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Habitat selection by American mink during summer is related to hotspots of crayfish prey

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Habitat selection by mammalian carnivores may be driven by prey availability, physical characteristics of the habitat, and landscape context. However, the cues used by carnivores to select habitat are often unclear. We examined the seasonal diet of American mink *Neovison vison* and determined if the abundance of a primary prey, crayfish, was an important driver of habitat use during summer in an agricultural landscape in Illinois. We also evaluated effects of stream size, water depth, riparian buffer width, and urbanization on occupancy of stream segments by mink. We collected mink scats during three seasons and tested for seasonal differences in the percentage of occurrence and volume percentage of prey classes in the diet of mink. Crayfish remains were the dominant component of mink scats during summer. In summer 2012, we performed occupancy surveys for mink and concurrently measured crayfish densities and habitat features in 59 stream segments. Site occupancy by mink was related positively to presence of local areas with high crayfish concentrations (hotspots) instead of local habitat characteristics that might indicate high prey densities. Mink also were associated negatively with degree of urbanization and stream size. Our study highlights the effectiveness of integrating data on diets and occupancy modeling to obtain insights on cues used by carnivores to select habitat.

Habitat selection by mammalian carnivores may be driven by prey availability, physical characteristics of the habitat, and landscape context. However, the cues used by carnivores to select habitat are often unclear. Within a home range, carnivores should select habitat patches that maximize the probability of encountering prey. They 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). Because prey habitat does not necessarily guarantee actual occurrence of prey at any given time, using direct measures of prey abundance could be more informative than using the amount of prey habitat as a surrogate for prey abundance (Keim et al. 2011). Moreover, habitat selection studies should be paired with mechanistic data such as diet metrics (Keim et al. 2011) to understand carnivore 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, South America and Asia (Macdonald and Harrington 2003, Bonesi and Palazon 2007). This semiaquatic mustelid is closely associated with watercourses, but is capable of spending extended periods of time away from water. For example, in central Illinois, USA, radio-marked mink were located >100 m away from the water's edge 14% of the time (A. Ahlers pers. comm.). Mink have seasonally variable diets due to temporal changes in relative availabilities of prey (Gerell 1967, Dunstone and Birks 1987, Brzeziński 2008). The diet of mink has been examined within its native range (Dearborn 1932, Sealander 1943, Korschgen 1958, Racey and Euler 1983, Arnold and Fritzell 1987, Ben-David et al. 1997, Hoffman et al. 2009), 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, studies linking diet with habitat selection behavior of mink are scarce. 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). In the invasive range, mink population density is correlated positively with the proportion of crayfish in the diet, and home range size is correlated negatively with the crayfish contribution (Melero et al. 2014). Spatial variability in abundance of this aquatic prey could explain habitat selection by mink during seasons when crayfish are plentiful.

Mink may select habitat in relation to crayfish abundance in two general 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 to presence of prey hotspots instead

of to average prey densities for sites. Studies across multiple taxa indicate prey hotspots can be important determinants of predator space use and foraging behavior (Thompson et al. 2001, Davoren et al. 2003, Gende and Sigler 2006, López-Bao et al. 2011). 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 correlates of habitat selection by mink. In the Midwestern United States, agricultural intensification, including drainage for row crops, and urbanization have reduced the amount of suitable habitat for semiaquatic wildlife (Zucker and Brown 1998), and limited the terrestrial habitat available to mink surrounding the small streams and agricultural ditches in which they occur. 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). Additionally, mink might avoid areas of human development (Racey and Euler 1983, Brzeziński et al. 2012), although information regarding effects of urbanization on mink is limited (Gehrt et al. 2010).

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. The severe drought of 2012 (Illinois Department of Natural Resources 2013) presented an ideal opportunity to examine predator–prey interactions during environmental conditions expected to occur more frequently under climate change.

We examined the seasonal diet of American mink and determined if a primary prey, crayfish, was an important driver of habitat selection by mink during summer of a severe drought year in an agricultural landscape. We hypothesized that diet of mink would reflect seasonal availability of prey. We 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. We also hypothesized that habitat selection by mink during summer would be related directly to prey abundance. Hence, we expected a higher probability of occupancy for mink at sites with crayfish hotspots or higher mean densities. We also hypothesized that stream and landscape characteristics would influence habitat selection by mink. We predicted site occupancy by mink would be related positively to water depth and stream size because larger streams contain more aquatic resources. We also predicted a positive association between occupancy and riparian buffer width because wider buffers provide more foraging opportunities. Finally, we expected a negative association between site occupancy by mink and degree of urbanization.

Material and methods

Study area

Our study was conducted in east–central Illinois, USA and was centered on Champaign-Urbana (40°12′N, 88°26′W). Fifty-nine 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 (> 2500 people), and 50% of which were located outside of this urban buffer (Cotner and Schooley 2011). Sampling for crayfish density and site occupancy by mink occurred at these 59 study sites. Each site was a 200-m stretch of wadeable stream, ranging from 1st to 5th order in size (average site wetted width = 0–23.3 m; average site depth = 0–0.97 m). Sites represented potential resource patches for mink so our measure of site occupancy corresponded to habitat use (Schooley et al. 2012). The median distance between one site and the nearest site was 3.4 km (range = 0.5–13.5 km). Sites were distributed across an urbanization gradient (proportion of impervious surface within a 500-m buffer around each site, Cotner and Schooley 2011), and had a wide range of riparian buffer widths (0–466 m). We also collected mink scats at an additional 60 locations to increase our sample size.

Scat collection

To evaluate seasonal variation in composition of mink diets, we collected scats during fall, winter and summer. 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 (Rezendes 1999). 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 fall 2011 (21 September–10 November), our 59 study sites were surveyed for mink scat by two trained searchers; scat was found at 18 sites. There was uncertainty regarding the source of one collected scat sample, resulting in an analysis of 17 scats from 18 sites for fall. In winter 2012 (4 January –9 March), the 18 sites were revisited and searched, and all found scats were collected. To maximize efficiency of our searching, we did not revisit the 41 sites at which we did not find scat in fall. To increase our sample size, we instead searched an additional 60 locations within our study area. These locations were underneath and within 50 m of bridges in areas that often included rock and other substrates where mink typically deposit scat. The collection locations were ≥ 1.5 km apart. This separation distance was based on an estimate of average length of mink home ranges in the study area (A. Ahlers pers. comm.), 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. We sorted remains into seven prey classes (crayfish, mammal, bird, fish, insect, reptile and unknown) under a dissecting microscope (10 ×) based on hair, teeth, bones, feathers, scales and exoskeleton fragments. The unknown prey class was mostly comprised of unidentifiable bone fragments. These general prey classes were adequate for testing our main prediction regarding seasonal shifts for crayfish in mink diets.

Diet composition was recorded for each of the three seasons (fall, winter, summer) using three metrics: percentage of occurrence (PO; the number of occurrences of each prey class divided by the total number of scat samples, times 100), relative frequency of occurrence (RFO; the number of occurrences of each prey class divided by the total number of occurrences of identified prey), and volume percentage (VOL; visually estimated as the percentage of each prey class in each scat). PO and RFO were highly correlated positively for all prey classes ($r > 0.80$), so we used PO for analyses. Each metric comes with caveats. PO may overestimate less digestible prey and underestimate more digestible prey, and overestimate the contribution of prey taken regularly but in small amounts. 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, we used both PO and VOL methods in our 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 PO 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 we expect biases due to digestibility of prey types to remain constant across time, and our analyses focus on relative differences among seasons, conclusions about seasonal variation in mink diet should be robust.

For the PO metric, we tested for variation in mink diet among seasons using χ^2-tests and Fisher's exact tests when $\geq 20\%$ of the expected frequencies were < 5 (Zar 1984). For the VOL metric, we tested for between-season differences in diet composition using multi-response permutation procedures (MRPP – Mielke and Berry 2001, Roberts and Taylor 2008). We employed a Bonferroni correction when making multiple, pair-wise seasonal comparisons ($\alpha = 0.0167$). 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. The MRPP analysis was conducted in PC-ORD 6.0 (McCune and Mefford 2011).

To quantify the diversity of prey found in the mink diet, we calculated the Shannon diversity index (Shannon 1948) and dietary evenness in each season using both PO and VOL metrics. We 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 Inst.).

Occupancy surveys and crayfish sampling

Occupancy surveys for mink and crayfish sampling were conducted at the 59 study sites from 18 May – 26 July 2012, during the core months of the severe drought of 2012, which included the second driest January to July period on record in Illinois (Illinois State Water Survey 2012a, Illinois Department of Natural Resources 2013). 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, but we dealt with imperfect detection in our modeling. Sign was likely left by mink with established home ranges because our sampling was not during the dispersal period (Larivière 1999).

Concurrently, crayfish (*Orconectes*, *Procambarus*, *Cambarus*) density was measured in each of the 59 sites by sampling 1-m^2 areas in 10-m segments of stream (20 samples per site). We divided the stream's wetted width in half, randomly selected either the left or right side to begin sampling, and alternated sides as we sampled upstream. A sample was taken at the first 'high-quality' crayfish habitat encountered on the selected area within each 10-m segment. In streams ≤ 1 m wide, the entire stream width was sampled. High-quality habitat consisted of in-stream gravel, cobble, and rocks; anchored woody debris; or submerged vegetation. If there was no high-quality habitat within a segment, we 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, Taylor and Soucek 2010). When necessary in low-flow areas, we 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.

We quantified three habitat covariates that could be correlated with crayfish density (Riggert et al. 1999, DiStefano et al. 2003): substrate particle size, number of crayfish burrows, and number of woody debris accumulations. At each sampling location, we created a transect perpendicular to the stream flow. We dropped a metal rod at 1-m intervals for the entire wetted width of the stream and measured the substrate particle size that the rod landed on using a gravelometer. These particle sizes were averaged to create one measure of substrate particle size per 10-m segment of stream. The number of active crayfish burrows was counted in each 10-m segment of stream. We also counted

the number of woody debris accumulations anchored in the streambed in each segment of stream.

Detection and occupancy covariates

We recorded covariates that could influence detection (p) of mink sign including observer, Julian date, number of days since rain, and recent rainfall – total rainfall (cm) for the seven days prior to each survey (Illinois State Water Survey, station no. 118740, Urbana, Illinois). Recent rainfall could wash away sign or raise water levels to hide sign (Schooley et al. 2012).

We measured 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 (five values) and averaged for each site (Cotner and Schooley 2011). Drainage area, wetted width, and stream order were correlated positively (all $r > 0.47$), so we 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 three variables ($r = 0.74$–0.94), so we used sizePC as a measure of stream size in our models (Cotner and Schooley 2011). We excluded water depth from the PCA because small streams have dynamic flow regimes tied to local precipitation events; they flood and subside faster than do large streams (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 within sites, so we evaluated three measures of crayfish density. For each site, we calculated average density of adult crayfish (adults m^{-2}), average density of total crayfish (adults + juveniles m^{-2}), and 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 sampled crayfish densities (median = 2 crayfish m^{-2}, $n = 1{,}180$; Supplementary material Appendix 1 Fig. A1). Although mink are likely to prey only on larger, adult crayfish, we used total crayfish density to define hotspots because mink could use the presence of juvenile crayfish as an indicator of where adults occur.

Occupancy modeling

We 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). We first selected the best model for detection (p), and then modeled occupancy. We used a maximum of two covariates for p and four covariates for ψ in a single model to avoid over-parameterization. We 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. We did not include two covariates in the same model if they were correlated at $r \geq 0.60$. We 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). Akaike weights (w_i) were summed for models that contained each of the three measures of crayfish density to determine (using across-model inference) which measure of prey abundance was the best predictor of occupancy by mink.

Results

Seasonal diet

We 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 and comprising > 83% of the diet by volume. However, percentage of occurrence of diet items differed among seasons ($\chi^2 = 23.7$, $DF = 12$, $p = 0.02$). Crayfish occurred most frequently in summer (Fisher's exact test: winter–summer, $p = 0.003$; fall–summer, $p = 0.016$; Fig. 1), when PO of mammals was lowest (Fisher's exact test, fall–summer, $p = 0.025$; Fig. 1). PO of mammals in the diet was greatest during fall and winter (Fig. 1). Fish occurred in 35.9% of scats, 8.1% by volume. PO of fish increased from fall to winter (Fisher's exact test $p = 0.076$), and both PO (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 (PO = 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 vertebrate prey. Based on PO, the contribution of the unknown prey class to the diet did not differ between seasons ($p > 0.72$ for all seasonal comparisons).

MRPP results for the VOL metric showed that diet composition for summer differed from diet composition for fall and winter (fall–winter, $A = 0.010$, $p = 0.15$; winter–summer, $A = 0.098$, $p < 0.001$; fall–summer, $A = 0.155$, $p < 0.001$). MRPP results highlight the greater contribution

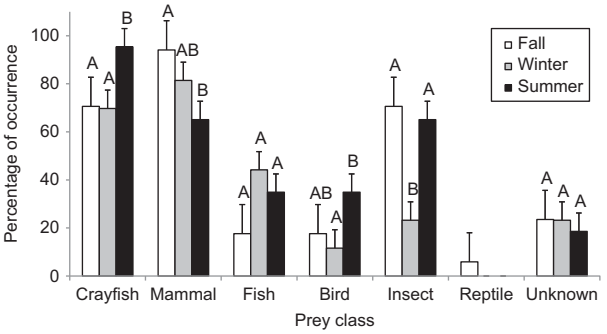

Figure 1. Mean percentage of occurrence (+ 1 SE) of seven prey classes in the diet of American mink in fall 2011 ($n = 17$ scat samples), winter 2012 ($n = 43$), and summer 2012 ($n = 43$). Within a prey class, bars with different letters indicate differences among seasons (Fisher's exact tests).

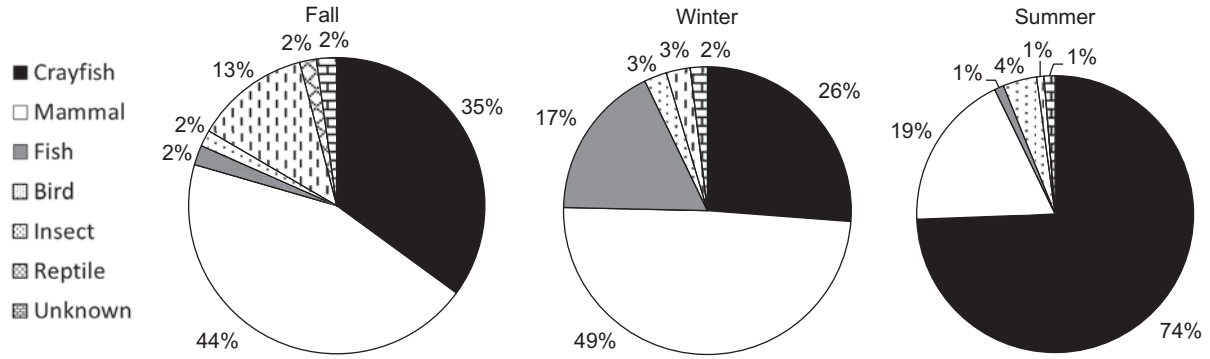

Figure 2. Volume percentage of seven prey classes in the diet of American mink in fall 2011 (n = 17 scat samples), winter 2012 (n = 43), and summer 2012 (n = 43).

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 MRPP results.

Based on the PO metric, the diversity indices for mink diet did not differ strongly among seasons (Table 1; Shannon diversity index: fall–winter, $t = 0.45$, $DF = 86$, $p = 0.65$; winter–summer, $t = 1.03$, $DF = 211$, $p = 0.31$; fall–summer, $t = 0.19$, $DF = 70$, $p = 0.85$). 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, $t = 0.19$, $DF = 91$, $p = 0.85$; winter–summer, $t = 4.00$, $DF = 244$, $p < 0.001$; fall–summer, $t = 3.23$, $DF = 103$, $p < 0.01$).

Summer habitat selection

A total of 7798 crayfish of four species (*Orconectes virilis*, *Orconectes propinquus*, *Procambarus acutus*, *Cambarus* spp.) were captured (2068 adults, 5730 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 strongly associated with the four habitat covariates used in occupancy modeling (all $p > 0.05$, Wolff 2013). Adult crayfish density was associated weakly and negatively with substrate particle size ($R^2 = 0.006$, $p = 0.02$) and the number of woody debris accumulations ($R^2 = 0.004$, $p = 0.03$), but not with the number of crayfish burrows ($R^2 < 0.001$, $p = 0.78$). Total crayfish density was not related to substrate ($R^2 < 0.001$, $p = 0.52$), but was related weakly and negatively to crayfish burrows ($R^2 = 0.005$, $p = 0.02$) and woody debris accumulations ($R^2 = 0.008$, $p < 0.01$). Crayfish hotspots were not associated with substrate ($R^2 = 0.003$, $p = 0.92$) or crayfish burrows ($R^2 = 0.007$, $p = 0.64$), but were associated negatively with woody debris accumulations ($R^2 = 0.164$, $p = 0.056$).

Mink sign was detected at 18 of 59 sites (naïve occupancy = 0.305). We decided the best model for detection was the competitive model ranked second ($\Delta AIC = 0.14$; Table 2), and we 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 ($\Delta AIC < 2$) contained crayfish hotspot as a covariate (Table 3). Occupancy probability was related positively to the presence of a crayfish hotspot at a site ($\beta_{hotspot} = 1.721$, $SE = 0.625$; Fig. 3). Estimated occupancy from the hotspot model was 0.562 for sites with crayfish hotspots, and 0.187 for sites without hotspots. Site occupancy by mink was related negatively to stream size ($\beta_{sizePC} = -0.598$, $SE = 0.463$; Fig. 3) and urbanization

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 percentage of occurrence data and volume percentage data.

	Percentage of occurrence			Volume		
Index	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 seven days prior to each survey (rainfall). $\Delta AIC = AIC$ 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	$-2 \times LL$
ψ(.), p(observer)	0	0.2849	3	103.34
ψ(.), p(observer, rainfall)	0.14	0.2657	4	101.48
ψ(.), p(observer, days since rain)	0.83	0.1881	4	102.17
ψ(.), p(observer, Julian date)	1.58	0.1293	4	102.92
ψ(.), p(observer, Julian date, days since rain)	2.80	0.0703	5	102.14
ψ(.), 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 seven 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	$-2 \times LL$
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

($\beta_{urban} = -1.793$, SE = 1.606; Fig. 3). Although water depth occurred in competitive occupancy models (Table 3), water depth did not substantially increase model fit based on log likelihoods; the top two models were essentially unchanged by including depth as a covariate. In addition, the model with depth alone performed worse than the intercept-only model. Riparian buffer width also was not a good predictor of site occupancy.

Discussion

The spatial variation in abundance of a common prey, crayfish, was the primary predictor of habitat selection during summer by American mink within a human-dominated landscape. Mink seemed to select sites 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 occupancy by mink than were average crayfish densities. Habitat occupancy by mink was also affected by stream and landscape characteristics; mink were associated negatively with both stream size and urbanization.

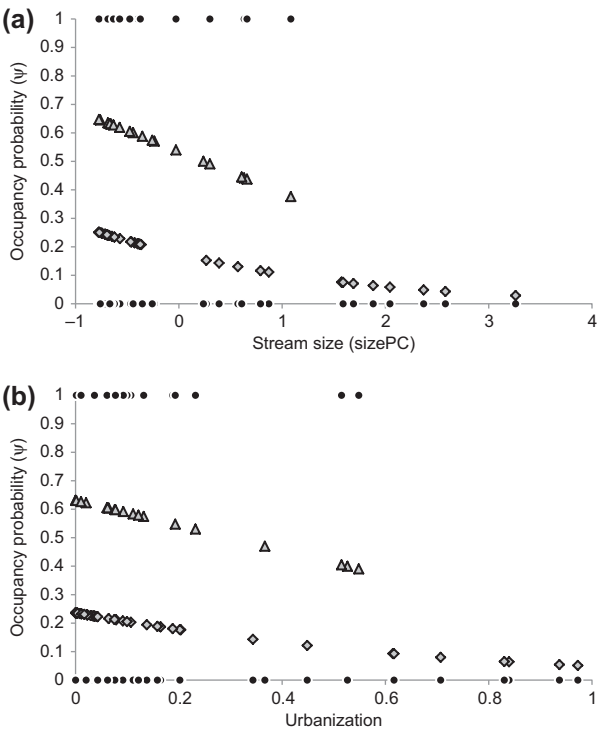

Figure 3. Relationships between probability of site occupancy by American mink and (a) stream size from the top occupancy model, and (b) urbanization from the 3rd best occupancy model (Table 3). Gray triangles indicate estimated occupancy at sites with crayfish hotspots. Gray diamonds indicate estimated occupancy at sites without crayfish hotspots. Black circles indicate naïve occupancy for sites (1 = occupied, 0 = unoccupied).

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 our study appeared 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 likely cue directly on crayfish. This tactic may be particularly effective 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.e. crayfish distributions may be patchy due to demographic processes instead of differences in habitat quality). In our study, habitat selection by mink also was influenced by urbanization. Mink had lower occupancy probabilities in urban areas (Fig. 3). 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 (Tigas et al. 2002, Dickson et al. 2005). However, little information exists regarding the effects of urbanization on mink (Gehrt et al. 2010). In Canada, cottage development around lakes reduced habitat heterogeneity, decreased mink activity, and altered diets of mink (Racey and Euler 1983). Radio-marked American mink around 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 human disturbance

typical of urban areas on the behavior of mink, and agree with our result.

Contrary to our prediction, site occupancy for mink was related negatively to stream size (Fig. 3). We expected mink to select larger streams because we assumed that larger streams had more available resources, and we do not have an explanation for this surprising result. In the invasive range, Zuberogoitia et al. (2006) found the use of small versus large streams by radiomarked mink was sex-dependent; females used small streams and males used large streams. Unfortunately, we cannot assess sex-dependent habitat selection with our occupancy surveys.

We did not detect a strong, positive relationship between occupancy probability for mink and water depth in contrast to previous research in our study area (Schooley et al. 2012). Our results may differ because of much less variable water levels during our 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 precent (42 of 59) of sites during our study had water depths below 0.4 m. Thus, we acknowledge that our results from this severe drought year may not extend to years of high precipitation. However, 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), our study may offer a glimpse into occupancy dynamics under climate change. Mink and other semiaquatic mammals are likely to experience increased environmental stochasticity that could create temporal variability in factors that influence habitat selection.

We measured a range of habitat variables typically used for assessing crayfish abundance (Riggert et al. 1999, DiStefano et al. 2003), but mink could have keyed in on an unmeasured habitat factor. For example, submerged vegetation provides protective cover for crayfish (Kershner and Lodge 1995) and reduces predation risk from aquatic and terrestrial predators (Wolff 2013). We did not measure submerged vegetation cover at crayfish hotspots in this study. However, we performed a post hoc analysis using submerged vegetation data collected between July and September 2012 at our study sites (Wolff 2013) to examine the relationship between submerged vegetation cover, crayfish hotspots, and site occupancy (Supplementary material Appendix 2). Crayfish hotspots were associated positively with submerged vegetation cover, but submerged vegetation did not explain much variation ($R^2 < 0.17$). Moreover, submerged vegetation cover was a poor predictor of site occupancy (worse than intercept-only model) compared to crayfish hotspots (Supplementary material Appendix 2 Table A1). Thus, we found little evidence that mink recognize areas with high cover of submerged vegetation as good locations to hunt.

The diet of mink in our 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 indicate greater dietary specialization on crayfish during summer. This increased contribution of crayfish to the diet appears to drive the habitat selection behavior of mink. 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). Our study area experienced an unseasonably mild winter during 2012. January and February temperatures in Illinois were 3.67°C and 2.61°C warmer than average, respectively (Illinois State Water Survey 2012b, 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.

Our 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 their 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. Our 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.

Our combined results for diet and occupancy modeling indicate the spatial distribution of mink during summer is greatly influenced by the abundance patterns of their preferred prey. Our data support recent evidence from Europe suggesting that availability of crayfish, and an increased prevalence of crayfish in the diet of American mink, may alter the spatial distribution of mink and aid in expansion of mink across its invasive range (Melero et al. 2014, Rodrigues et al. 2014). Further examination of this predator–prey interaction in North America could lead to a better understanding of mink ecology in places where the co-occurrence of mink and crayfish is novel. More generally, the importance of prey hotspots merits further investigation to understand the mechanisms underlying habitat selection by carnivores.

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Supplementary material (available online as Appendix wlb.00031 at <www.wildlifebiology.org/readers/appendix>). Appendix 1–2.