance. However, if uncertainties in

identification existed, the scat was not collected. Scat samples from a single site were combined in plastic bags and stored at -15°C. In winter 2012 (4 January – 9 March), the 18 sites at which scat was found during fall were revisited and searched, and all detected scats were collected. In an attempt to maximize my time searching, I did not revisit the 41 sites at which I did not find scat. To increase my sample size, I then searched an additional 60 locations for mink scats. From a given location, I moved downstream to the nearest intersecting road bridge and performed an exhaustive search underneath and within 50 m of the bridge. Areas under bridges often include rock and other substrates where mink typically deposit scat. I then moved to a new location at the next downstream bridge ≥1.5 km away and conducted a similar search. This distance between scat collection locations was based on an estimate of average length of mink home ranges in the study area (A. Ahlers, *unpublished data*), and increased the likelihood of independence of scat samples. In summer 2012 (25 June – 31 July), the 18 sites and 60 scat collection locations were revisited. Scat was also collected opportunistically within the same three seasons during a concurrent study of radio-marked mink.

Diet analysis

Each scat was soaked in warm water to facilitate separation of prey remains, washed through a sieve (0.8-mm mesh), and air-dried. I sorted remains into 7 prey classes (crayfish, mammal, bird, fish, insect, reptile, and unknown) under a dissecting microscope (10x) based on hair, teeth, bones, feathers, scales, and exoskeleton fragments. The unknown prey class was mostly comprised of unidentifiable bone fragments. Plant material was excluded from analyses because it was considered incidental intake or adhesion upon collection.

Diet composition was recorded for each of the three seasons (fall, winter, summer) using three metrics: relative frequency of occurrence percentage (RFO; the number of occurrences of each prey class divided by the total number of occurrences of identified prey, times 100), frequency of occurrence percentage (FO; the number of occurrences of each prey class divided by the total number of scat samples, times 100), and volume percentage (VOL; visually estimated as the percentage of each prey class in each scat). RFO and FO were highly correlated positively for all prey classes ($r > 0.80$), so I used FO for analyses. Each metric comes with caveats. FO may overestimate less digestible prey and underestimate more digestible prey. VOL does not account for variation in scat sizes and also could underestimate the contribution of highly digestible prey (Klare et al. 2011). To minimize the influence of biases associated with a single metric, I used both FO and VOL methods in my analyses (Zabala and Zuberogoitia 2003). However, extrapolations from scat samples to the actual relative amounts of each prey type consumed should be made with caution. When making seasonal comparisons with FO data, it should be more difficult to detect differences among prey classes because the contribution of rare food items is exaggerated. VOL data are more likely to reveal differences in the relative amounts of prey types in scats, and thus detect seasonal specialization even if the overall variety of diet items per scat changes little. Because I expect biases due to digestibility of prey types to remain constant across time, and my analyses focus on relative differences among seasons, conclusions about seasonal variation in mink diet should be robust.

For the FO metric, I tested for variation in mink diet among seasons using chi-square tests and Fisher's exact tests when ≥20% of the expected frequencies were <5 (Zar 1984). For the VOL metric, I could not use these same statistical tests because the volume percentages of prey classes were highly dependent (sum to 100%). Therefore, I used non-metric

multidimensional scaling (NMS—Kruskal 1964) to visualize seasonal diets, in which the

distance between scat samples in ordination space represents the degree of dietary dissimilarity.

I then tested for between-season differences in diet composition for the VOL metric using multi-

response permutation procedures (MRPP—Mielke and Berry 2001; Roberts and Taylor 2008). I

employed a Bonferroni correction ($\alpha = 0.05$) when making multiple, pair-wise seasonal

comparisons. An effect size A was calculated to measure the overall dietary agreement among

scat samples within the same season (McCune and Grace 2002; Roberts and Taylor 2008).

Within-season homogeneity of scat samples is greater than expected by chance when $A > 0$,

equal when $A = 0$, and less when $A < 0$ (Roberts and Taylor 2008). The reptile prey class

occurred in only one scat sample during fall, and was excluded from analyses of VOL. NMS

and MRPP analyses were conducted in PC-ORD 6.0 (McCune and Mefford 2011).

I calculated the Shannon diversity index (Shannon 1948) and dietary evenness in each

season using both FO and VOL metrics. I also calculated food niche breadth using Levins

(1968) B index: $B = \sum(p_i^2)^{-1}$ in which p_i is the proportion of scats containing prey class i.

Differences in Shannon diversity index values between seasons were assessed using Student's t-

tests, with variances calculated according to Zar (1984). Statistical tests were performed in SAS

9.2 (SAS Institute Inc. 2010).

Occupancy surveys and crayfish sampling

Occupancy surveys were conducted for mink at the 59 study sites from 18 May – 26 July

2012. Two trained observers independently surveyed each site once. Each observer walked

along both sides of the 200-m stream segment and searched for sign within 5 m of the water's

edge (Schooley et al. 2012). A site was considered occupied by mink if scat or tracks were

detected. Sign may be left by mink with established home ranges that overlap study sites, or by transient mink passing through a site.

Concurrently, crayfish (*Orconectes*, *Procambarus*, *Cambarus*) density was measured at each site by sampling 1-m^2 areas in 10-m segments of stream (20 samples per site). I divided the stream's wetted width in half, randomly selected either the left or right side to begin sampling, and alternated sides as I sampled upstream. A sample was taken at the first potentially suitable crayfish habitat encountered on the selected area within each 10-m segment. In streams ≤1 m wide, the entire stream width was sampled. Potentially suitable habitat consisted of in-stream gravel, cobble, rocks, buried woody debris, or submerged vegetation. If there was no suitable habitat within a segment, I sampled the first 1-m^2 area at the downstream end of the segment. A seine net was placed perpendicular to the stream flow, and a 1-m^2 area of substrate upstream of the net was disturbed so that all crayfish were washed into the seine net (Mather and Stein 1993; Flinders and Magoulick 2003). When necessary in low-flow areas, I dragged the seine net through the sampling area while disturbing the substrate to collect crayfish. Upon collection, crayfish were classified as juvenile (<15 mm carapace length) or adult, and adults were identified to species. All crayfish species were pooled for analyses.

Detection and occupancy covariates

I recorded covariates that could influence detection (*p*) of mink sign including observer, Julian date, rainfall, and number of days since rain. I summed total rainfall (cm) for the 7 days prior to each survey (Illinois State Water Survey, station #118740, Urbana, Illinois). Recent rainfall could wash away sign or raise water levels to hide sign (Schooley et al. 2012).

I measured local habitat and landscape covariates for occupancy including crayfish density, water depth (m), average riparian buffer width (m), degree of urbanization (0-1), drainage area (km^2), wetted width (m), and stream order (1-5). Water depth (thalweg) and riparian buffer width were measured at 50-m intervals (5 values) and averaged for each site (Cotner and Schooley 2011). Drainage area, wetted width, and stream order were correlated positively (all $r > 0.47$; Appendix B: Table 2), so I used principal components analysis (PCA) to create orthogonal principal components (PC). The first PC (sizePC) explained 75.9% of the variation and was correlated positively with all 3 variables ($r = 0.74 – 0.94$), so I used sizePC as a measure of stream size in my models (Cotner and Schooley 2011). I excluded water depth from the PCA because small streams have dynamic flow regimes tied to local precipitation events and they flood and subside faster than do large streams in my study area (Ahlers et al. 2010). Thus, small streams can have deep waters during a sampling period because water depth is influenced by more than stream size. In addition, water depth alone can be a predictor of site occupancy and colonization by mink (Schooley et al. 2012).

Crayfish were patchily distributed and densities varied within a single site, so I evaluated three measures of crayfish density. For each site, I calculated (1) average density of adult crayfish (adults/m^2), (2) average density of total crayfish (adults + juveniles/m^2), and (3) presence-absence of a crayfish "hotspot." A site was considered to contain a prey hotspot if ≥ 1 of the 20 kick-seine samples had a total crayfish density in the top 15% (≥ 15 crayfish/m^2; $n = 171$) of all estimated crayfish densities (median $= 2$ crayfish/m^2, $n = 1,180$; Appendix C: Fig. 1). Although mink are likely to prey only on larger, adult crayfish, I included both adult and total crayfish density because mink could use the presence of small, juvenile crayfish as an indicator of where adults might occur.

Occupancy modeling

I estimated the probability of site occupancy (ψ) by mink using single-season occupancy models that accounted for imperfect detection (MacKenzie et al. 2006) in Program PRESENCE 5.8 (Hines 2006). I developed a candidate set of 12 occupancy models that included within-stream covariates (stream size, water depth) and landscape-level covariates (riparian buffer width, degree of urbanization). The candidate set contained models that tested each covariate separately, and also combinations of within-stream and landscape covariates. I did not include two covariates in the same model if they were correlated at $r \geq 0.60$ (Appendix B: Table 2). I ran this candidate set alone and with each of the three measures of crayfish density (48 total models), and ranked models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) for cross-model evaluation. Akaike weights (w_i) were summed for models that contained each of the three measures of crayfish density to determine which measure of prey abundance was the best predictor of occupancy by mink. I first selected the best model for detection (p), then modeled ψ. I used a maximum of 4 covariates for ψ and 2 covariates for p in a single model to avoid over-parameterization.

RESULTS

American mink diet

I analyzed 103 scat samples (fall = 17, winter = 43, summer = 43). Crayfish and mammals were the most common diet items for mink throughout the year, occurring in >76% of all scats (Fig. 1) and comprising >83% of the diet by volume (Fig. 2). However, frequency of occurrence of diet items differed among seasons ($\chi^2 = 23.7$, *d.f.* = 12, $P = 0.02$). Crayfish

occurred most frequently in summer (Fisher's exact test: winter-summer, $P = 0.003$; fall-summer, $P = 0.016$; Fig. 1), when FO of mammals was lowest (Fisher's exact test, fall-summer, $P = 0.025$; Fig. 1). FO of mammals in the diet was greatest during fall and winter (Fig. 1). Fish occurred in 35.9% of scats, 8.1% by volume. FO of fish increased from fall to winter (Fisher's exact test $P = 0.076$), and both FO (44.2%) and VOL (17.5%) were greatest in winter. Birds occurred in 22.3% of scats, but only comprised 3% of the total scat volume. Similarly, insects occurred commonly in the diet (FO = 48.5%) but made up a small percentage of the dietary volume (3.6%). The unknown prey class was most likely the remains of mammals and birds, but could have included other prey, such as amphibians. Based on FO data, the contribution of this prey class to the diet did not differ between seasons ($P > 0.72$ for all seasonal comparisons; Appendix A: Table 2).

NMS ordination of the VOL metric reinforced the seasonal patterns for mink diet and also emphasized the variation among scats within seasons (Fig. 3). Summer scats were particularly constrained along Axis 1 because they contained primarily crayfish and secondarily mammal remains. In contrast, scats from fall and winter were less constrained and included greater contributions from other prey classes. MRPP results for the VOL metric showed that diet composition for summer differed from diet composition for fall and winter (pair-wise comparisons with Bonferroni corrected $\alpha = 0.0167$: fall-winter, $A = 0.010$, $P = 0.15$; winter-summer, $A = 0.098$, $P < 0.001$; fall-summer, $A = 0.155$, $P < 0.0001$). NMS and MRPP results highlight the greater contribution of crayfish to the diet in summer than in fall and winter (Fig. 2). Repeating the analysis excluding the unknown prey class did not qualitatively affect NMS and MRPP results (Appendix A: Table 3, Fig. 1).

Based on the FO metric, the diversity indices for mink diet did not differ strongly among seasons (Table 1; Shannon diversity index: fall-winter, $t = 0.45$, $d.f. = 86$, $P = 0.65$; winter-summer, $t = 1.03$, $d.f. = 211$, $P = 0.31$; fall-summer, $t = 0.19$, $d.f. = 70$, $P = 0.85$). Based on the VOL metric, summer diets of mink had the lowest evenness, narrowest niche breadth, and lowest diversity (Table 1). Diet of mink was least diverse during summer when they focused on crayfish (Shannon diversity index: fall-winter, $t = 0.19$, $d.f. = 91$, $P = 0.85$; winter-summer, $t = 4.00$, $d.f. = 244$, $P < 0.0001$; fall-summer, $t = 3.23$, $d.f. = 103$, $P < 0.01$).

Summer habitat selection

A total of 7,798 crayfish of 4 species (*Orconectes virilis*, *Orconectes propinquus*, *Procambarus acutus*, *Cambarus* spp.) were captured (2,068 adults, 5,730 juveniles). Average densities of adult crayfish per site ranged from 0 to 16.8 crayfish/m^2 (median = 0.45 crayfish/m^2), and total crayfish densities per site ranged from 0 to 41.8 crayfish/m^2 (median = 2.55 crayfish/m^2). Crayfish hotspots were present at 20 of 59 sites (33.9%). None of the three measures of crayfish abundance were highly correlated with habitat covariates used in occupancy modeling (Appendix B: Table 2) or positively correlated with additional variables characterizing stream substrates (Appendix C: Table 1).

Mink sign was detected at 18 of 59 sites (naïve occupancy = 0.305). I decided the best model for detection was the competitive model ranked second by AIC ($\Delta AIC = 0.14$; Table 2), and I used this model for subsequent evaluation of occupancy covariates. The top detection model contained observer alone, but adding rainfall to that model improved the log likelihood substantially (Table 2). Detection (p) was related positively to rainfall ($\beta_{rainfall} = 0.652$, $SE = 0.501$).

Akaike weights (w_i) summed across occupancy models indicated that among the three

measures of crayfish abundance, the best predictor of site occupancy by mink was presence of a

hotspot (hotspot w_i = 0.821, total crayfish density w_i = 0.100, adult crayfish density w_i = 0.032).

All competitive models (ΔAIC < 2) contained crayfish hotspot as a covariate (Table 3; see

Appendix B: Table 1 for full table). Occupancy probability was related positively to the

presence of a crayfish hotspot at a site ($\beta_{hotspot}$ = 1.721, SE = 0.625; Fig. 4). Estimated occupancy

from the hotspot model was 0.562 for sites with crayfish hotspots, and 0.187 for sites without

hotspots (Table 3). Site occupancy by mink was related negatively to stream size (β_{sizePC} = -

0.598, SE = 0.463; Fig. 4) and urbanization (β_{urban} = -1.793, SE = 1.606; Fig. 4). Although water

depth occurred in competitive occupancy models (Table 3), water depth did not substantially

increase model fit based on log likelihoods; the top 2 models were essentially unchanged by

including depth as a covariate. In addition, the model with depth alone performed worse than the

intercept-only model (Appendix B: Table 1). Riparian buffer width also was not a good

predictor of mink occupancy (Appendix B: Table 1).

DISCUSSION

The spatial distribution of a common prey, crayfish, was the primary driver of habitat

selection during summer by American mink within a human-dominated landscape. Mink appear

to select locations based directly on high prey concentrations instead of habitat characteristics

that might indicate high prey densities. Mink shifted strongly to feeding mainly on crayfish

during summer, and mink were more likely to occupy stream segments that contained crayfish

hotspots. Crayfish hotspots were a far better predictor of mink occupancy than were average

crayfish densities. Habitat occupancy by mink was also affected by stream and landscape characteristics; mink were associated negatively with both urbanization and stream size.

To increase the chance of encountering prey and maximizing energetic gains in a patchy environment (MacArthur and Pianka 1966; Charnov 1976), predators may either select prey habitat or select locations most used by prey (Flaxman and Lou 2009, Keim et al. 2011). Mink in my study appear to select foraging habitat based on locations most used by prey—hotspots with high densities of adult and juvenile crayfish. Given that crayfish density was not highly correlated with any measured habitat variable, mink seemingly cannot use habitat cues to identify good locations to hunt for crayfish and must instead cue directly on crayfish. This tactic may be particularly true in human-dominated landscapes in which stream habitat structure is altered due to channelization, habitat heterogeneity is low, and prey distribution might mostly reflect spatial population dynamics. I measured a range of habitat variables used for assessing crayfish abundance (Riggert et al. 1999; DiStefano et al. 2003), but mink could be keying in on a habitat factor that I did not measure. For example, I did not measure the cover of submergent macrophytes at crayfish hotpots. Macrophytes provide protective cover for crayfish from predators (Kershner and Lodge 1995), and thus may be associated with crayfish abundance. It is possible that mink recognize areas with high cover of submergent macrophytes as good locations to hunt.

My results have implications for the efficacy of habitat models for species management. For instance, Loukmas and Halbrook (2001) concluded that the poor performance of a habitat suitability model for mink was primarily due to lack of habitat variables for key prey. If mink cue in on its prey directly, then improving model performance will be difficult if habitat variables are used as surrogates for prey abundance. However, quantification of prey abundance

can be difficult, time-consuming, and expensive, especially for a generalist predator that consumes a variety of prey items. My approach of using seasonal diet data to identify key prey and direct resource measurement could be the most efficient strategy for developing predictive habitat models for predators.

In my study, habitat selection by mink was also influenced by urbanization and stream size. Mink had a lower occupancy probability in urban areas (Fig. 4). The ability of mammalian carnivores to adapt to urban areas is influenced by characteristics such as body size, reproductive potential, diet, behavior, and habitat requirements (Gehrt et al. 2010). Urbanization fragments natural habitats (McKinney 2002), which can cause the decline or local extinction of carnivore species (Crooks 2002). Roads and human development act as barriers to dispersal (Forman and Alexander 1998; Riley et al. 2006) and increase mortality risk from vehicle collisions (Dickson et al. 2005; Tigas et al. 2002). However, little information exists regarding the effects of urbanization on mink (Gehrt et al. 2010). In Canada, cottage development around lakes reduced habitat heterogeneity, causing decreased mink activity near human development and altered diets of mink (Racey and Euler 1983). Radio-marked American mink in Polish lakes also avoided areas near human settlements (Brzeziński et al. 2012). These studies were not set in urban areas, but they demonstrate the negative impact of habitat alteration and human disturbance typical of urban areas on the behavior of mink, and agree with my result. Contrary to my prediction, site occupancy for mink was related negatively to stream size (Fig. 4). I expected mink to select larger streams with more available resources, and I do not have an explanation for this surprising result.

I did not detect a strong, positive relationship between occupancy probability for mink and water depth in contrast to previous research in my study area (Schooley et al. 2012). Our

results may differ because of much less variable water levels during my study, which took place during the severe drought of 2012. In contrast, Schooley et al.'s (2012) study included a year with extreme flooding (2008 was 2nd wettest year on record; Changnon and Black 2009). Different factors may influence mink habitat selection under different environmental conditions. Schooley et al. (2012) noted that colonization of vacant sites was variable if water depths were ≤0.4 m, but consistently high if water depths were >0.4 m. Seventy-one percent (42 of 59) of sites during my study had water depths below 0.4 m. Thus, I acknowledge that my study is a "snapshot" during an abnormally dry year and my results may not extend to years of high precipitation. However, it is important to put these occupancy dynamics in perspective because climate models for the Midwestern United States predict an increase in the frequency of summer drought and spring flooding events (Wuebbles and Hayhoe 2004; Trenberth 2011). Mink and other semiaquatic mammals are likely to experience increased environmental stochasticity that could create temporal variability in factors that influence habitat selection.

The diet of mink in my study reflected the seasonal availability of prey. Although crayfish and mammals were important year-round food sources for mink, crayfish occurred most frequently and in the highest volume in the summer diet. Low diversity, evenness, and niche breadth values during summer indicate greater dietary specialization on crayfish at this time of year. This specialization appears to drive the habitat selection behavior of mink during this season. Some species of crayfish move into deeper water and severely reduce activity at low water temperatures (Aiken 1968). This behavior may make crayfish less available to terrestrial and semiaquatic predators during winter. Conversely, fish increased in frequency and volume in the diet from fall to winter. Other diet studies of mink have observed increased fish consumption during winter as a result of increased vulnerability of fish (Gerell 1967; Magnusdottir et al.

2012). Low water temperatures decrease the mobility of fish, making them more vulnerable to predation (Parsons and Smiley 2003; Brown et al. 2011). My study area experienced an unseasonably mild winter during scat collection in 2012. January and February temperatures in Illinois were 3.67°C and 2.61°C warmer than average, respectively (Illinois State Water Survey 2012b; Illinois State Water Survey 2012c). Thus, many streams did not freeze over, but were still cold enough to decrease the mobility of fish, thus allowing mink constant access to vulnerable fish prey.

The combined results of my diet analysis and occupancy modeling indicate that the locations that mink choose to occupy during summer are greatly influenced by the abundance patterns of their preferred prey. Prey availability can drive space use for other carnivores (e.g., Halpin and Bissonette 1988; Murray et al. 1994). For mink, crayfish hotspots were more important than average crayfish densities for predicting habitat occupancy. The importance of prey hotspots for semiaquatic predators, and the relationship between habitat use by predators and direct measures of prey abundance are difficult to evaluate. More empirical evidence is necessary to fully understand the mechanisms that drive habitat selection by carnivores across variable landscapes.

Table 1. Three indices summarizing the diet of American mink (*Neovison vison*) across three seasons: fall 2011, winter 2012, and summer 2012, in Illinois, USA. Indices were calculated both using frequency of occurrence percentage data and volume percentage data.

Index	Frequency of occurrence			Volume		
	Fall	Winter	Summer	Fall	Winter	Summer
Shannon diversity index	1.65	1.60	1.68	1.30	1.27	0.81
Evenness	0.85	0.90	0.93	0.67	0.71	0.45
Food niche breadth	4.49	4.38	4.77	2.96	2.92	1.70

Table 2. Ranking of detection (p) models for American mink in Illinois based on Akaike's Information Criterion (AIC). Detection covariates included observer, Julian date, days since rain, and rainfall for 7 days prior to each survey (rainfall). ΔAIC = AIC for a given model minus AIC for the top model. K = number of model parameters, w_i = Akaike weights, and LL is the log-likelihood. Models better than the intercept-only model are presented.

Model	ΔAIC	w_i	K	-2*LL
$\psi(.), p(\text{observer})$	0	0.2849	3	103.34
$\psi(.), p(\text{observer, rainfall})$	0.14	0.2657	4	101.48
$\psi(.), p(\text{observer, days since rain})$	0.83	0.1881	4	102.17
$\psi(.), p(\text{observer, Julian date})$	1.58	0.1293	4	102.92
$\psi(.), p(\text{observer, Julian date, days since rain})$	2.80	0.0703	5	102.14
$\psi(.), p(.)$	3.06	0.0617	2	108.40

Table 3. Ranking of occupancy models for American mink in Illinois based on Akaike's Information Criterion (AIC). Detection covariates included observer and rainfall for the 7 days prior to each survey (rainfall). Occupancy covariates included presence-absence of a crayfish hotspot (hotspot), stream size (sizePC), water depth, and degree of urbanization. ΔAIC = AIC for a given model minus AIC for the best model. K = number of model parameters, w_i = Akaike weights, and LL is the log-likelihood. Competitive models (ΔAIC <2) and the intercept-only model without occupancy covariates are presented.

Model	ΔAIC	w_i	K	-2*LL
ψ(hotspot, sizePC), p(observer, rainfall)	0	0.1533	6	91.28
ψ(hotspot), p(observer, rainfall)	0.12	0.1444	5	93.40
ψ(hotspot, urbanization), p(observer, rainfall)	0.62	0.1124	6	91.90
ψ(hotspot, sizePC, urbanization), p(observer, rainfall)	0.74	0.1059	7	90.02
ψ(hotspot, depth), p(observer, rainfall)	1.87	0.0602	6	93.15
ψ(hotspot, sizePC, depth), p(observer, rainfall)	1.87	0.0602	7	91.15
ψ(.), p(observer, rainfall)	6.20	0.0069	4	101.48
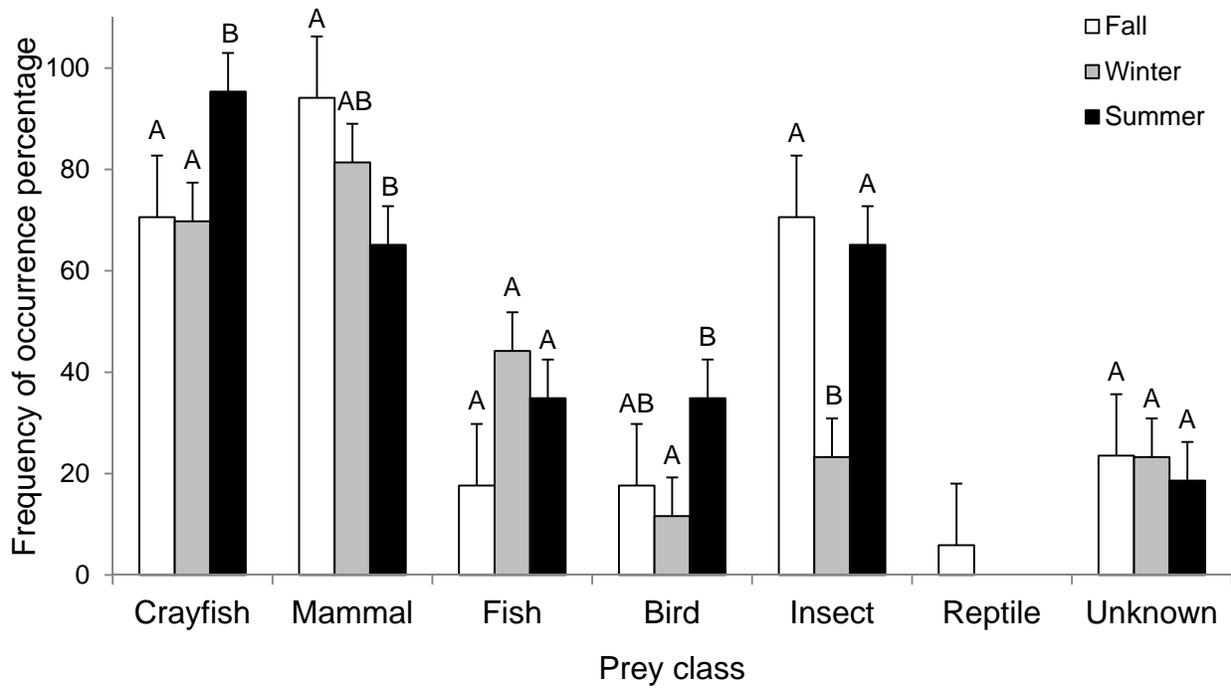
Figure 1. Mean frequency of occurrence (+ 1 *SE*) of 7 prey classes in the diet of American mink in fall 2011 (*n* = 17 scat samples), winter 2012 (*n* = 43), and summer 2012 (*n* = 43). Within a prey class, bars with different letters indicate differences among seasons (Fisher's exact tests).
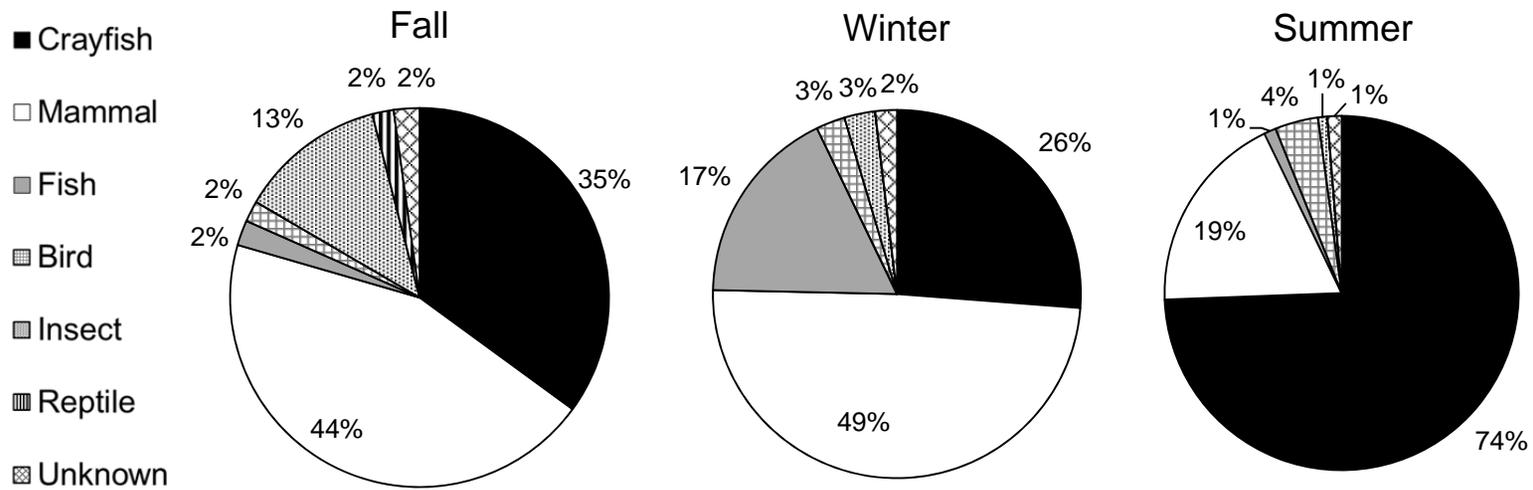
Figure 2. Volume percentage of 7 prey classes in the diet of American mink in fall 2011 (*n* = 17 scat samples), winter 2012 (*n* = 43), and summer 2012 (*n* = 43).
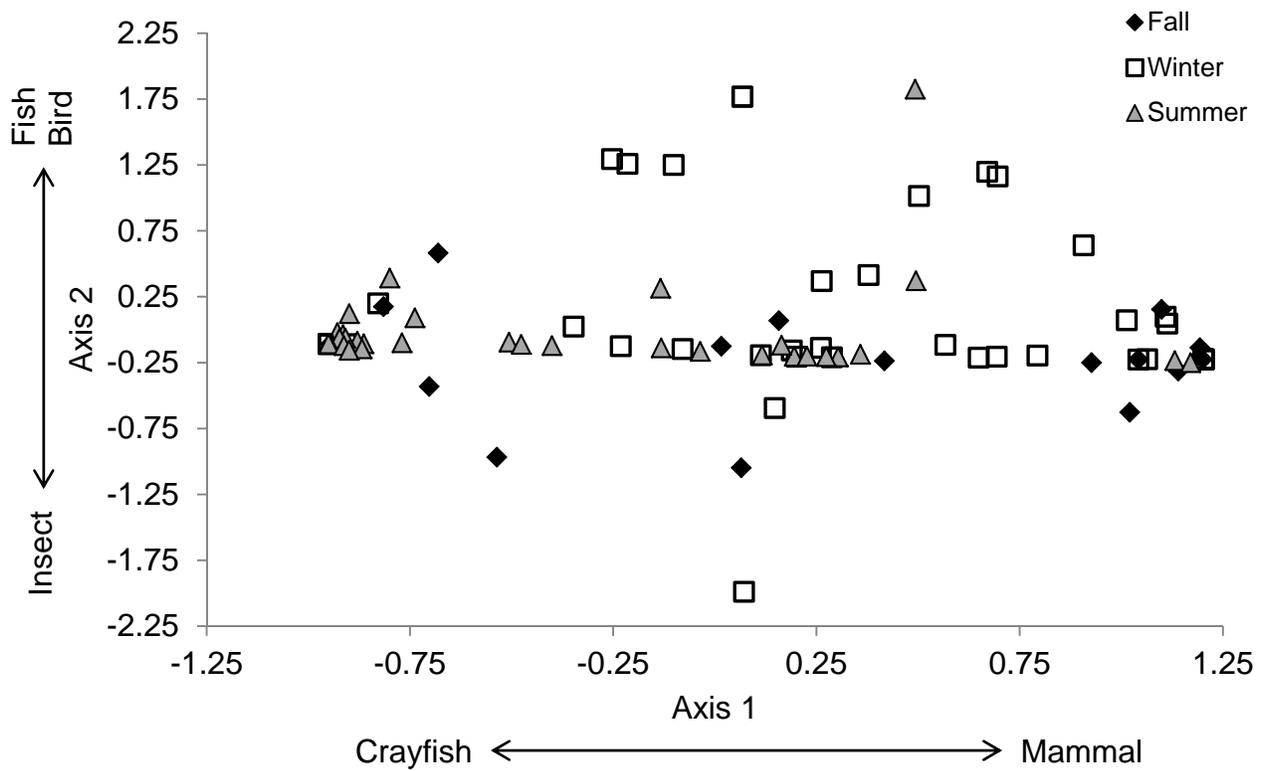
Figure 3. Non-metric multidimensional scaling ordination of the volume percentage of prey classes in American mink scats in fall 2011 ($n = 17$ scat samples), winter 2012 ($n = 43$), and summer 2012 ($n = 43$). Each point represents one scat sample. Distances between points represent the degree of dietary dissimilarity.
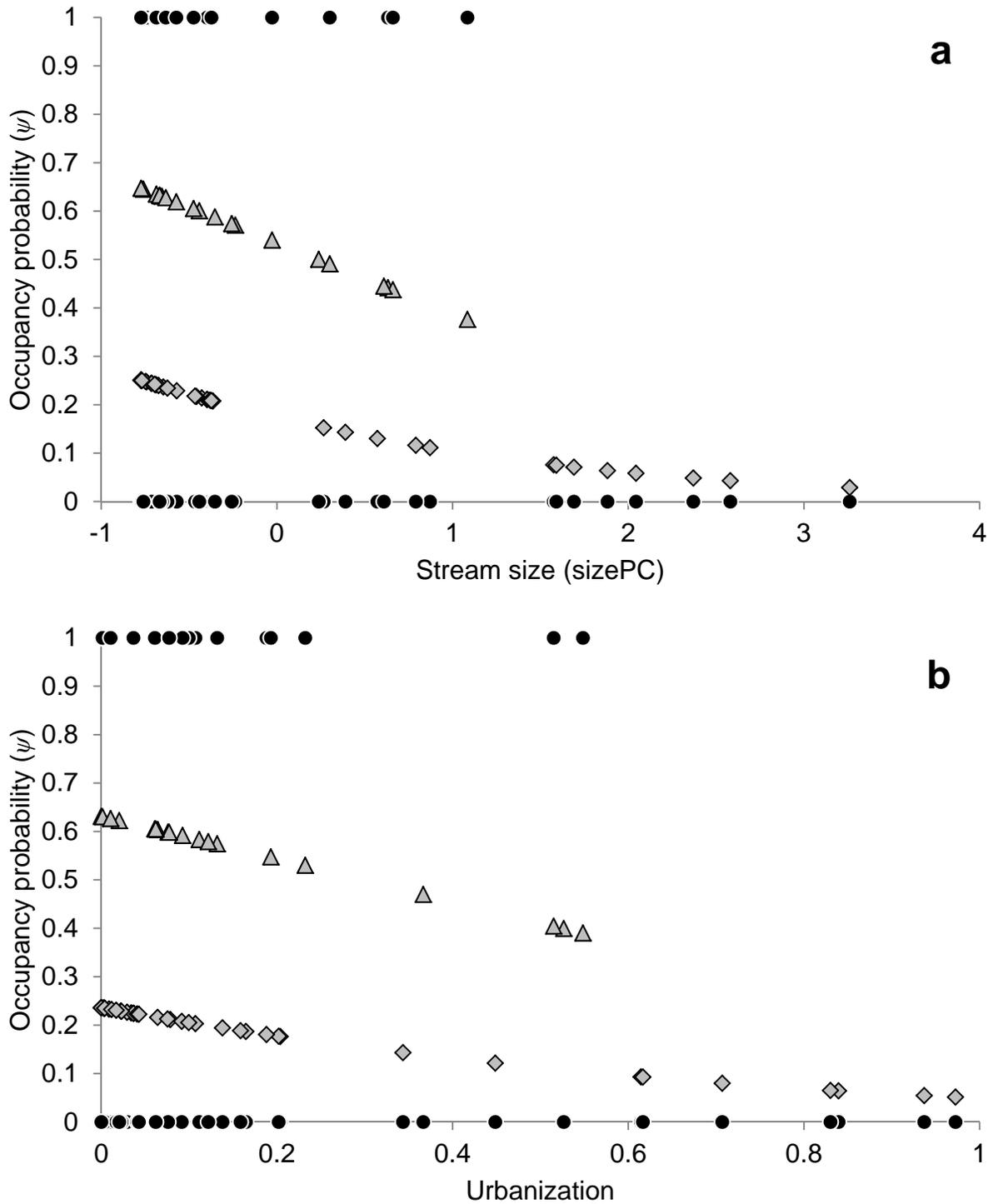
Figure 4. Relationships between probability of site occupancy by American mink and (a) stream size from the top occupancy model (see Table 3), and (b) urbanization from the 3rd best occupancy model (Table 3). Gray triangles indicate estimated occupancy at sites with crayfish hotspots. Gray diamonds indicate estimated occupancy at sites without crayfish hotspots. Black circles indicate naïve occupancy for sites.

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CHAPTER 3: PREDATION RISK FOR CRAYFISH CHANGES BETWEEN DROUGHT AND NON-DROUGHT YEARS

INTRODUCTION

Predator-prey interactions form ecologically significant links between terrestrial and aquatic ecosystems (Polis et al. 1997). Terrestrial and semiaquatic predators may depend on aquatic prey (Jędrzejewska et al. 2001, Marchand and Litvaitis 2004), and predation on aquatic prey by terrestrial predators may provide a pathway by which the productivity of aquatic systems is transferred to land (Schmitz et al. 2010). Similarly, aquatic prey may be depredated by both aquatic and terrestrial predators, and the relative predation risk from each could affect the abundance, behavior, and distribution of aquatic prey species (Stein and Magnuson 1976, Sih et al. 1985, Kershner and Lodge 1995). Climate change is expected to increase variability in precipitation in the Midwestern United States; climate models predict an increase in frequency of summer drought and spring flooding events (Wuebbles and Hayhoe 2004, Trenberth 2011). These changes will lead to increased temporal fluctuations in water depths and flow regimes of streams that could have consequences for predator-prey interactions in riparian ecosystems. Because access to aquatic prey may be affected by water depth for many terrestrial predators, relative predation risk from terrestrial and aquatic predators may differ under drought and wet conditions. Understanding how predation risk of aquatic prey may change between drought and non-drought conditions can be useful for predicting potential impacts of climate change on aquatic species.

Crayfish are important components of aquatic food webs because of their role as habitat modifiers (Momot 1995), consumers (Creed 1994, Lodge et al. 1994), and prey (Stein 1977). Crayfish commonly occur in the diet of aquatic (Saiki and Ziebell 1976, Nyström et al. 2006) and terrestrial riparian predators (e.g., raccoon [*Procyon lotor*; Dorney 1954]; great blue heron

[*Ardea herodias*; Hunt et al. 1995]; American mink [*Neovison vison*; Gerell 1967]). Predation

risk for crayfish is affected by habitat characteristics and the predator community. Risk from

aquatic predators such as fish is typically greater in deep water than in shallow water (Mather

and Stein 1993, Flinders and Magoulick 2007, Clark et al. 2013), particularly for smaller crayfish

because fish are gape-limited predators (Englund and Krupa 2000). Crayfish of all sizes are at

risk from terrestrial predators in shallow waters (Englund and Krupa 2000), and terrestrial

predators are more likely to depredate larger, adult crayfish than small juveniles (Correia 2001).

Therefore, low water levels during drought may provide easy access to crayfish by terrestrial

predators, increasing predation risk for the largest size classes.

Predation risk also is related negatively to substrate particle size or the presence of other

structural features that can provide hiding cover. For example, crayfish are at a greater risk in

sand than in cobble or macrophyte-dominated habitats that provide refuges from predation

(Kershner and Lodge 1995). Experimental manipulations of substrate indicate the presence of

large, rocky refugia increases crayfish survival (Clark et al. 2013). Cover provided by

submerged vegetation or substrates with large particle sizes could be particularly critical for

avoidance of terrestrial predators when water levels are low during drought. Both biotic and

abiotic factors that affect predation risk are likely to differ under different hydrologic conditions

influenced by climate change. Therefore, it is important to measure the relative importance of

risk factors during drought and non-drought years to understand how environmental stochasticity

from climate change will alter predation risk.

Predation risk may also be affected by landscape features. Predator-prey interactions are

altered by land-use modifications such as agriculture production (Shapira et al. 2008) and

urbanization (Francis et al. 2009, Rodewald et al. 2011). Agricultural intensification in the

Midwestern United States has led to stream channelization (Mattingly et al. 1993), and urbanization is associated with extreme degradation of stream habitat (Paul and Meyer 2001) and biotic homogenization (McKinney 2006). Land conversions and drainage for row-crop agriculture have reduced the amount of natural habitat (Zucker and Brown 1998) and have restricted some riparian predators to linear habitats along small streams and agricultural ditches. These riparian buffers vary considerably in characteristics such as width and vegetation structure (Ahlers et al. 2010), which should affect their attractiveness to terrestrial predators. Although the landscape surrounding a stream remains fairly constant between years, interactions between water depth and landscape characteristics may change risk between drought and non-drought years.

I compared predation risk for crayfish within a human-dominated landscape in a year of severe drought to that in a non-drought year. Specifically, I evaluated effects of crayfish size, within-stream characteristics, and landscape context on crayfish mortality using an experiment in which tethered crayfish were exposed to aquatic and riparian predators. I hypothesized that predation risk would vary between drought and non-drought years because of changes in water depth. Because crayfish are likely at greater risk from aquatic predators in deep water and from terrestrial predators in shallow water, I predicted that terrestrial predators would be responsible for more predation events during the drought than during the non-drought year. High water levels during the non-drought year should restrict access by wading predators to crayfish. Thus, hiding cover provided by submerged vegetation or substrates with large particle sizes should be more important when water levels are low and risk from terrestrial predators is high. Many aquatic predators are gape-limited, but terrestrial predators can eat crayfish of all sizes in my

study system, so I also predicted that smaller crayfish would have greater predation risk than would larger crayfish when water levels are high.

I hypothesized that landscape context of streams would affect predation risk of crayfish in three ways. First, predators that also forage for terrestrial prey should be less likely to encounter crayfish in streams surrounded by wider riparian buffers because there are more available terrestrial foraging opportunities. However, foraging in streams by terrestrial predators may become more attractive when water levels are low in drought years and aquatic prey such as crayfish are more vulnerable, reducing any dilution effect of riparian buffers on predation risk. Second, fish predators should be less abundant in urbanized areas (Steedman 1988, Wang et al. 1997, Paul and Meyer 2001), but terrestrial predators such as raccoons may be more abundant (Gehrt et al. 2006). Therefore, drought years that shift predation toward terrestrial predators may increase relative predation risk in more urbanized streams. Third, larger streams contain a greater diversity of aquatic predators (Sheldon 1968, Horwitz 1978, Osborne and Wiley 1992) including larger fish (Evans and Noble 1979, Rahel and Hubert 1991). In these streams, risk from aquatic predators is greater than risk from terrestrial predators, and risk should be less affected by annual variation in precipitation because large streams should retain deeper water better than small streams in drought years.

METHODS

Study area

My study was conducted in the human-dominated landscape of east-central Illinois, U.S.A., centered on Champaign-Urbana (40°12'N, 88°26'W). Currently, 85% of the landscape is dedicated to corn (*Zea mays*, 45%) and soybean (*Glycine max*, 40%) production. Urban

sprawl is associated with an increased human population size (e.g., 11.9% population increase in Champaign County in the last decade). Forty-five study sites were distributed across 4 watersheds (Sangamon, Kaskaskia, Embarras, and Vermilion) and across an urbanization gradient (defined below) with a median nearest-neighbor distance of 3.8 km (range = 0.5 – 17.8 km). Each site was a 200-m stretch of stream, ranging from 1st to 5th order in size, and included a wide range of riparian buffer widths (0 – 466 m). My study area experienced a severe drought in 2012, and multiple streams reached record lows for streamflow during my study (Illinois Department of Natural Resources 2013). However, by March 2013, most streams in Illinois returned to normal or above normal flows (Illinois Department of Natural Resources 2013).

Predation risk experiment

I quantified how predation risk for crayfish changed between drought and non-drought conditions in relation to crayfish size, within-stream traits, and landscape context by tethering crayfish in streams. I used crayfish mortality as a measure of predation risk. The field experiment was conducted at 45 sites in 2012 (23 July – 27 September), and at 44 of the same sites in 2013 (3 June – 29 July). One site could not be resampled in 2012 because it was under construction and inaccessible.

I collected crayfish immediately downstream of each site, or within 8 km and in the same drainage as the site if crayfish were not available near the site. Crayfish were stored in a laboratory aquarium until they were deployed. I measured carapace length (mm) using digital calipers. Crayfish were tethered with 30 cm of monofilament fishing line (6-lb. test) attached to tent stakes that were then hammered into the streambed. I used cyanoacrylate (Super Glue) to secure the monofilament to the dorsal side of the crayfish carapace. Preliminary tests of this

tethering technique showed that crayfish were unable to escape tethers. Other studies have successfully tethered crayfish using similar techniques (Kershner and Lodge 1995, Flinders and Magoulick 2007, Dekar and Magoulick 2013). All missing crayfish were assumed to have been depredated, excluding individuals that molted (exuviae present).

At each site, 4 crayfish were placed 1 m from the bank and 50 m apart within the 200-m stream reach (2012, $n = 180$ crayfish; 2013, $n = 176$ crayfish). The 50-m spacing was intended to minimize spatial autocorrelation of predation events due to predator trap-lining. My sites comprised a range of stream morphologies, so crayfish communities were variable across sites. I used only common species found at a given site (based on sampling from summer 2012, see Chapter 2) for the tethering experiment. Three species were used in total, but all 4 crayfish at a site were always of the same species. The 3 species were virile crayfish (*Orconectes virilis*: 2012, $n = 116$; 2013, $n = 116$), northern clearwater crayfish (*Orconectes propinquus*: 2012, $n = 40$; 2013, $n = 32$), and White River crayfish (*Procambarus acutus*: 2012, $n = 24$; 2013, $n = 28$). I did not include "species" as a covariate for statistical modeling because the main effect of species identity on predation risk would be due to body size differences, which was already indexed by carapace length.

Crayfish were exposed for 3 nights, and mortality was recorded after the third night. A predation event occurred if a crayfish was missing. Survival included all crayfish that were living or dead-intact and still attached to the tether.

Potential predators of crayfish included raccoons, American mink, river otters (*Lontra canadensis*), muskrats (*Ondatra zibethicus*), great blue herons, green herons (*Butorides striatus*), sora (*Porzana carolina*), various Passeriformes species, various duck species (Anatidae), bullfrogs (*Rana catesbeiana*), snapping turtles (*Chelydra serpentine*), and various fish species.

These animals differ in size, and terrestrial predators vary in diving ability. A trail camera (Wildgame Innovations, LTD, Grand Prairie, Texas) with the capacity to record short videos was placed on the stream bank and aimed at the tethered crayfish to record predation events. Cameras were tied to wooden stakes (5.1 x 7.6 x 122 cm) that were driven into the stream bank. Cameras had a passive infrared sensor that activated when motion and heat were detected within 15 m, and had an infrared flash range of 15 m. Other studies of crayfish predation made general inferences about the predator community based solely on field surveys (Englund and Krupa 2000, Dekar and Magoulick 2013). I used cameras in an attempt to attribute predation events to specific terrestrial predators. Cameras were not successful in recording aquatic predators because of low visibility at sites with turbid water or high cover of submerged vegetation.

Camera footage (video segments 15 – 30 s long) was reviewed and predation events were attributed to specific predator species if there was proof that the animal depredated a crayfish. There were instances in which a camera did not capture the exact moment of a predation event, but the predator could be reasonably inferred by combining multiple video sequences. For example, in some streams with high visibility there were video sequences in which (1) a crayfish was present in one clip, (2) a raccoon was foraging near the crayfish in the next clip, and (3) the crayfish was gone in the last clip. I included these cases of "probable" terrestrial predation (2012: $n = 6$, 8.1% of predation events; 2013: $n = 4$, 4.5% of predation events) in my analyses of predator-specific mortality risk to increase my sample size. Exclusion of these cases did not qualitatively affect my results. All predation events in which no terrestrial predator was observed were assumed to occur underwater and were attributed to aquatic predators.

Within-stream and landscape covariates

For each crayfish, I recorded 3 within-stream covariates and 3 landscape covariates that could influence predation risk. Within-stream covariates (submerged vegetation cover, substrate particle size, and water depth) were measured within a 1-m^2 area centered on each crayfish location when crayfish were deployed. Submerged vegetation cover (%) was visually estimated to the nearest 5%. Substrate was quantified using a substrate cross (two 1-m long metal rods that intersect perpendicularly at the other's midpoint). I dropped the cross at each crayfish location and measured the substrate particle size class (mm) using a gravelometer at each endpoint and at the center of the cross (5 total values). I then averaged the 5 values to create 1 measure of particle size (mm). Water depth (m) was measured with a meter stick at each crayfish location.

Landscape covariates were measured at the site level and included riparian buffer width, degree of urbanization, and stream size. Riparian buffer width (m) was measured at 50-m intervals (5 values) and averaged for each site. Urbanization was the proportion of impervious surface within a 500-m buffer of each site (scale of $0 - 1$). Riparian width and urbanization had been measured previously for my sites (Cotner and Schooley 2011). Stream size was a composite measure calculated using principle components analysis (PCA) and included 3 variables. Wetted width (m), stream order ($1 - 5$), and drainage area (km^2) were highly correlated ($r > 0.83$), so I used PCA to create orthogonal principal components (PC). The first PC (sizePC) explained 90.7% of the variation and was positively correlated with all 3 variables ($r = 0.95 - 0.96$), so I used sizePC as a measure of stream size (Cotner and Schooley 2011). I tested for differences in crayfish size and within-stream covariates between years using Wilcoxon signed-rank tests.

Modeling effects of covariates on predation risk

I evaluated the effects of crayfish size, within-stream covariates, and landscape covariates on predation risk for crayfish separately for 2012 and 2013 using generalized linear mixed models (PROC GLIMMIX; SAS Institute Inc. 2010). I modeled the response variable as binary (0 = crayfish survival, 1 = predation event) and used a logit link function. Site was treated as a random block effect, and the 7 covariates were fixed effects. I used the Laplace approximation in PROC GLIMMIX in which marginal likelihoods are estimated using maximum likelihood techniques, instead of pseudo-likelihoods, which allowed me to use Akaike's Information Criterion (AIC, Burnham and Anderson 2002) to evaluate models. Because R-side random effects are not permitted with the Laplace approximation, I did not combine data for the two years in a repeated measures analysis.

I ranked candidate models using AIC. To avoid an unreasonably large candidate model set and over-parameterization of models, I used a 2-stage approach that resulted in 1 model containing the best predictors of predation risk for each year. First, I evaluated within-stream covariates to determine which variables influenced predation risk within 1-m^2 of each crayfish. The candidate set consisted of the 3 within-stream covariates tested individually and in additive combinations (7 models). I repeated this candidate set with and without carapace length included in each model. At this first stage, I used ΔAIC values and log-likelihoods to determine the "best" model, which was retained for the second stage. The "best" model was not necessarily the model with ΔAIC = 0; the "best" model could be a competitive model (ΔAIC $\leq$ 2) with supported covariates. Second, I evaluated effects of the landscape covariates on predation risk. This candidate set consisted of the 3 landscape covariates tested individually and in additive combinations (5 models). The landscape candidate set had 2 fewer models than the within-

stream candidate set because riparian width and sizePC were highly correlated ($r = 0.76$) and not included in the same model.

The candidate model sets for within-stream covariates were identical between years, and contained all possible model subsets, so covariate importance could be compared both between and within years using summed Akaike weights (w_i, Burnham and Anderson 2002). In particular, I used summed Akaike weights to determine whether within-stream covariates affected predation risk of crayfish differently in a drought year (2012) versus a non-drought year (2013). Because of different "best" models in the first stage of this process (see Results), landscape model sets in the second stage differed between years, and I could not use summed Akaike weights to compare the relative importance of landscape covariates between years.

Modeling predator-specific mortality risk

I examined whether carapace length, within-stream covariates, and landscape covariates influenced the type of predator (terrestrial or aquatic) responsible for predation events (2012, $n = 74$; 2013, $n = 89$). Again, I used PROC GLIMMIX in SAS 9.2 to create generalized linear mixed models. The binary response variable was predator type (1 = terrestrial, 2 = aquatic), and covariates were fixed effects. Site was a random block effect. Each covariate was tested individually (7 models), and ranked using AIC. Models that outperformed the intercept-only model indicated predator type varied according to that covariate, and the relationship between the predator type and the covariate was indicated by the β parameter estimate. I ran this analysis for each year separately.

Predation risk experiment

Stream conditions varied between the severe drought year (2012) and the non-drought year (2013). Water depths were lower (p <0.001) in 2012 (median = 0.20 m, 25th percentile – 75th percentile = 0.13 m – 0.28 m) than in 2013 (median = 0.34 m, 0.22 m – 0.48 m). Substrate particle size was smaller (p = 0.007) in 2012 (median = 4.0 mm, 4.0 mm – 7.7 mm) than in 2013 (median = 5.5 mm, 4.0 mm – 10.3 mm). Submerged vegetation cover was not different (p = 0.88) between years (2012: median = 7.5%, 0% – 80%; 2013: median = 10%, 0% – 50%). The size of crayfish (carapace length) used in the tethering experiment was smaller (p <0.001) in 2012 (median = 29.8 mm, 25.9 mm – 33.7 mm) than in 2013 (median = 37.2 mm, 33.6 mm – 42.8 mm). See Appendix D for the distributions of within-stream covariates in 2012 and 2013.

Crayfish had to be censored from analyses in both years. In 2012, 4 crayfish molted and 3 stakes were lost, resulting in a final sample size of 173 crayfish. In 2013, 5 stakes were lost, resulting in a sample size of 171 crayfish.

In 2012, 74 of 173 (42.8%) crayfish were depredated. Terrestrial predators were definitively identified in 14 predation events (12 raccoon, 1 great blue heron, 1 common grackle [*Quiscalus quiscula*]), and an additional 6 predation events were attributed to "probable terrestrial predators" (5 raccoon, 1 great blue heron). The remaining 54 predation events were credited to aquatic predators (1 bullfrog, 53 unknown). Crayfish mortality was higher in 2013 (χ^2 = 2.97, df = 1, p = 0.085); 89 of 171 (52.0%) crayfish were depredated. Four terrestrial predators were definitively identified (3 raccoon, 1 great blue heron), and an additional 4 predation events were attributed to "probable terrestrial predators" (3 raccoon, 1 great blue heron). Unknown aquatic predators were responsible for 81 predation events.

Predictors of predation risk

The influence of crayfish size, within-stream covariates, and landscape covariates on predation risk differed between 2012 and 2013. During the drought of 2012, carapace length was not a predictor of predation risk (Fig. 5); the intercept-only model outperformed the model with carapace length (Table 4). In 2012, the best within-stream model was the top-ranked model, which included only submerged vegetation (Table 4). Predation risk was related negatively to the percentage of submerged vegetation cover at a crayfish location (β = -0.019, SE = 0.005; Fig. 6). There were competitive models (ΔAIC <2) that included additional covariates, but the most influential variable by far was submerged vegetation cover, as indicated by the summed Akaike weights (Table 5). The addition of other covariates to the submerged vegetation model did not improve model fit substantially (Table 4). Therefore, I retained the submerged vegetation model for my analysis of landscape effects in 2012. All landscape models were competitive with the submerged vegetation model (Table 4). However, only the inclusion of urbanization and sizePC substantially improved model fit (log-likelihoods), indicating these covariates influenced predation risk. In 2012, predation risk for crayfish was related negatively to urbanization (β = -0.886, SE = 0.748; Fig. 7) and positively to stream size (sizePC, β = 0.303, SE = 0.211; Fig. 8).

In 2013, carapace length was a predictor of predation risk (Table 6). Predation risk was related positively to carapace length (β = 0.131, SE = 0.043; Fig. 5). There were 8 competitive within-stream models, and each contained carapace length (Table 6). Two within-stream covariates, submerged vegetation and substrate particle size, improved model fit when included with carapace length (Table 6). Summed Akaike weights indicated these covariates were of

similar relative importance (Table 5). Predation risk was related negatively to submerged

vegetation cover (β = -0.010, SE = 0.006; Fig. 6) and to substrate (β = -0.033, SE = 0.025).

Water depth was a poor predictor of predation risk (Table 5). Thus, I retained the model with

carapace length, submerged vegetation, and substrate for my analysis of landscape effects in

2013. There were 2 competitive landscape models (Table 6), both of which outperformed the

model containing only within-stream covariates. Predation risk was related negatively to

urbanization (β = -1.715, SE = 1.084; Fig. 7) and positively to sizePC (β = 1.651, SE = 0.398;

Fig. 8).

Comparison of summed Akaike weights between years indicated submerged vegetation

cover was the most influential within-stream variable during the severe drought, but submerged

vegetation was relatively less important during the non-drought year (Table 5). Carapace length

had the greatest importance when water levels were high in 2013.

Predator-specific mortality risk

Aquatic predators were responsible for more predation events (81 of 89; 91%) when

water levels were high in 2013 than during the drought of 2012 (54 of 74; 73%; χ^2 = 9.24, df = 1,

p = 0.002). In 2012, water depth and carapace length influenced the type of predator that

depredated a crayfish (Table 7). Terrestrial predators depredated crayfish more often in

shallower water, and aquatic predators depredated crayfish more often in deeper water (β = -

54.104, SE = 33.901; Fig. 9a). Terrestrial predators also depredated larger crayfish than did

aquatic predators (β = 0.418, SE = 0.212; Fig. 9b).

In 2013, water depth was the only covariate that explained variation in which predator

type was responsible for predation events (Table 7). Similar to 2012, terrestrial predators

depredated crayfish more often in shallower water, whereas aquatic predators depredated

crayfish more often in deeper water (β = -23.158, SE = 14.333; Fig. 10). Exclusion of

"probable" terrestrial predators from analyses did not qualitatively affect results in 2012 or 2013

(Appendix E: Table 1).

DISCUSSION

Different water levels of streams in a drought versus non-drought year caused the factors

influential on predation risk for crayfish to change in a human-dominated landscape. During the

severe Midwestern drought of 2012, cover of submerged vegetation was the most important

factor affecting predation risk, whereas crayfish size was the main factor in 2013 when streams

had returned to normal or above-normal streamflow. Crayfish were always at the greatest risk

from aquatic predators, although there was a shift towards more risk from terrestrial predators

during the drought. Landscape characteristics were also influential in both years; predation risk

was related positively to stream size and negatively to urbanization. These results indicate

increased variability in hydrology expected under climate change will alter predation risk for

crayfish but that landscape context also matters.

Overall predation risk was not increased during the drought. In fact, the trend was for

lower risk during the drought year (43%) than the non-drought year (52%). Aquatic predators

were predominant in both years, but there was an increase in predation by terrestrial predators

during the drought presumably because lower water levels provided more access to crayfish.

The foraging efficiency of wading predators decreases with increasing water depth (Power

1987), and I found that terrestrial predators depredated more crayfish in shallow water. High

water levels in 2013 restricted terrestrial predators, but apparently gave aquatic predators more

access to crayfish which led to a higher proportion of predation events by aquatic predators than during the drought. My results confirm previous findings that risk from aquatic predators is greatest in deep water (Mather and Stein 1993, Flinders and Magoulick 2007), and that terrestrial predators consume large crayfish in shallow water (Englund and Krupa 2000).

The relative importance of within-stream habitat variables differed between years. Cover of submerged vegetation was important in both years. However, during the drought when risk from terrestrial predators was highest, cover of submerged vegetation was the single most influential habitat feature affecting predation risk. Survival of crayfish was greatest in locations with high cover of submerged vegetation where crayfish could take refuge and decrease their vulnerability (see also Kershner and Lodge 1995). Vegetation cover also is an important habitat feature for reducing predation risk of other aquatic prey (Savino and Stein 1982, Camp et al. 2012).

Submerged vegetation and substrates with large particle sizes serve similar protective purposes for crayfish. Substrates with larger particle sizes, such as cobble or rocks, provide a greater number of suitable interstitial spaces in which crayfish can hide than substrates with smaller particle sizes, such as sand or silt (Stein and Magnuson 1976, Kershner and Lodge 1995, Clark et al. 2013). In the non-drought year, substrate and submerged vegetation had similar relative influences on predation risk, but both were of secondary importance to crayfish size. The increase in substrate particle size from 2012 to 2013 was driven by the placement of only a few crayfish in substrates with large particle sizes (Appendix D: Fig. 2), and these few sites were enough to demonstrate the relationship between substrate and predation risk. However, most streams in my study area have homogenized substrates with low variability in substrate particle size (Appendix D: Fig. 2). Most crayfish were placed on sand or silt substrates that did not

provide shelter from predators. Therefore, cover of submerged vegetation became most important when exposure to terrestrial predators was high during the drought and there was not suitable substrate in which to seek shelter.

I hypothesized terrestrial predators would select larger crayfish because terrestrial predators can handle crayfish of all sizes, whereas aquatic predators would select smaller crayfish because fish are gape-limited predators. Terrestrial predators such as raccoons and herons can target larger prey because they can easily manipulate prey and consume it piecemeal if prey is too large to swallow whole (Power 1987). During the drought, terrestrial predators did depredate larger crayfish, but there was no overall relationship between predation risk and crayfish size. However, contrary to my prediction, in the non-drought year when water levels were higher and aquatic predators were responsible for a greater proportion of predation events, larger crayfish were at greater risk than smaller crayfish. Previous tethering studies have demonstrated that fish predators select for small crayfish (<20 mm CL; DiDonato and Lodge 1993, Englund and Krupa 2000, Clark et al. 2013). If a stream were to contain only small fish, then crayfish could grow beyond the gape-limitation of their fish predators, thus decreasing predation risk. However, the crayfish I used in 2013 all had a carapace length (CL) $\geq$22 mm (Appendix D: Fig. 4) and would fit into the "medium" or "large" size classes used in other studies. DiDonato and Lodge (1993) did not find significant differences in mortality between medium (23 – 25 mm CL) and large (33 – 35 mm CL) size classes. Clark et al. (2013) also observed similar survival of medium (20 – 30 mm CL) and large (>30 mm CL) crayfish. Therefore, it is not surprising that I did not find a negative relationship between predation risk and crayfish size because "small" crayfish were not used in my study.

Optimal foraging theory predicts that a predator should forage so as to maximize its net rate of energy gain, therefore consuming the largest prey possible while expending the least amount of energy (MacArthur and Pianka 1966). The size of prey that fish predators select depends on the mouth size of the fish and prey handling time (Werner 1974, Hoyle and Keast 1987). Hoyle and Keast (1987) experimentally determined the optimal size of different prey (tadpoles, fish, crayfish) of largemouth bass (*Micropterus salmoides*) with regard to handling time. An optimal ratio of crayfish total length to bass length was calculated to be 0.22 (Hoyle and Keast 1987). At this ratio, the crayfish at the low end of the size distribution used in my study (Appendix D: Fig. 4) would be the optimal size for about a 20-cm bass. A 45-cm bass would select crayfish at the high end of the size distribution used in my study if it was foraging optimally. The larger streams in my study area held fish of this large size (personal observation). My results indicate that at sites that contained aquatic predators big enough to consume large crayfish, they preferentially did so. Large crayfish may be more vulnerable to large aquatic predators because they are more visible than small crayfish, especially when exposed on substrates with small particle sizes. I suggest that deeper waters in 2013 allowed larger fish access to crayfish, and drove the relationship between predation risk and crayfish size.

This relationship is also supported by the positive association between predation risk and stream size. Stream size is associated positively with fish species richness (Sheldon 1968, Horwitz 1978, Osborne and Wiley 1992), and larger areas support more individuals (Angermeier and Schlosser 1989). Fish communities tend to increase in trophic complexity as streams transition from headwaters to larger streams, with large predatory fish occurring more in larger streams (Evans and Noble 1979, Rahel and Hubert 1991). Fish predation on crayfish can be species-specific, and the streams in my study area contain fish species known to prey upon the

crayfish species used in my tethering experiment (Larimore and Bayley 1996). For example, largemouth bass, smallmouth bass (*Micropterus dolomieu*), longnose gar (*Lepisosteus osseus*), and green sunfish (*Lepomis cyanellus*) are known predators of *Orconectes propinquus* (Hobbs 1993). Largemouth bass, smallmouth bass, longnose gar, and shortnose gar (*Lepisosteus platostomus*) consume *Orconectes virilis* (Hobbs 1993). These and other predatory fish inhabit the streams in my study area (Larimore and Bayley 1996). The positive relationship between crayfish mortality and stream size appears to be a result of increased predation pressure from aquatic predators as stream size increases.

I hypothesized that predation risk would be less affected by annual variation in precipitation in larger streams because larger streams should retain deeper water better than small streams in drought years. My study area contains permanent and intermittent streams, but only streams that held water were used in the experiment. I originally planned to use 60 study sites for the experiment in 2012, but 8 of these streams were dry all summer, and an additional 7 streams that originally held water in May were partially or completely dry by July. All of these sites were located in 1st or 2nd order headwater streams. Therefore, predation risk appears to be consistently higher in larger streams that hold more water and contain larger aquatic predators. More variable precipitation events in the future will influence the timing of stream drying and flooding events, and thus the factors that affect predation risk.

Predation risk was also related negatively to urbanization. I predicted that an abundance of terrestrial predators (i.e., raccoons) in urban areas and increased predation by terrestrial predators when water levels were low would cause predation risk to increase in urban areas during drought. However, I detected the opposite effect in both the drought and non-drought year; predation risk was lower in urban areas. Considering the large contribution of aquatic

predators to predation events, this relationship may reflect changes in the fish community across the urbanization gradient. Urbanization is associated with decreases in diversity and abundance of fish, which may be driven by pollutants, sedimentation, and flow modification typical of urban areas (Paul and Meyer 2001). Such altered fish communities could cause risk in urban areas to be low regardless of water levels, however I do not have data on the fish communities at my study sites. Contra my hypothesis, I did not detect a significant effect of riparian buffer size on predation risk for crayfish in either year, perhaps because of the predominance of aquatic predation in my study.

Overall, I found that severe drought did not increase predation risk for crayfish in streams; risk was actually lower during the drought. Risk was driven primarily by aquatic predation, although there was an increase in predation by terrestrial predators during the drought. Although the change in levels of predation risk for crayfish between drought and non-drought years was subtle, the difference in the influence of variables that affected predation risk was pronounced.

Table 4. Ranking of generalized linear mixed models for predation risk for crayfish ($n = 173$) in Illinois during the drought of 2012 based on Akiake's Information Criterion (AIC). Within-stream models were tested with and without crayfish size (carapace). The top "within-stream model" was included in every "landscape" model. Within-stream covariates included submerged vegetation cover (subveg), substrate particle size (substrate), and water depth. Landscape covariates included stream size (sizePC), urbanization, and riparian buffer width (ripwidth). ΔAIC = AIC for a given model minus AIC for the top model. K = number of model parameters. w_i = Akaike weights. LL is the log-likelihood. Within-stream models in the 95% confidence set, plus the intercept-only model, are presented. All landscape models are presented.

Model set	Model	ΔAIC	w_i	K	-2*LL
Within-stream	subveg	0	0.324	3	214.68
	subveg + substrate	1.19	0.179	4	213.87
	carapace + subveg	1.63	0.144	4	214.31
	subveg + depth	2.00	0.119	4	214.68
	carapace + subveg + substrate	2.74	0.082	5	213.42
	subveg + substrate + depth	3.17	0.066	5	213.85
	carapace + subveg + depth	3.61	0.053	5	214.29
	intercept-only	13.10	0.000	2	229.78
Landscape	subveg + sizePC	0	0.238	4	212.22
	subveg	0.46	0.189	3	214.68
	subveg + urbanization + sizePC	0.61	0.175	5	210.83
	subveg + urbanization	0.86	0.155	4	213.08
	subveg + ripwidth	0.93	0.149	4	213.15
	subveg + urbanization + ripwidth	1.84	0.095	5	212.06

Table 5. Relative importance of carapace length and within-stream covariates in affecting predation risk for crayfish in Illinois for 2012 and 2013 based on Akaike weights summed across statistical models. Within-stream covariates include cover of submerged vegetation, substrate particle size (substrate), and water depth.

Covariate	Summed Akaike weights	
	2012	2013
Carapace length	0.310	0.994
Submerged vegetation	0.999	0.552
Substrate	0.358	0.561
Water depth	0.270	0.379

Table 6. Ranking of generalized linear mixed models for predation risk for crayfish ($n = 171$) in Illinois in 2013 based on Akiake's Information Criterion (AIC). Within-stream models were tested with and without crayfish size (carapace). The top "within-stream model" was included in every "landscape" model. Within-stream covariates included submerged vegetation cover (subveg), substrate particle size (substrate), and water depth. Landscape covariates included stream size (sizePC), urbanization, and riparian buffer width (ripwidth). ΔAIC = AIC for a given model minus AIC for the top model. K = number of model parameters. w_i = Akaike weights. LL is the log-likelihood. Within-stream models in the 95% confidence set, plus the intercept-only model, are presented. All landscape models are presented.

Model set	Model	ΔAIC	w_i	K	-2*LL
Within-stream	carapace + subveg + substrate	0	0.196	5	204.52
	carapace + substrate	0.54	0.150	4	207.06
	carapace	0.69	0.139	3	209.21
	carapace + subveg + substrate + depth	0.78	0.133	6	203.3
	carapace + subveg	0.81	0.131	4	207.33
	carapace + subveg + depth	1.59	0.089	5	206.11
	carapace + substrate + depth	1.82	0.079	5	206.34
	carapace + depth	1.89	0.076	4	208.41
	intercept-only	10.15	0.001	2	220.67
Landscape	carapace + subveg + substrate + urban + sizePC	0	0.584	7	175.35
	carapace + subveg + substrate + sizePC	0.69	0.414	6	178.04
	carapace + subveg + substrate + ripwidth	12.68	0.001	6	190.03
	carapace + subveg + substrate + urban + ripwidth	13.93	0.001	7	189.28
	carapace + subveg + substrate	25.17	0.000	5	204.52
	carapace + subveg + substrate + urban	25.69	0.000	6	203.04

Table 7. Ranking of generalized linear mixed models for predator-specific mortality risk for crayfish in Illinois in 2012 and 2013 based on Akiake's Information Criterion (AIC). Covariates were tested for their effect on the type of predator responsible for predation events. Covariates included crayfish size (carapace), submerged vegetation cover (subveg), substrate particle size (substrate), water depth, stream size (sizePC), urbanization, and riparian buffer width (ripwidth). ΔAIC = AIC for a given model minus AIC for the top model. K = number of model parameters. w_i = Akaike weights. LL is the log-likelihood.

| Year	Model	ΔAIC	w_i	K	-2*LL
2012	depth	0	0.750	3	64.35
	carapace	2.65	0.199	3	67.00
	intercept-only	7.61	0.017	2	73.96
	subveg	8.84	0.009	3	73.19
	urban	9.37	0.007	3	73.72
	substrate	9.52	0.006	3	73.87
	ripwidth	9.60	0.006	3	73.95
	sizePC	10.06	0.005	3	74.41
2013	depth	0	0.669	3	47.10
	intercept-only	4.38	0.075	2	53.48
	ripwidth	4.55	0.069	3	51.65
	sizePC	5.19	0.050	3	52.29
	carapace	5.22	0.049	3	52.32
	urban	6.11	0.032	3	53.21
	subveg	6.31	0.029	3	53.41
	substrate	6.35	0.028	3	53.45
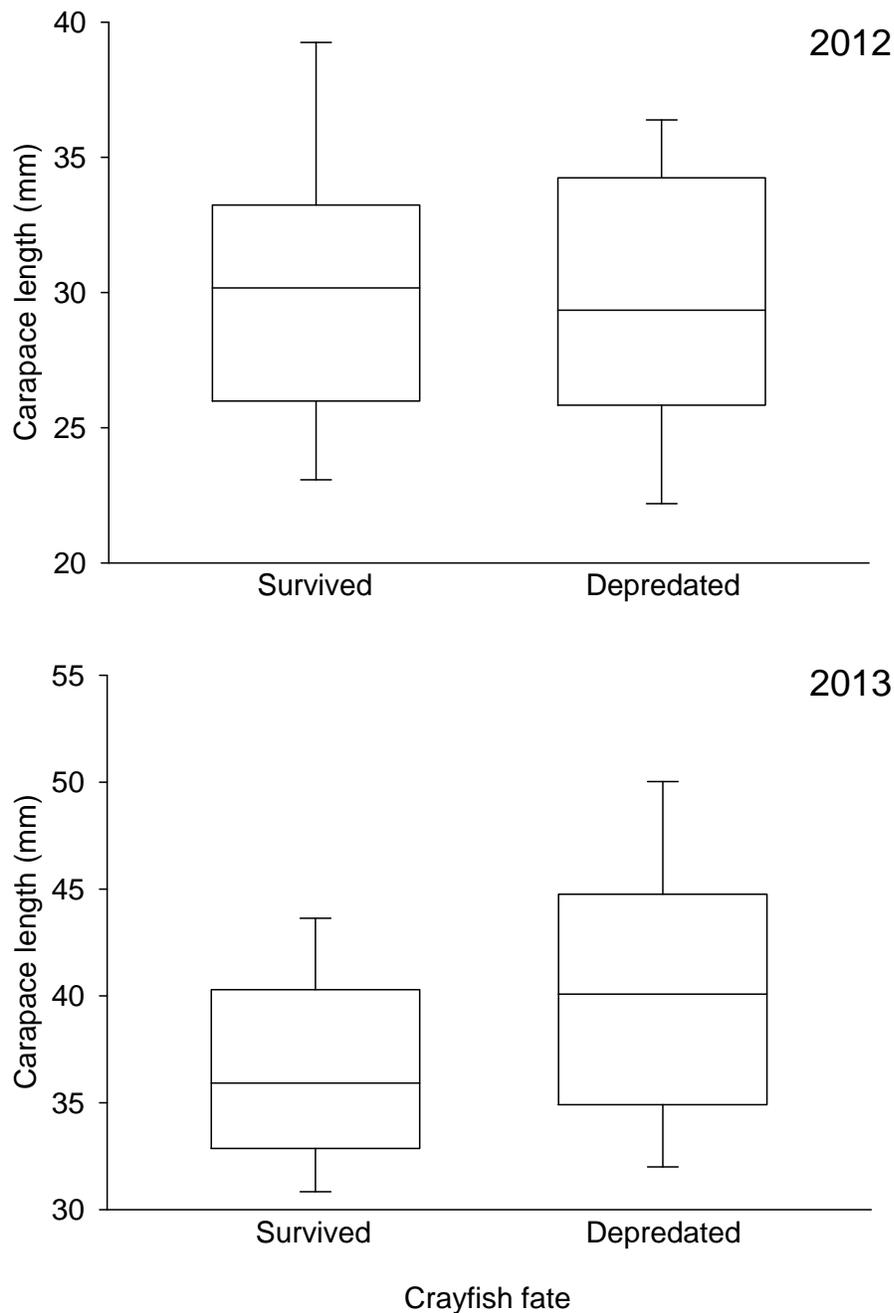
Figure 5. Size of crayfish (carapace length) that survived and were depredated in 2012 (survived, $n = 99$; depredated, $n = 74$) and 2013 (survived, $n = 82$; depredated, $n = 89$) in Illinois. Carapace length was a predictor of predation risk in 2013, but not 2012. Horizontal lines are medians, boxes indicate 25th and 75th percentiles, and whiskers indicate the 10th and 90th percentiles. Note the different ranges of the Y-axis.
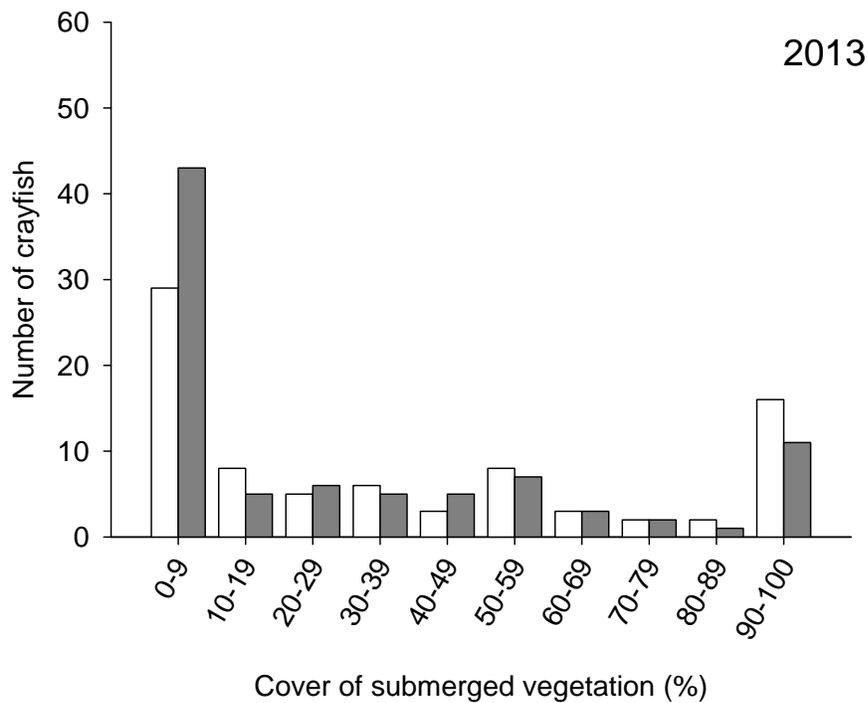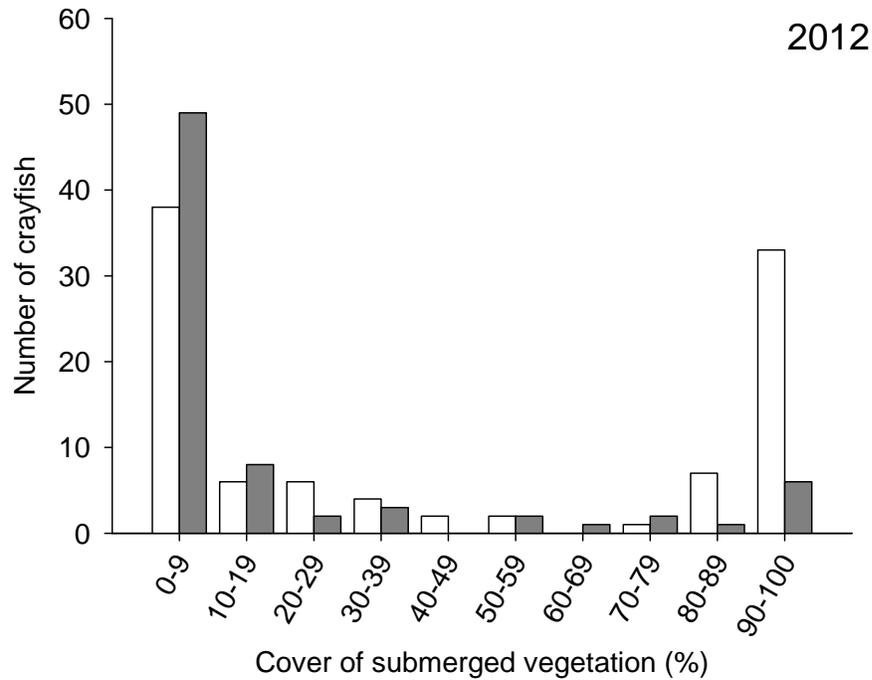
**Figure 6.** Number of crayfish that survived and were depredated in 2012 (survived, $n = 99$; depredated, $n = 74$) and 2013 (survived, $n = 82$; depredated, $n = 89$) in Illinois. Crayfish are grouped into 10% bins based on cover of submerged vegetation within 1 m^2. White bars represent crayfish that survived. Gray bars represent crayfish that were depredated.
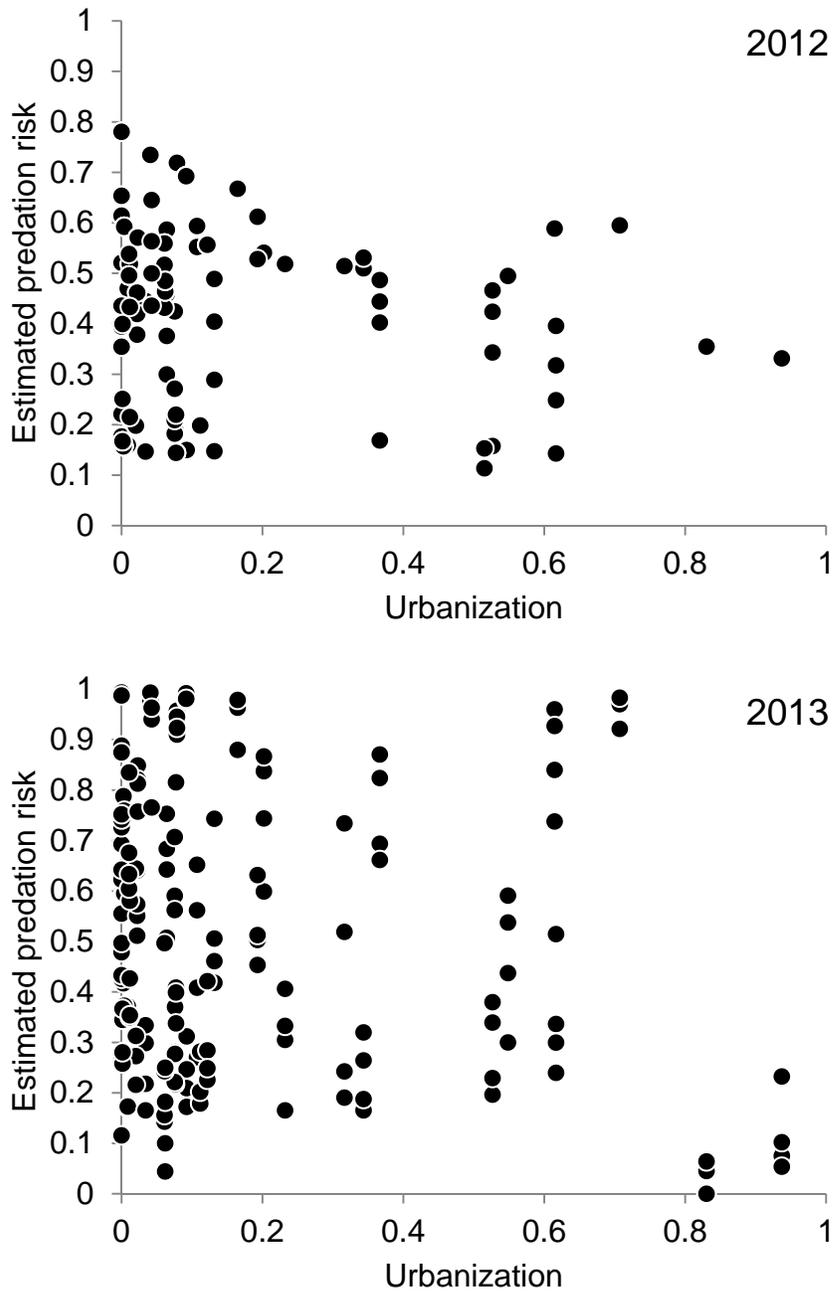
Figure 7. Relationship between estimated predation risk for crayfish and urbanization in 2012 and 2013 in Illinois. Estimated predation risk was predicted from the 3rd best "landscape model" in 2012 (Table 4) and the top "landscape model" in 2013 (Table 6). Each point represents a crayfish (2012, $n = 173$; 2013, $n = 171$).
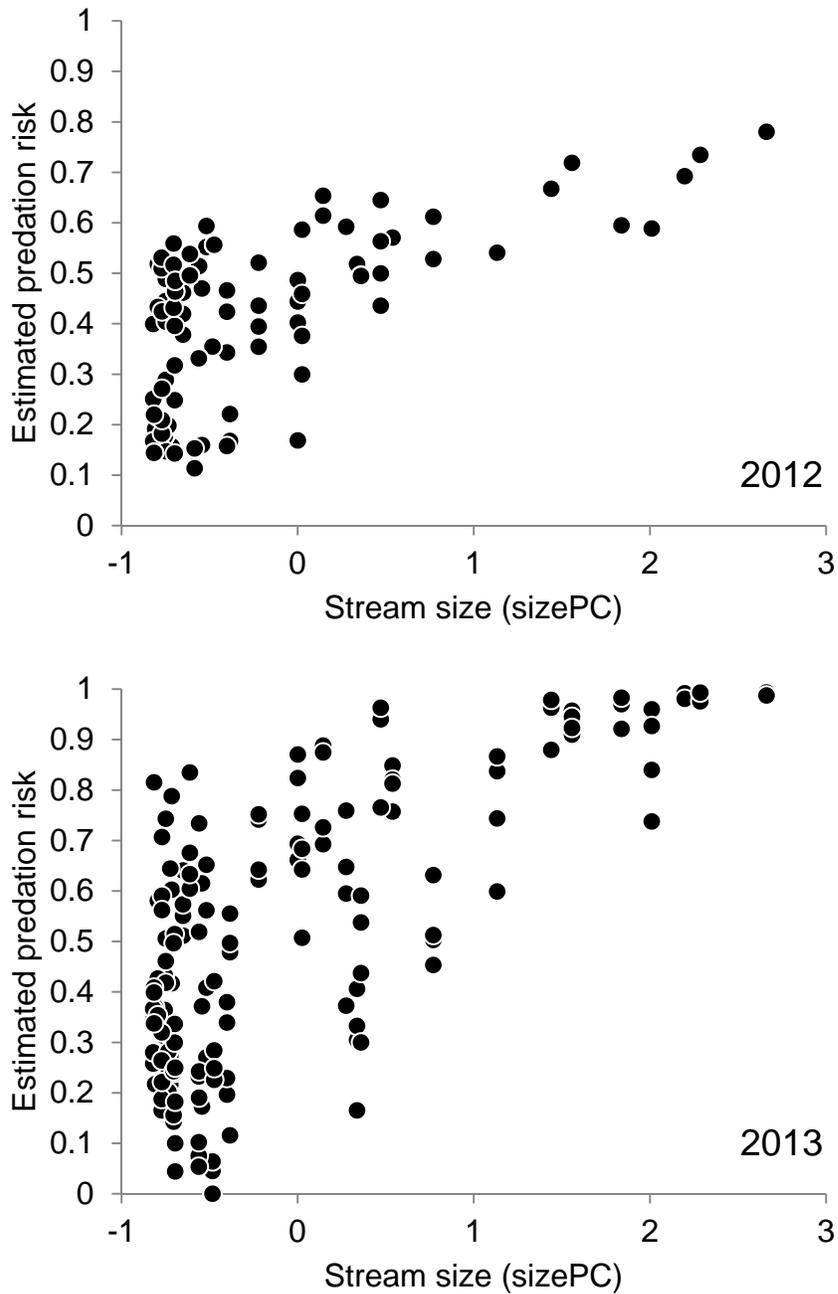
Figure 8. Relationship between estimated predation risk for crayfish and stream size in 2012 and 2013 in Illinois. Predation risk was predicted from the 3rd best "landscape model" in 2012 (Table 4) and the top "landscape model" in 2013 (Table 6). Each point represents a crayfish (2012, $n = 173$; 2013, $n = 171$).
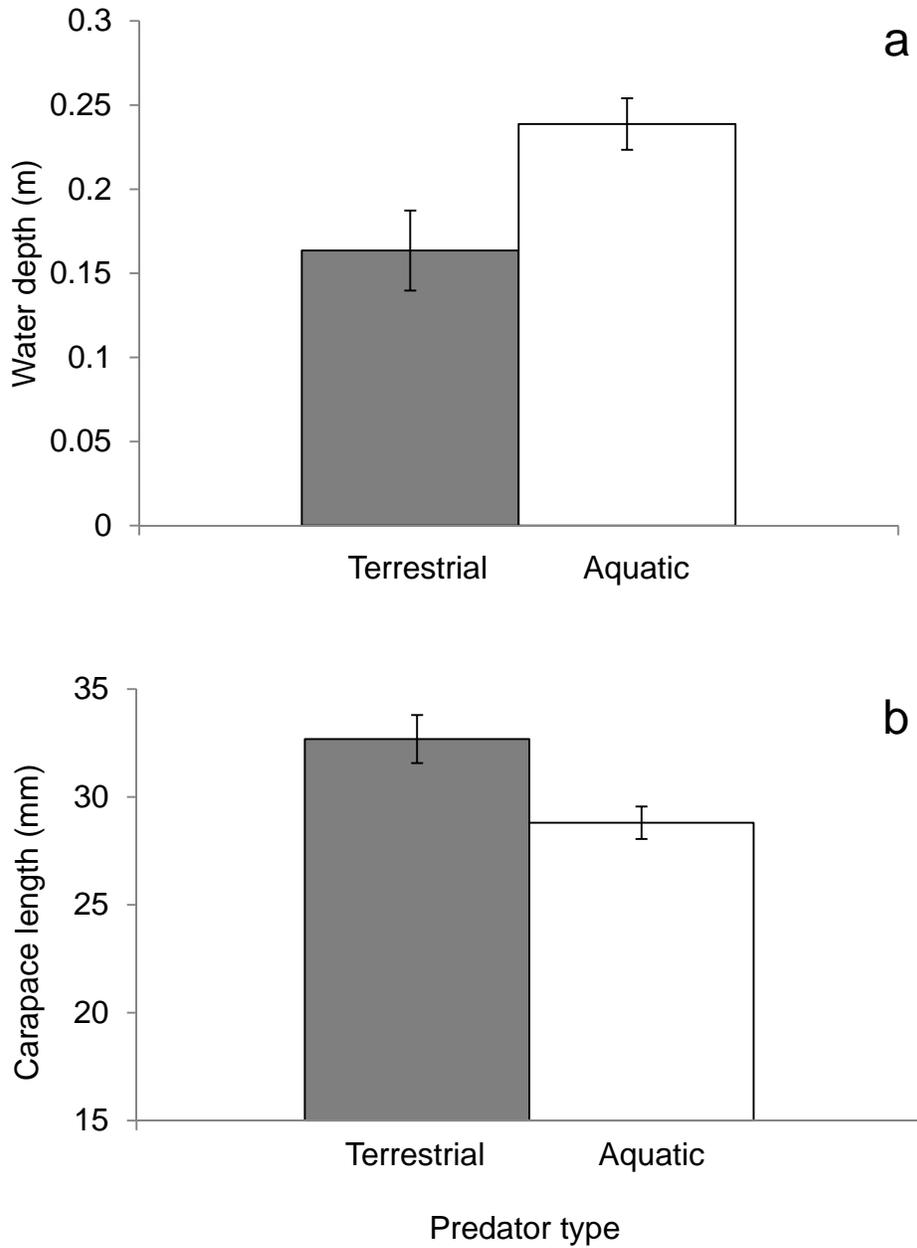
Figure 9. Water depth (a) and crayfish size (b) for crayfish depredated by terrestrial ($n = 20$) and aquatic ($n = 54$) predators in Illinois in 2012. Means ±1 SE presented.
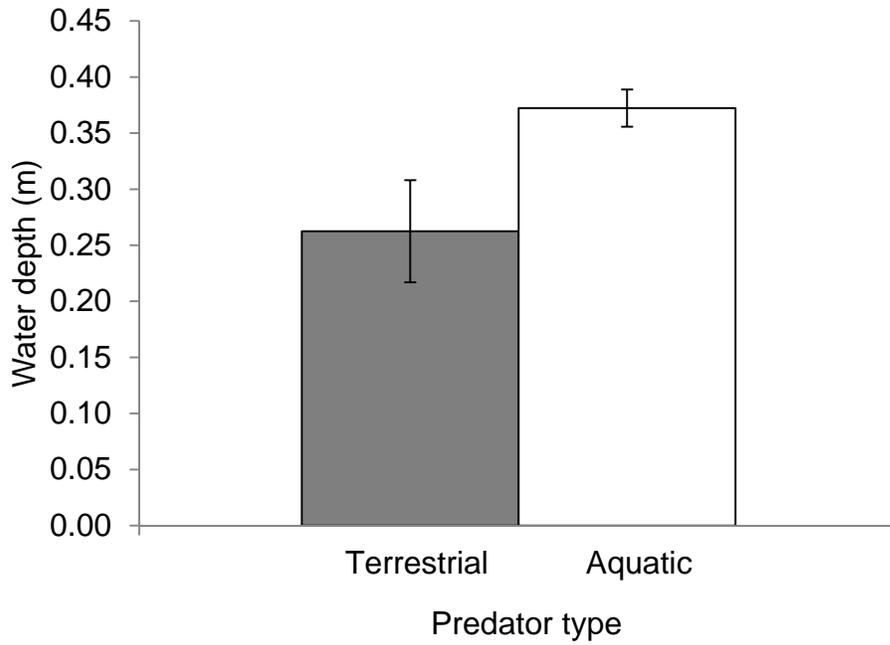
Figure 10. Water depths (mean ±1 SE) for crayfish depredated by terrestrial (*n* = 8) and aquatic (*n* = 81) predators in Illinois in 2013.

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CHAPTER 4: SUMMARY

Predator-prey interactions form ecologically significant links at the interface of terrestrial and aquatic ecosystems, and may be of particular importance in human-dominated landscapes. In the Midwestern United States, agricultural intensification and urbanization have reduced the amount of native habitat for wildlife, and riparian zones provide much of the remaining habitat for terrestrial, semiaquatic, and aquatic species. It is important to understand space use of predators and assess the vulnerability of prey in this landscape. In the face of climate change, it is particularly important to evaluate how these entities might be affected in the future. My research examined predator-prey interactions in a human-dominated landscape both from the perspective of a semiaquatic predator (mink) and of an aquatic prey (crayfish).

My study of the diet and habitat selection behavior of American mink demonstrated that the spatial distribution of a common prey item, crayfish, was the primary driver of habitat selection by mink during summer of a severe drought. I found that mink occupied habitats based directly on high prey concentrations instead of habitat characteristics that might indicate high prey densities. Stream and landscape characteristics also affected habitat occupancy; mink were associated negatively with both urbanization and stream size. My results indicate different factors may influence habitat selection by mink under different environmental conditions.

I compared the effects of biotic and abiotic factors on predation risk for crayfish in drought year to a non-drought year. I found that severe drought did not cause predation risk for crayfish in streams to increase, and that risk was actually slightly lower during the drought. Different hydrologic conditions caused the relative influence of biotic and abiotic factors to change between drought and non-drought years. Submerged vegetation was an important refuge for crayfish during the drought, when crayfish were more vulnerable to predation from terrestrial

predators. Aquatic predators were predominant in both years, but higher water levels during the

non-drought year appeared to give larger fish more access to crayfish, particularly in larger

streams.

My research demonstrates the complexity of predator-prey interactions in this human-

dominated ecosystem. Although habitat selection and predation risk are spatially and temporally

dynamic, certain patterns existed that helped improve our understanding of predator behavior

and prey vulnerability.

APPENDIX A: AMERICAN MINK DIET SUPPLEMENTARY MATERIAL

Table A1. Summary of (a) relative frequency of occurrence percentage, (b) frequency of occurrence percentage, and (c) volume percentage of prey items in the diet of mink in fall 2011 ($n = 17$), winter 2012 ($n = 43$), and summer 2012 ($n = 43$).

(a)	Relative frequency of occurrence percentage			
	Fall	Winter	Summer	Total
Crayfish	23.5	27.5	30.4	28.1
Mammal	31.4	32.1	20.7	26.8
Fish	5.9	17.4	11.1	12.5
Bird	5.9	4.6	11.1	7.8
Insect	23.5	9.2	20.7	16.9
Reptile	2.0	0.0	0.0	0.3
Unknown	7.8	9.2	5.9	7.5

(b)	Frequency of occurrence percentage			
	Fall	Winter	Summer	Total
Crayfish	70.6	69.8	95.3	80.6
Mammal	94.1	81.4	65.1	76.7
Fish	17.6	44.2	34.9	35.9
Bird	17.6	11.6	34.9	22.3
Insect	70.6	23.3	65.1	48.5
Reptile	5.9	0.0	0.0	1.0
Unknown	23.5	23.3	18.6	21.4

(c)	Volume percentage			
	Fall	Winter	Summer	Total
Crayfish	35.0	26.2	74.4	47.8
Mammal	44.4	49.1	18.4	35.5
Fish	2.2	17.5	1.1	8.1
Bird	1.8	2.5	3.9	3.0
Insect	12.5	2.7	0.9	3.6
Reptile	1.8	0.0	0.0	0.3
Unknown	2.2	1.9	1.3	1.7

Table A2. Fisher's exact test p-values for differences in frequency of occurrence percentage of prey classes between seasons. The null hypothesis is that the contribution of a prey class does not differ between seasons. The reptile prey class is excluded because there was only 1 occurrence in 103 scat samples. Fall ($n = 17$); Winter ($n = 43$); Summer ($n = 43$). *Significant seasonal difference at $\alpha = 0.05$

Prey class	Fall-Winter	Winter-Summer	Fall-Summer
Crayfish	1.000	0.003*	0.016*
Mammal	0.423	0.143	0.025*
Fish	0.076	0.509	0.228
Bird	0.676	0.020*	0.228
Insect	0.001*	0.0002*	0.769
Unknown	1.000	0.792	0.726

Table A3. Multi-response permutations procedures results, excluding reptile and unknown prey classes. A = effect size. A Bonferroni corrected $\alpha = 0.0167$ was used because of multiple pair-wise comparisons. Overall $A = 0.1388$, $P < 0.0001$. *Significant seasonal difference.

| Comparison	A	P
Fall-Winter	0.0103	0.1404
Winter-Summer	0.0978	< 0.001*
Fall-Summer	0.1578	< 0.0001*

Table A4. Matrix of Pearson correlation coefficients (*r*) for the three dietary diversity indices calculated from (a) frequency of occurrence and (b) volume data. *Significant correlation (*P* <0.05).

(a)	Shannon Diversity Index	Evenness	Levins niche breadth
Shannon Diversity Index	1.000	0.240	0.880
Evenness	.	1.000	0.673
Levins niche breadth	.	.	1.000

(b)	Shannon Diversity Index	Evenness	Levins niche breadth
Shannon Diversity Index	1.000	0.980	0.999*
Evenness	.	1.000	0.985
Levins niche breadth	.	.	1.000
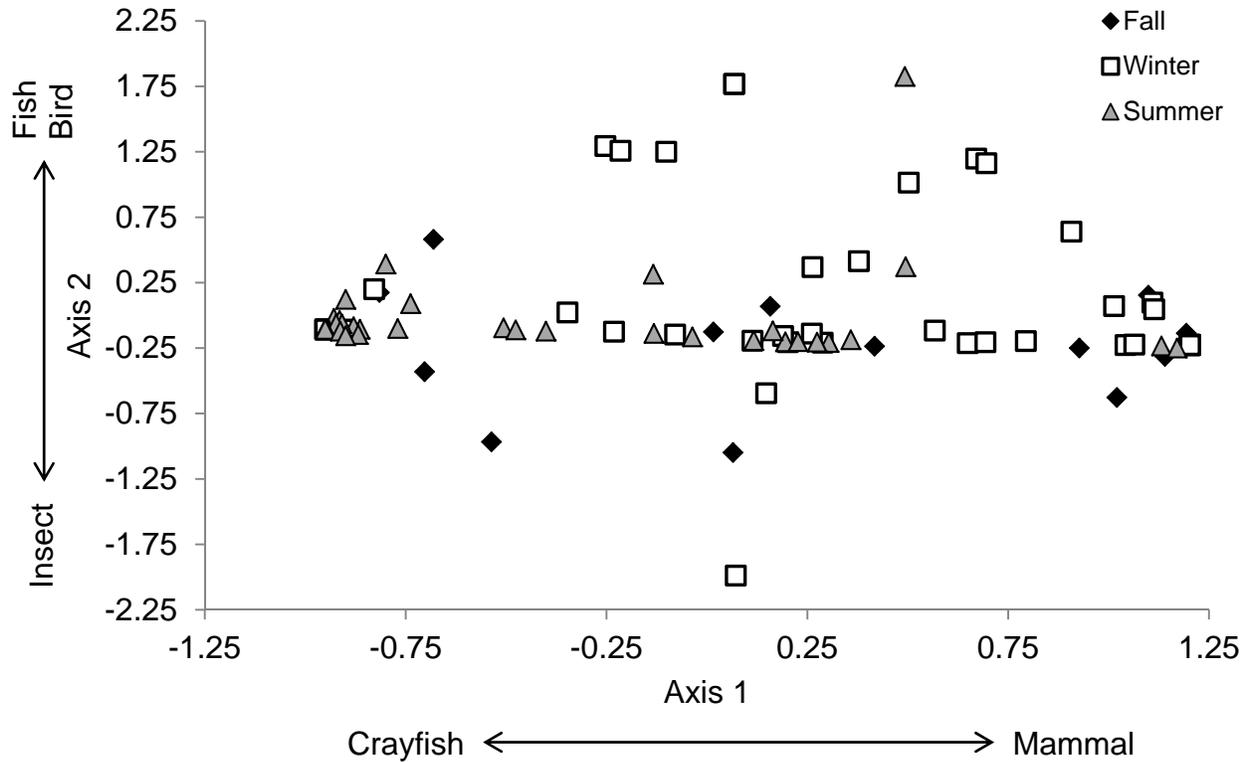
Figure A1. Non-metric multidimensional scaling ordination of the volume percentage of prey classes in American mink scats in fall 2011 (*n* = 17 scat samples), winter 2012 (*n* = 43), and summer 2012 (*n* = 43), excluding reptile and unknown prey classes. Each point represents one scat sample. Distances between points represent the degree of dietary dissimilarity.

APPENDIX B: OCCUPANCY MODELING SUPPLEMENTARY MATERIAL

Table B1. Ranking of occupancy models for American mink in Illinois based on Akaike's Information Criterion (AIC). Detection covariates included observer and rainfall for the 7 days prior to each survey (rainfall). Occupancy covariates included presence-absence of a crayfish hotspot (hotspot), total crayfish density, adult crayfish density, stream size (sizePC), water depth, urbanization, and riparian width. ΔAIC = AIC for a given model minus AIC for the best model. K = number of model parameters, w_i = Akaike weights, and LL is the log-likelihood.

Model	ΔAIC	w_i	K	-2*LL
ψ(hotspot, sizePC), p(observer, rainfall)	0	0.1458	6	91.28
ψ(hotspot), p(observer, rainfall)	0.12	0.1373	5	93.40
ψ(hotspot, urbanization), p(observer, rainfall)	0.62	0.1070	6	91.90
ψ(hotspot, sizePC, urbanization), p(observer, rainfall)	0.74	0.1007	7	90.02
ψ(hotspot, depth), p(observer, rainfall)	1.87	0.0572	6	93.15
ψ(hotspot, sizePC, depth), p(observer, rainfall)	1.87	0.0572	7	91.15
ψ(hotspot, ripwidth), p(observer, rainfall)	2.09	0.0513	6	93.37
ψ(hotspot, urbanization, depth), p(observer, rainfall)	2.43	0.0433	7	91.71
ψ(hotspot, urbanization, ripwidth), p(observer, rainfall)	2.60	0.0397	7	91.88
ψ(hotspot, sizePC, depth, urbanization), p(observer, rainfall)	2.61	0.0395	8	89.89
ψ(hotspot, ripwidth, depth), p(observer, rainfall)	3.58	0.0243	7	92.86
ψ(total density, sizePC), p(observer, rainfall)	3.92	0.0205	6	95.20
ψ(hotspot, ripwidth, depth, urbanization), p(observer, rainfall)	4.21	0.0178	8	91.49
ψ(total density), p(observer, rainfall)	4.22	0.0177	5	97.50
ψ(total density, sizePC, urbanization), p(observer, rainfall)	5.12	0.0113	7	94.40
ψ(total density, urbanization), p(observer, rainfall)	5.32	0.0102	6	96.60
ψ(total density, sizePC, depth), p(observer, rainfall)	5.40	0.0098	7	94.68

Table B1. (cont.)

Model	ΔAIC	w_i	K	-2*LL
ψ(sizePC), p(observer, rainfall)	5.62	0.0088	5	98.90
ψ(sizePC, urbanization), p(observer, rainfall)	5.98	0.0073	6	97.26
ψ(total density, depth), p(observer, rainfall)	6.17	0.0067	6	97.45
ψ(total density, ripwidth), p(observer, rainfall)	6.18	0.0066	6	97.46
ψ(.), p(observer, rainfall)	6.20	0.0066	4	101.48
ψ(urbanization), p(observer, rainfall)	6.39	0.0060	5	99.67
ψ(adult density, sizePC), p(observer, rainfall)	6.40	0.0059	6	97.68
ψ(adult density), p(observer, rainfall)	6.58	0.0054	5	99.86
ψ(total density, sizePC, depth, urbanization), p(observer, rainfall)	6.64	0.0053	8	93.92
ψ(sizePC, depth), p(observer, rainfall)	7.16	0.0041	6	98.44
ψ(adult density, sizePC, urbanization), p(observer, rainfall)	7.25	0.0039	7	96.53
ψ(total density, urbanization, depth), p(observer, rainfall)	7.28	0.0038	7	96.56
ψ(total density, urbanization, ripwidth), p(observer, rainfall)	7.31	0.0038	7	96.59
ψ(adult density, urbanization), p(observer, rainfall)	7.36	0.0037	6	98.64
ψ(sizePC, depth, urbanization), p(observer, rainfall)	7.57	0.0033	7	96.85
ψ(adult density, sizePC, depth), p(observer, rainfall)	7.93	0.0028	7	97.21
ψ(total density, ripwidth, depth), p(observer, rainfall)	8.01	0.0027	7	97.29
ψ(depth), p(observer, rainfall)	8.09	0.0026	5	101.37
ψ(ripwidth), p(observer, rainfall)	8.18	0.0024	5	101.46
ψ(urbanization, depth), p(observer, rainfall)	8.30	0.0023	6	99.58

Table B1. (cont.)

| Model	ΔAIC	w_i	K	-2*LL
ψ(urbanization, ripwidth), p(observer, rainfall)	8.34	0.0023	6	99.62
ψ(adult density, depth), p(observer, rainfall)	8.52	0.0021	6	99.80
ψ(adult density, ripwidth), p(observer, rainfall)	8.57	0.0020	6	99.85
ψ(adult density, sizePC, depth, urbanization), p(observer, rainfall)	8.83	0.0018	8	96.11
ψ(total density, ripwidth, depth, urbanization), p(observer, rainfall)	9.20	0.0015	8	96.48
ψ(adult density, urbanization, depth), p(observer, rainfall)	9.31	0.0014	7	98.59
ψ(adult density, urbanization, ripwidth), p(observer, rainfall)	9.36	0.0014	7	98.64
ψ(ripwidth, depth), p(observer, rainfall)	10.08	0.0009	6	101.36
ψ(ripwidth, depth, urbanization), p(observer, rainfall)	10.29	0.0008	7	99.57
ψ(adult density, ripwidth, depth), p(observer, rainfall)	10.46	0.0008	7	99.74
ψ(adult density, ripwidth, depth, urbanization), p(observer, rainfall)	11.30	0.0005	8	98.58

Table B2. Matrix of Pearson correlation coefficients (*r*) for occupancy covariates. Covariates included total crayfish density, adult crayfish density, degree of urbanization, riparian width, water depth, stream size (sizePC), drainage area, wetted width, and stream order. Drainage area, stream order, and wetted width were combined using principal components analysis to create the stream size covariate, sizePC. *n* = 59. *Significant correlation (*P* <0.05).

|	Total density	Adult density	Urbanization	Riparian width	Water depth	SizePC	Drainage area	Wetted width	Steam order
Total density	1.000	0.628*	-0.209	-0.171	-0.052	-0.103	0.237	-0.223	-0.217
Adult density	.	1.000	-0.206	-0.163	-0.070	-0.134	0.213	-0.224	-0.272*
Urbanization	.	.	1.000	-0.100	0.008	0.047	0.002	0.117	-0.005
Riparian width	.	.	.	1.000	0.554*	0.617*	0.266*	0.667*	0.631*
Water depth	.	.	.	.	1.000	0.577*	0.284*	0.634*	0.552*
SizePC	.	.	.	.	.	1.000	0.738*	0.941*	0.920*
Drainage area	.	.	.	.	.	.	1.000	0.536*	0.476*
Wetted width	.	.	.	.	.	.	.	1.000	0.875*
Steam order	.	.	.	.	.	.	.	.	1.000

Table C1. Matrix of Pearson correlation coefficients (r) for crayfish densities and habitat covariates for crayfish. Covariates included adult crayfish density, juvenile crayfish density, total crayfish density, number of active crayfish burrows, number of total crayfish burrows, number of woody accumulations anchored in the stream substrate, and substrate particle size. $n = 1,180$ for all covariates except substrate ($n = 992$). *Significant correlation ($P < 0.05$).

|	Adult density	Juvenile density	Total density	Active burrows	Total burrows	Woody accumulations	Substrate
Adult density	1.000	0.149*	0.534*	0.009	-0.034	-0.067*	-0.076*
Juvenile density	.	1.000	0.916*	-0.085*	-0.071*	-0.073*	0.060
Total density	.	.	1.000	-0.070*	-0.075*	-0.090*	0.020
Active burrows	.	.	.	1.000	0.853*	-0.043	-0.087*
Total burrows	.	.	.	.	1.000	0.024	-0.073*
Woody accumulations	.	.	.	.	.	1.000	-0.030
Substrate	.	.	.	.	.	.	1.000
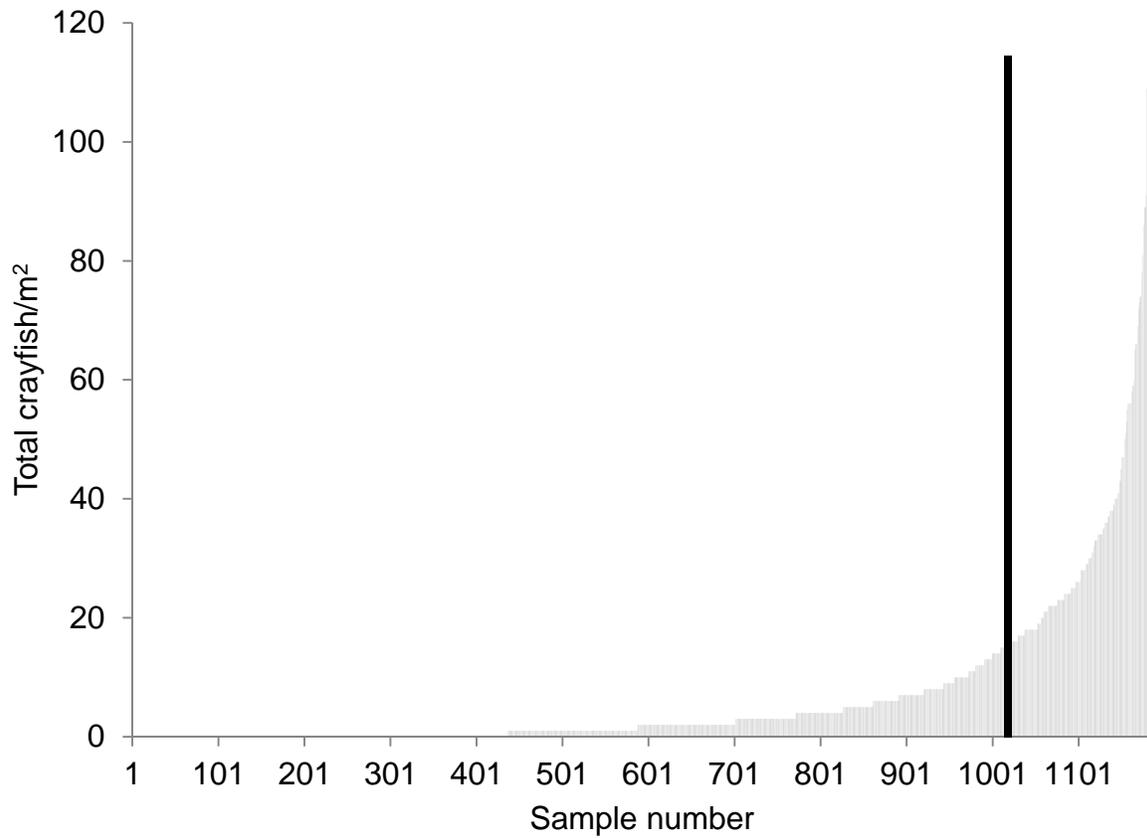
Figure C1. Crayfish densities ranked from smallest to largest. Twenty kick seine samples were collected at 59 sites ($n = 1,180$). The black line is the 85th percentile. Sites with ≥ 1 crayfish density to the right of the line (≥ 15 crayfish/m^2) were considered to contain a hotspot.
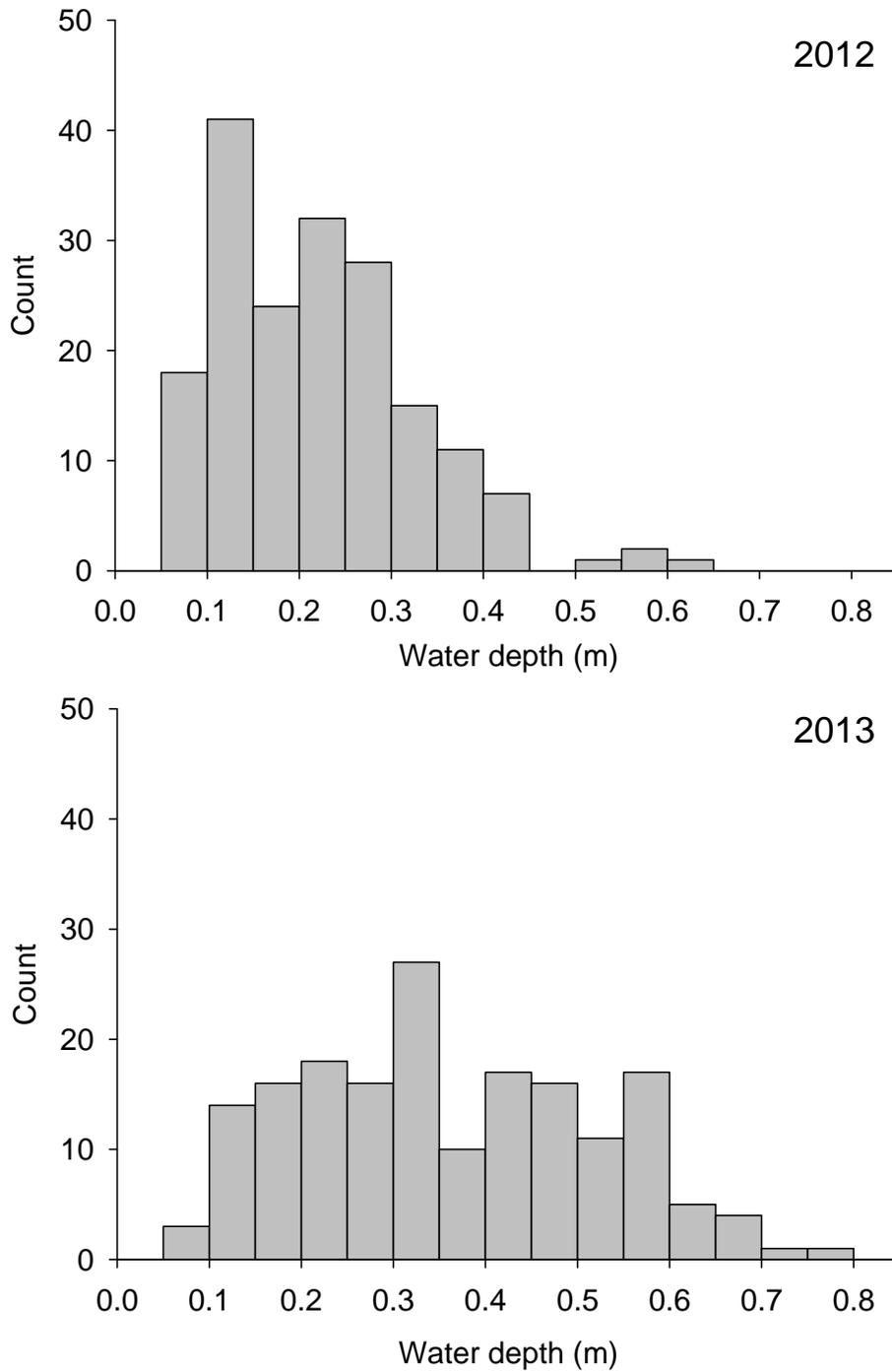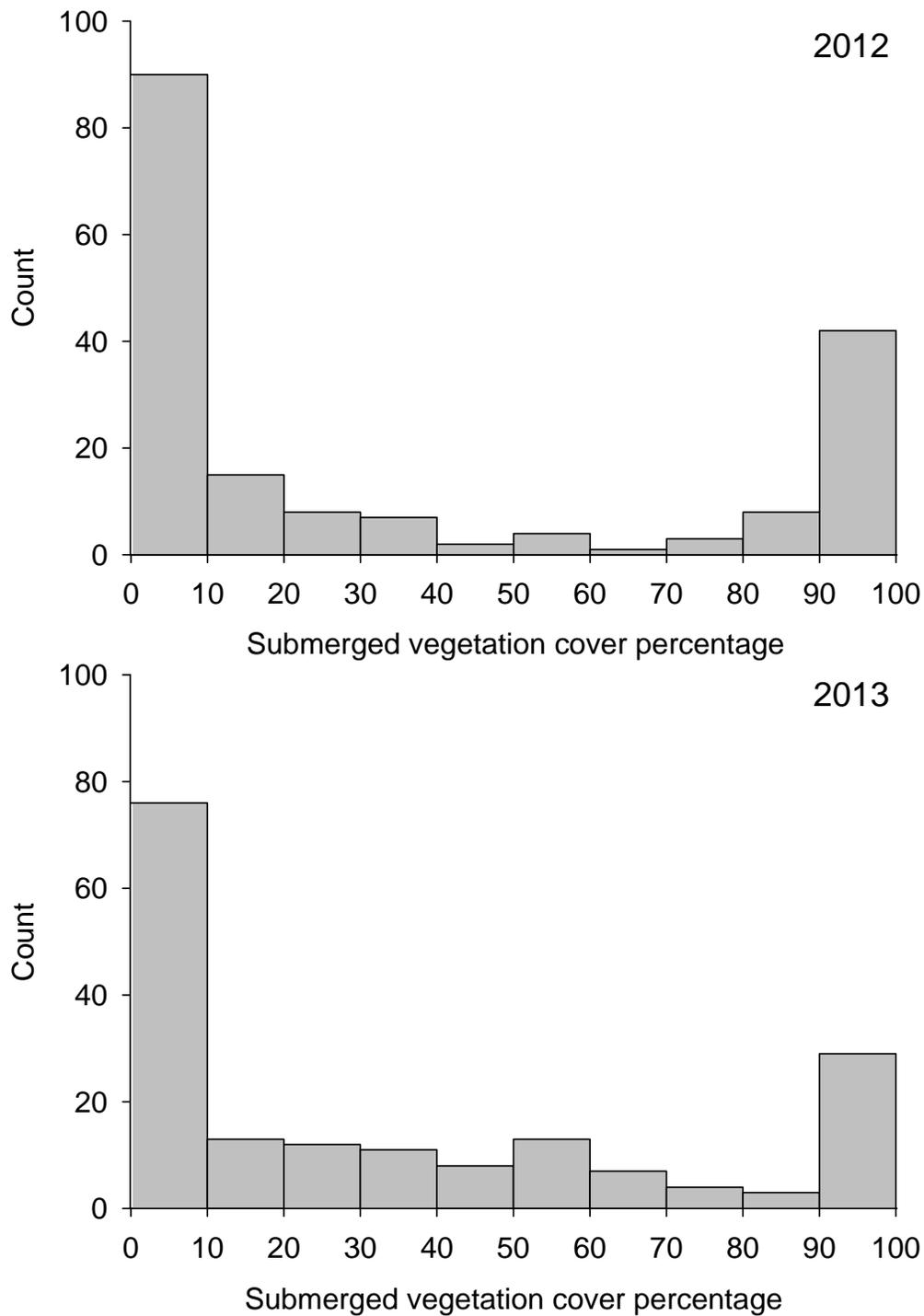
Figure D1. Histograms of water depths at crayfish locations in 2012 ($n = 180$) and 2013 ($n = 176$). Water depth was significantly higher in 2013 (Wilcoxon signed-rank test).
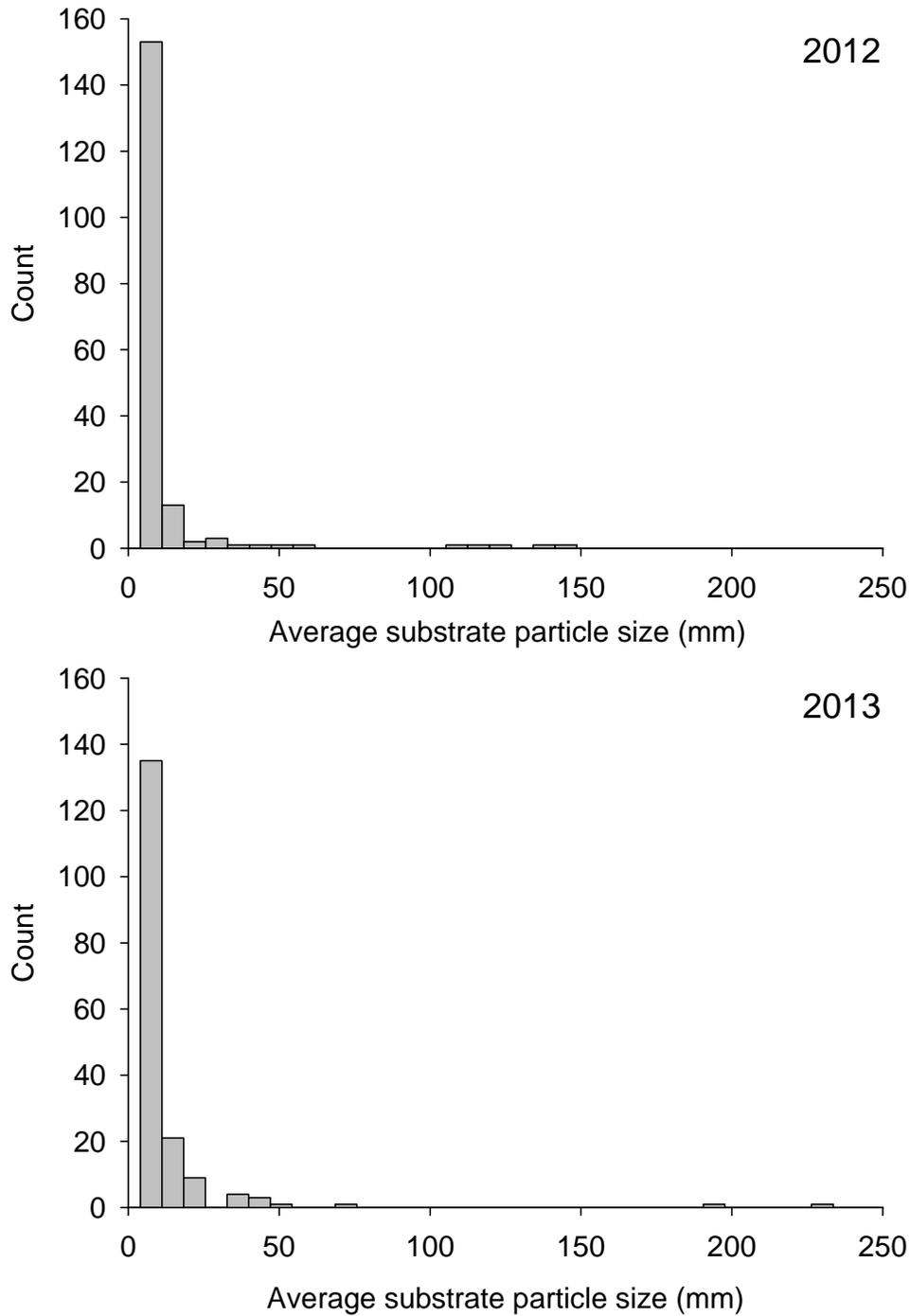
Figure D2. Histograms of average substrate particle sizes at crayfish locations in 2012 (*n* = 180) and 2013 (*n* = 176). Substrate particle size was significantly larger in 2013 (Wilcoxon signed-rank test).

Figure D3. Histograms of the percentage of submerged vegetation cover at crayfish locations in 2012 ($n = 180$) and 2013 ($n = 176$). Submerged vegetation cover did not differ significantly between years (Wilcoxon signed-rank test).
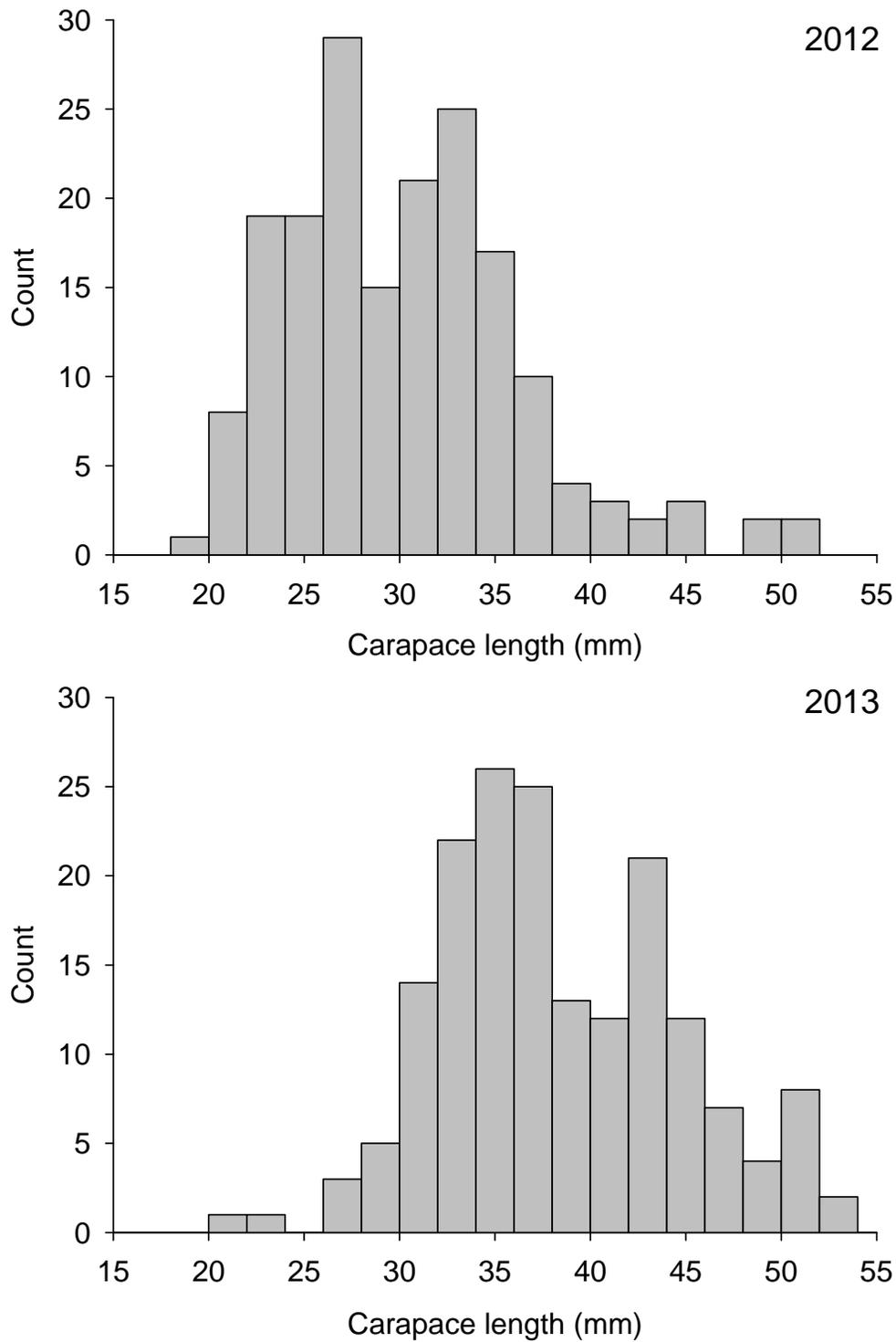
Figure D4. Histograms of size of crayfish (carapace length) used in 2012 ($n = 180$) and 2013 ($n = 176$). Crayfish were significantly larger in 2013 (Wilcoxon signed-rank test).

Table E1. Ranking of generalized linear mixed models for predator-specific risk for crayfish in Illinois in 2012 and 2013 based on Akiake's Information Criterion (AIC). "Probable" terrestrial predators were excluded from the analysis. Covariates were tested for their effect on the predator type (2012: terrestrial, $n = 14$; aquatic, $n = 54$; 2013: terrestrial, $n = 4$; aquatic, $n = 81$) responsible for predation events. Covariates included crayfish size (carapace), submerged vegetation cover (subveg), substrate particle size (substrate), water depth, stream size (sizePC), urbanization, and riparian buffer width (ripwidth). ΔAIC = AIC for a given model minus AIC for the top model. K = number of model parameters. w_i = Akaike weights. LL is the log-likelihood.

Year	Model	ΔAIC	w_i	K	-2*LL
2012	depth	0	0.915	3	49.97
	carapace	5.51	0.058	3	55.48
	intercept-only	9.54	0.008	2	61.51
	substrate	10.04	0.006	3	60.01
	subveg	11.10	0.004	3	61.07
	urban	11.26	0.003	3	61.23
	sizePC	11.27	0.003	3	61.24
	ripwidth	11.43	0.003	3	61.40
2013	depth	0	0.342	3	22.60
	intercept-only	1.26	0.182	2	25.86
	subveg	2.50	0.098	3	25.10
	substrate	2.59	0.094	3	25.19
	sizePC	2.89	0.081	3	25.49
	ripwidth	3.19	0.069	3	25.79
	urban	3.22	0.068	3	25.82
	carapace	3.26	0.067	3	25.86

Table E2. Potential terrestrial predators of crayfish observed on camera at sites in 2012 ($n = 45$) and 2013 ($n = 44$). Various Passeriformes species and duck species were pooled, respectively.

Potential predator	Number of occurrences		Naïve site occupancy	
	2012	2013	2012	2013
raccoon	24	22	0.533	0.500
great blue heron	14	20	0.311	0.455
Passeriformes	8	22	0.178	0.500
duck	8	21	0.178	0.477
muskrat	3	7	0.067	0.159
mink	3	4	0.067	0.091
otter	3	1	0.067	0.023
sora	2	0	0.044	0.000
green heron	0	2	0.000	0.045
fox	0	1	0.000	0.023