WETLAND HABITAT USE BY SEMIAQUATIC FAUNA IN A HYDROMODIFIED AND FRAGMENTED LANDSCAPE

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ABSTRACT

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Northwest Ohio has been heavily impacted by ditching and draining of the landscape as well as impoundment and pond construction. These features can reduce baseflows, alter wetland hydroperiods, or otherwise impair ecosystem services. However, they may also create aquatic habitat, serve as refuges from wetland habitat loss and promote connectivity of wildlife populations. It is critical to identify the effects of hydromodification on semiaquatic fauna such as the common muskrat (Ondatra zibethicus), the American mink (Neovison vison) and cambarid crayfishes (Cambaridae), which may be sensitive to associated changes in fine- and coarse-scale wetland habitat and landscape characteristics. To evaluate potential wetland habitat use patterns, sign and nocturnal spotlight surveys were conducted in the Oak Openings Region from May 15th to October 18th 2021. Habitat, environmental and spatial data were also collected. As predicted, focal organisms used modified wetlands to a lesser degree, although the effect depended on organism and wetland type. As expected further, muskrats and crayfishes were more likely to use higher order or deep streams/ditches; crayfishes were more likely to use seasonal and restored wetlands. Results were consistent with isolation-area based predictions of habitat use insofar as mink and muskrats were more likely to use large nonlinear wetlands, and muskrats used less isolated wetlands. Crayfish and, unexpectedly, mink used more isolated wetlands. Open canopy and anthropogenic landcover classes in the landscape neighborhood of wetlands featured in many habitat use models. Fine-scale habitat variables tended to predict habitat use as well as or better than coarser-scale variables. Treating presence or relative activity of each organism as a predictor variable in habitat use models of the other organisms produced competitive models, although results for mink occurrence were inconsistent with predictions based on predator-prey relationships. Results support restoration of historical wetland conditions, implementation of spatially-informed conservation strategies, consideration of local landcover types in conservation planning, and careful selection of predictor variables in models of habitat use.

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GENERAL INTRODUCTION

Wetlands in the lower forty-eight United States have been reduced in areal extent by more than 50% (as much as 90% in states such as Ohio) since the late 18th century (Dahl 1990). Ditching, tiling and draining, in addition to expansion of urban areas and associated impermeable surfaces, contributes to channelization, increased flooding, and reduced baseflow of waterways globally (Poff et al. 1997). Additionally, ponds constructed for flood control, water provisioning, nutrient and sediment retention, recreation and other purposes have proliferated such that ponds number more than 2.6 million in the contiguous United States (Renwick 2005). While construction of ditches and ponds can degrade aquatic ecosystems, these features can also create aquatic habitat, serve as refuges from wetland habitat loss and promote connectivity of wildlife populations (Gee et al. 1997, Akasaka and Takamura 2012, Chester and Robson 2013, Pryke et al. 2015, Kukkala and Moilanen 2016, Clifford and Hefferman 2018).

Habitat-use patterns by semiaquatic fauna of the Oak Openings Region of northwest Ohio are likely to reflect this hydromodification and associated altered hydrological and habitat conditions. Hydromodification following Anglo-American settlement of the Oak Openings Region has lowered its water table, reduced surface water residence time, and introduced many constructed ponds and ditches (Brewer and Vankat 2004, Grigore 2016). Protected areas encompass 12% of the region in Northwest Ohio, incorporating diverse land cover types and wetland habitat characteristics (Abella et al. 2007, Martin and Root 2020).

Semiaquatic fauna that occur in this region include common muskrats (*Ondatra zibethicus*), cambarid crayfishes (*Cambaridae*) and American mink (*Neovison vison*). These focal organisms are common in wetlands of the American Midwest, fill a variety of niches, and use habitat across a range of scales. Therefore, differential habitat use by these organisms may reflect variable fine- and landscape-scale habitat suitability, accessibility and functioning of wetlands to a variety of fauna in the Oak Openings Region. This study evaluated habitat use of focal semiaquatic organisms to explore the relationship between these factors and wetland habitat use to inform conservation and management of modified wetlands and landscapes.

Primary questions addressed included: (1) what fine- and landscape-scale habitat suitability factors influenced habitat use in the semi-natural and hydrologically unique conditions of the Oak Openings Region? (2) were highly modified or constructed wetlands used similarly to less modified wetlands? (3) how did spatial factors like wetland size and isolation affect habitat use? (4) was habitat use by each focal organism related to that of the others?

This thesis is organized into three chapters. Chapter I reviews the impacts of hydromodification on wetland habitat in the Oak Openings and summarizes documented habitat use patterns of focal semiaquatic organisms. Chapter II discusses habitat use patterns by focal organisms observed in linear wetlands (streams and ditches) of the Oak Openings Region. Chapter III discusses habitat use patterns by focal organisms observed in nonlinear wetlands (ponds, scrapes, swamps, etc.) of the region. Fine-scale and landscape-scale habitat characteristics are considered as well as spatial factors.

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CHAPTER I: LITERATURE REVIEW

Introduction

Hydromodification, the Oak Openings Region and resident semiaquatic fauna

Hydromodification, in addition to expansion of urban areas and associated impermeable surfaces, contributes to channelization, increased flooding, and reduced baseflow of waterways globally (Poff et al. 1997). Additionally, ponds constructed for flood control, water provisioning, nutrient and sediment retention, recreation and other purposes have proliferated such that ponds number more than 2.6 million in the contiguous United States (Renwick 2005). While construction of ditches and ponds can degrade aquatic ecosystems, these features can also create aquatic habitat, serve as refuges from wetland habitat loss and promote connectivity of wildlife populations (Gee et al. 1997, Akasaka and Takamura 2012, Chester and Robson 2013, Pryke et al. 2015, Kukkala and Moilanen 2016, Clifford and Hefferman 2018).

A representative example of modern landscapes impacted by hydromodification is found in Northwest Ohio. Ditching and tiling for agriculture and human settlement has drained Great Black Swamp almost completely, which covered over 3800 square kilometers of Northwest Ohio and parts of Indiana (Kaatz 1955). However, the Oak Openings Region, a unique complex of ecological communities established on remnant glacial lakeshore-derived sandy soils, remains less developed than surrounding urban and agricultural areas. Regardless, this complex is especially vulnerable to regional hydromodification due in part to its natural geological and hydrological characteristics.

The Oak Openings Region is underlain by a shallow aquifer that facilitated the development of seasonally dry wet prairies, swamps, streams and other wetlands, although permanent wetlands did occur (Brewer and Vankat 2004). This shallow aquifer was historically highly connected with its few natural streams and overlain with unconsolidated, conductive sand (Shade and Valkenberg 1975, Brewer and Vankat 2004). Hydromodification following Anglo-American settlement of the region has since lowered the water table, reduced surface water residence time, and introduced many constructed ponds and ditches (Brewer and Vankat 2004, Grigore 2016). These influences and concomitant urban and agricultural development have greatly reduced and fragmented the biodiverse ecosystems of the Oak Openings Region, although approximately 27% of the area remains classified as natural or seminatural (Schetter and Root 2011).

Due to hydrological and habitat changes related to human impacts, many wetlands in this region may represent degraded habitat. However, ditches and constructed ponds are numerous in the area and may exhibit some favorable habitat characteristics. For example, ditches can serve as movement corridors or habitat for a variety of species (root voles: Mauritzen et al. 1999, green frogs: Mazerolle 2005, bobcats and ocelots: Nordlof 2015, gallinules: van Rees et al. 2018).

Muskrats, crayfishes and minks (hereafter referred to collectively as focal organisms) are common semiaquatic fauna that fill a variety of niches in hydromodified wetlands of the American Midwest including those of the Oak Openings Region. The common muskrat (*Ondatra zibethicus*) is a semiaquatic burrowing rodent that mostly forages on wetland vegetation. Crayfishes (*Cambaridae*) are largely omnivorous and detritivorous aquatic macroinvertebrates. Muskrats and crayfishes are important prey items for the mustelid generalist carnivore, the American mink (*Neovison vison*), as well as other predators (Hamilton 1940, Lariviere 1999, Ahlers et al. 2010, Wolff et al. 2015). Muskrats and crayfishes are wetland ecosystem engineers that exhibit sensitivity to aquatic ecosystem degradation (e.g., Schilderman et al. 1999, Ahlers et al. 2010, Reynolds and Souty-Grosset 2012, Carreira et al. 2014, Kua et al.

2020). As generalist predators, minks can exploit alternative prey items and consequently exert more pressure on some prey species (Barreto et al. 1998, MacDonald et al. 2002, Roemer et al. 2009). Focal organisms also exhibit variable behavioral ecologies corresponding to their size, foraging requirements and niches (Table 1.1). For example, mink home ranges during the summer vary in linear dimension from many hundreds to thousands of meters (e.g. Gorga 2012, Haan and Halbrook 2015), those of many crayfishes are on the order of less than a meter to tens of meters (e.g. Black 1963, Hazlett et al. 1974), and those of muskrats are on the order of tens to hundreds of meters (e.g. Proulx and Gilbert 1983, Ahlers et al. 2010). Consequently, monitoring habitat use by these focal organisms offers a broad ecological lens through which wetland functioning and impacts of conservation concern can be observed.

Table 1.1. List of common muskrat (*ondatra zibethicus*), crayfishes (*Cambaridae*) and American minks (*Neovison vison*) and their habitat preferences, behavioral requirements, and mortality risks in North America.

Organism	Linear home range size	Water	Substrate	Cover	Diet	Development	Mortality risks
Muskrat	Tens to hundreds of meters	Deep, perennial	Can support burrows	Wide riparian buffers, dense aquatic vegetation	Graminoids, especially aquatic macrophytes	Tolerant of urban and rural land cover	Predation by minks, other mesocarnivores, birds of prey; trapping by humans; starvation
Crayfish	Less than a meter to tens of meters	Varies	Can support burrows	Aquatic vegetation and debris	Variety (omnivorous/ detritivorous)	Relatively intolerant of non-natural land cover	Predation by a variety of taxa, especially fishes; desiccation; pollution
Mink	Hundreds to thousands of meters	Deep, perennial	Unknown	Dense buffer vegetation	Muskrats, crayfishes, fishes, waterfowl, amphibians, etc. (carnivorous)	Relatively intolerant of urban land cover and developed wetlands	Predation by other mesocarnivores and birds of prey; vehicular collision and trapping by humans

Fine-scale factors affecting habitat use by focal organisms

Although numerous factors influence habitat use by these organisms (Table 1.1), hydrological characteristics tend to be among the most influential. For example, Ahlers et al. (2015) found that stream occupancy by minks, as well as their common muskrat prey, strongly tracked summer precipitation in an environment characterized by decreased stream base-flow due to ditching and draining of the landscape for agriculture. While some crayfish species are more able to tolerate dry conditions than muskrats by burrowing to the water table, wetlands with significantly decreased hydroperiods can nevertheless be associated with desiccation related mortality and reductions in fitness of crayfishes (Acosta and Perry 2001). In general, Muskrats, crayfishes and minks may benefit from larger, deeper wetlands for increased resources therein and refuge from terrestrial predators (Ahlers et al. 2016, Cotner and Schooley 2011, Schooley et al. 2012, Thoma and Jezerinac 2000). Potential habitat selection for persistent water sources is pertinent for semiaquatic fauna of the Oak Openings Region, where natural streams are limited and stream flow is highly variable (Brewer and Vankat 2004).

Other factors that have been established as important for habitat use by muskrats and/or crayfishes including percent macrophyte cover, wetland morphology, and riparian buffer size and composition (e.g. Ahlers 2010, Burksey and Simon 2010, Proulx and Gilbert 1983). However, muskrats and crayfishes can utilize degraded habitats lacking preferred habitat features in some cases (e.g. Ahlers et al. 2010, Ramalho and Anastácio 2015). Existing studies suggest that minks and/or muskrats use relatively dense, nearshore cover and abundant trees as cover from predation, rest sites, or foraging; minks may avoid more developed banks (e.g. Ahlers et al. 2016, Haan and Halbrook 2014, Mason and MacDonald 1983, Racey and Euler 1983, Yamaguchi et al. 2003). Canopy cover is related to wetland productivity in the Oak Openings

Region (Plenzler and Michaels 2015) and therefore may relate to habitat use by primary consumers such as crayfishes or muskrats. In spite of studies documenting the importance of mink habitat use covariates, predictive models based on fine-scale habitat variables have generally not performed well (e.g., Loukmas and Halbrook 2001, Martinig 2017).

While natural streams likely exhibit more favorable wetland habitat qualities, evidence of minks using ditches extensively in the species native range has been documented and minks have been directly observed using seasonally dry ditches in their invasive range (A. A. Ahlers, personal communication, Philcox and Grogan 1997, Zschille et al. 2012).

Spatial and landscape factors affecting habitat use by focal organisms

Models incorporating landscape-scale factors have also suggested variables relating to habitat use. Muskrats may use habitat in stream reaches with greater proportions of, or proximity to, urban development and agricultural land cover in the surrounding landscape (Ahlers et al. 2010, Ahlers et al. 2015). Crayfishes may prefer streams in watersheds with greater proportions of natural land cover types and lower proportions of anthropogenic land cover types, although reach-scale habitat factors are stronger predictors (Burksey and Simon 2010). Studies of landscape-scale influences on mink habitat use have shown conflicting effects at different scales or in different landscape contexts, although urban development or proximity to urban development at the landscape scale appears to be an influential factor (e.g. Ahlers et al. 2016, Holland et al. 2019).

Given that semiaquatic fauna use upland habitat for at least some of their life history, understanding how terrestrial context of water bodies influences habitat use is also important. Muskrats seldom distance themselves from surface water; for example, Ahlers et al. (2010) never observed radio-tracked muskrats more than 3 m away from stream banks. Ahlers et al. (2015)

related this finding to earlier studies suggesting that muskrats are reluctant to disperse through upland even when drought compromises their habitat, during which they can be exposed to elevated predation risk while traveling in upland areas (Errington 1939; 1943). As with muskrats, crayfishes can also be subject to high mortality during drying-related movements (Ramalho and Anastácio 2015).

Although mink activity is consistently concentrated near surface water, forays into upland areas away from water do occur (Arnold and Fritzell 1990, Lariviere 1999, Yamaguchi et al. 2003, Ahlers et al. 2015). For example, minks in the Prairie Pothole Region tend to occupy large circular home ranges containing many disconnected wetlands in comparison to the relatively linear home ranges of minks in other areas (Arnold and Fritzell 1990, Sargeant et al. 1993). The former configuration inherently requires more overland movement to access water than the latter wherein successive stream reaches tend to be directly connected. Nevertheless, these movements are associated with elevated mortality risk for minks (Ahlers et al. 2015). In North America, some of these risks include predation by birds of prey and larger mesocarnivores as well as collision by motor vehicles (Lariviere 1999). Exposure to these risks during overland movements may outweigh the foraging benefits of small wetlands isolated from other wetlands and streams. Maintaining large, fragmented territories incorporating these features may not be worth the mortality risk associated with traveling between them, especially if they contain fewer resources (MacDonald et al. 2002, Brzeziński et al. 2017). Conversely, some studies have reported negative effects of stream proximity to large, persistent, artificial wetlands or local availability of surface water on mink occupancy in streams; this may suggest preferential use of these permanent lentic wetlands over streams when both are available within a home range (Ahlers et al. 2016, Holland et al. 2019).

Interspecific interactions affecting habitat use by focal organisms

Mink habitat use is related to availability of preferred prey items (Arnold and Fritzell 1987, Arnold and Fritzell 1990, Yamaguchi et al. 2003, Wolff et al. 2015, Holland et al. 2018). In fact, Wolff et al. (2015) found that crayfish hotspots were better predictors of mink occupancy than habitat variables. Similarly, Ahlers et al. (2015) found that minks were more likely to abandon sites lacking preferred muskrat prey. While muskrats and crayfishes lack a predator-prey relationship with each other, it is possible that their overlap in sensitivity to hydrological conditions, facilitation of structural/vegetational heterogeneity, consumption of aquatic vegetation, and requirement for substrate that can support burrows (Kua et al. 2020, Reynolds and Souty-Grosset 2012, Proulx and Gilbert 1983, Thoma and Jezerinac 2000, Toner et al. 2010) could result in positively correlated habitat use of these two prey organisms.

Interspecific interactions can be modified by abiotic factors. For example, spatial factors influence the relationship between minks and water voles: water voles can exhibit higher occurrence rates in smaller, more isolated wetlands that minks are less likely to use, whereas the reverse pattern can be observed in larger, less isolated wetlands where minks can exert extreme predation pressure (Brzeziński et al. 2017, MacDonald et al. 2002). In a similar manner, the smaller home range size requirements of muskrats and crayfishes may facilitate a predation refugium effect of small habitat patches sufficiently isolated from preferred mink or predatory fish habitat patches (Arnold and Fritzell 1990, Brzeziński et al. 2017, MacDonald et al. 2002). In terms of hydrological factors, the benefits of more stable hydrological regimes to crayfishes could be offset by potential extreme predation pressure by fish in waters deep or persistent enough to sustain the latter, although availability of aquatic vegetation or debris as predation refugia can promote co-existence (Kellogg and Dorn 2012, Wolff et al. 2016). Furthermore, riparian crayfishes may be more vulnerable to terrestrial predators when drought reduces water depths (Wolff et al. 2016), which in turn may offset benefits of waters too shallow or seasonal for predatory fishes.

Hydromodification may also modify interspecific interactions among semiaquatic fauna to the detriment of one or more species involved. For example, the American mink, an active, generalist predator of a wide variety of aquatic and semiaquatic prey species (Lariviere 1999), can exert elevated predation pressure in environments affected by hydromodification. While studies documenting the effects of mink predation on North American wetland species are limited, those that have been documented in the species' native and invasive range (waterfowl: Krapu et al. 2004, water voles: Lawton and Woodroffe 1991, MacDonald et al. 2002, waders: Niemczynowicz et al. 2017) may be of conservation relevance. In one study, Krapu et al. (2004) observed that a constructed canal in the North American Prairie Pothole region acted as a permanent freshwater refugium for minks during dry periods of reduced surface water availability in disconnected wetlands which potentially stabilized mink abundance, increased predation pressure by minks, and thereby reduced gadwall duckling survival by as much as 56%.

Investigating non-random associations of these organisms may be informative as to their ecological relationships especially in the context of hydromodified or otherwise disturbed environments. Furthermore, because the occurrence of each organism is a function of the whole suite of abiotic and biotic factors in their environment, monitoring the organisms themselves may be a more efficient method to evaluate ecosystem function than monitoring the numerous potential habitat variables in their environment.

Methods used to evaluate habitat use

Sign searches

Muskrat tracks and scat are easily distinguished from those of other large rodents such as beavers and groundhogs. Mink tracks and scat are also readily identified in areas lacking similarly sized mustelids (Schooley et al. 2012). Furthermore, as muskrats and minks tend to be restricted to a relatively narrow area at the interface of aquatic and terrestrial habitats, sign surveys can be focused within a small area; consequently, presence-absence data can be obtained relatively efficiently for these organisms (Bluett et al. 2006, Bonesi et al. 2006, Bonesi and Macdonald 2004, Harrington et al. 2008, Loukmas and Halbrook 2001, Schooley et al. 2012, Wolff et al. 2015). Mink rafts can also be deployed at sites to increase detection probability (Schooley et al. 2012). These consist of a two-foot by four-foot buoyant plywood and polystyrene base with a hole cut in the center, above which sits a tunnel of sufficient size for a mink or muskrat to enter (Figure 1.1). A tracking cartridge embedded with a clay-sand mixture sits in the hole so that any mink or muskrat that climbs onto the raft and into the tunnel will leave tracks in the mixture (Figure 1.1). It is not necessary to use bait.

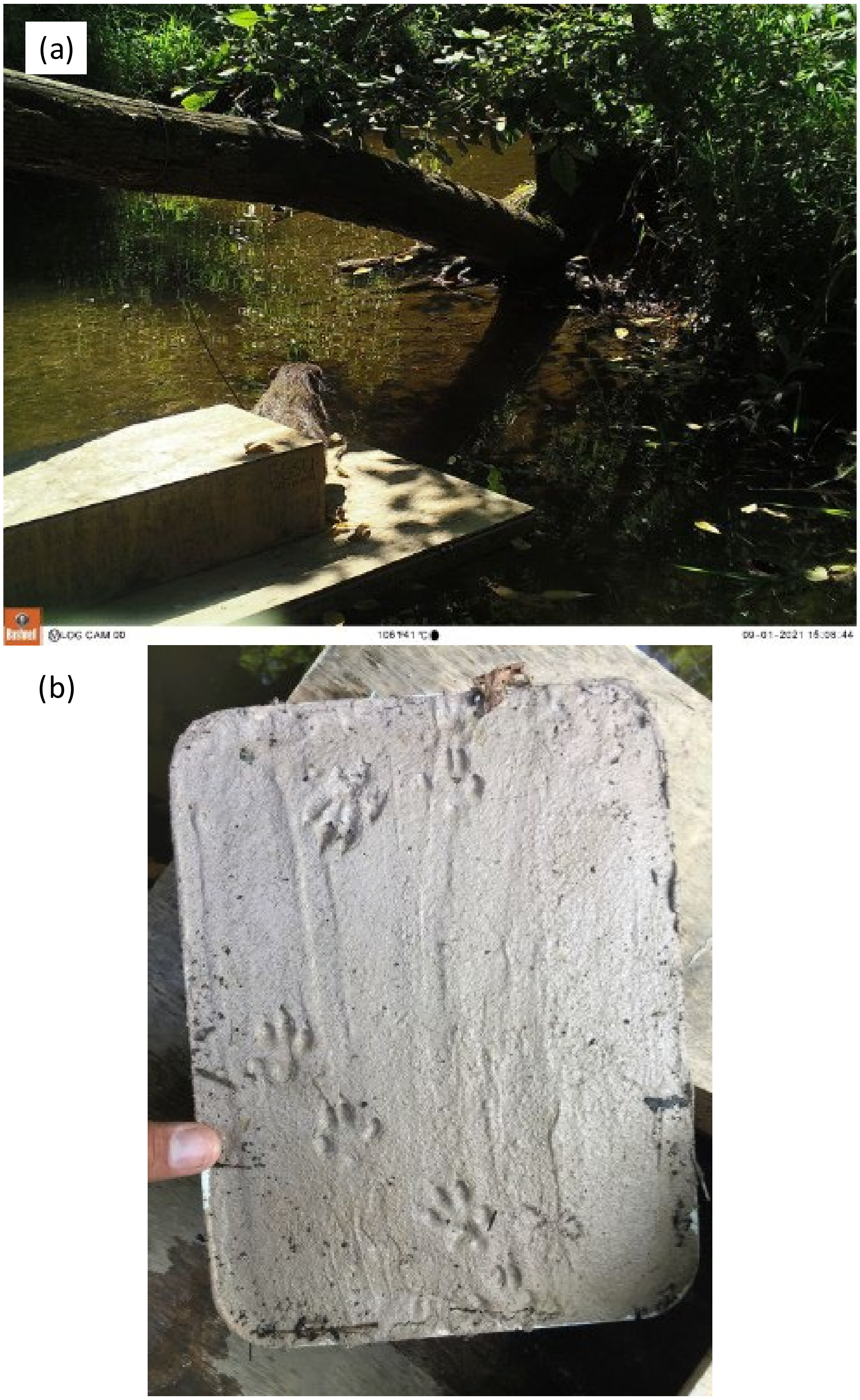

Figure 1.1. Images of (a) a groundhog (*Marmota monax*) on a mink raft and (b) a tracking cartridge from a mink raft displaying mustelid (*Mustelidae* sp.) tracks in Northwest Ohio, USA, 2021.

Spotlight surveys

Nocturnal spotlight surveys can be used to detect crayfishes (Bonk et al. 2019, Crandall 2016). Spotlight surveys require less effort than trapping methods and eliminate risk of harming crayfishes and non-target wildlife, although estimates related to abundance derived from these surveys may be biased (Bonk et al. 2019). After sunset, flashlights are used to scan shallow portions of wetlands from their banks for a pre-determined length of time, whereupon any crayfish or crayfish eye-shine observed is recorded.

Habitat use and detection covariates

Traditional habitat use models incorporate variables thought to influence the habitat use or selection process so that inference can be drawn as to the relative influence of different variables; however, other survey, site or observer-specific variables may influence the observation process and therefore the detectability of the animal of interest rather than its probability of using a sampling unit (MacKenzie et al. 2018). Habitat use covariates for mink and muskrats have included water depth on account of the dependence of these species on persistent water, whereas detection covariates have included time of year in the form of Julian date (i.e., number of days elapsed since the beginning of the year) given that survey ability can increase with time or that certain species exhibit seasonal changes in activity (Schooley et al. 2012). Other potential detection covariates include precipitation prior to sign surveys, which can wash away or submerge potential sign before spoor-based surveys; it is therefore appropriate to require that surveys be conducted only after a pre-determined number of days has passed since a substantial precipitation event, or to record cumulative precipitation amount in the days preceding each survey as a potential covariate (Ahlers et al. 2015, Schooley et al. 2012). Presence and extent of sandbars or similar substrates can be recorded to account for differences in the capacities of different sites to register tracks (Schooley et al. 2012). Temperature influences crayfish activity and is therefore relevant to crayfish detectability during surveys (Burksey and Simon 2010).

Landscape-scale habitat use covariates

In addition to fine-scale measures of habitat use, GIS-derived measures of channel sinuosity and stream order have been used as measures of stream physical structure in studies of muskrat and mink habitat use (Holland et al. 2019, Strahler 1957). Relative extent of land cover classes such as urban development and agriculture may be relevant to habitat use for focal organisms (e.g. as in Burksey and Simon 2010, Ahlers et al. 2015). Consequently, buffers of varying size depending on the scale of interest can be generated around sites and statistics summarizing the relative proportions of different land cover raster values within buffers can be calculated (Ahlers et al. 2015).

Analysis

Binary response logistic regression (generalized linear models with binomial error distribution and logit link) can be used in studies of habitat use to predict probability of species occurrence as a function of relevant environmental covariates (Pierce and Ferrier 2010). Collinear candidate covariates should be scrutinized as models incorporating them together will be characterized by high parameter uncertainty. Maximum likelihood estimates (MLEs) can be obtained for parameters including probability of success (animal detection/presence), p, at each site and covariate coefficient, β, for each covariate. The modeled strength of effect of each habitat covariate on p is suggestive of its relative importance as a habitat use variable. Information theoretic methods that incorporate both model likelihood and parsimony such as Aikaike’s Information Criterion corrected for small sample sizes (AICc) can be used to evaluate the relative support for each model of a candidate set fit to the same data (Burnham and Anderson 2004).

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CHAPTER II: HABITAT USE BY SEMIAQUATIC FAUNA IN LINEAR WETLANDS OF THE OAK OPENINGS REGION

Introduction

Wetlands in the lower forty-eight United States have been reduced in areal extent by more than 50% (as much as 90% in states such as Ohio) since the late 18th century (Dahl 1990). Ditching, tiling and draining, in addition to expansion of urban areas and associated impermeable surfaces, contributes to channelization, increased flooding, and reduced baseflow of waterways globally (Poff et al. 1997). While construction of ditches can degrade aquatic ecosystems, these features can also create aquatic habitat, serve as refuges from wetland habitat loss and promote connectivity of wildlife populations (Chester and Robson 2013, Clifford and Hefferman 2018, Gee et al. 1997, Kukkala and Moilanen 2016, Pryke et al. 2015, Akasaka and Takamura 2012).

Habitat-use patterns by semiaquatic fauna of the Oak Openings Region of northwest Ohio are likely to reflect this hydromodification and associated altered hydrological and habitat conditions. Hydromodification following Anglo-American settlement of the Oak Openings Region has lowered its water table, reduced surface water residence time, and introduced many constructed ponds and ditches (Brewer and Vankat 2004, Grigore 2016). Protected areas encompass 12% of the region in Northwest Ohio, incorporating diverse land cover types and wetland habitat characteristics (Abella et al. 2007, Martin and Root 2020).

Semiaquatic fauna that occur in this region include common muskrats (*Ondatra zibethicus*), cambarid crayfishes (*Cambaridae*) and American mink (*Neovison vison*). These focal organisms are common in wetlands of the American Midwest, fill a variety of niches, and use habitat across a range of scales. Therefore, differential habitat use by these organisms may reflect variable fine- and landscape-scale habitat suitability and functioning of wetlands to a variety of fauna in the Oak Openings Region.

This study evaluated linear wetland (streams and ditches) habitat use by focal semiaquatic organisms to explore the relationship between these factors and wetland habitat use. Study objectives included: (1) evaluation of which fine- and landscape-scale habitat suitability factors (especially the degree of ditching and channelization of features) most relate to use of linear wetlands in the semi-natural and hydrologically unique conditions of the Oak Openings Region, and (2) examination of whether focal organism occurrence could be predicted by the presence or activity of other focal organisms and whether such relationships were consistent with expected ecological interactions.

I expected that linear wetland size (as measured by Strahler order) or depth would exert the most influence on habitat use by muskrats and minks given the enhanced drainage of wetlands associated with landscape-scale hydromodification as well as the dependence of these organisms on persistent water availability. Ditches or channelized streams would likely be utilized as habitat by all focal organisms, although to a lesser degree than less modified streams due to unstable flow regimes, increased disturbance associated with ditch maintenance, lack of well-developed floodplains, and other conditions. All focal organisms would likely co-occur non-randomly because of some degree of niche overlap, although co-occurrence would likely be more strongly explained by predator-prey relationships (Arnold and Fritzell 1990, Wolff et al. 2015, Ahlers et al. 2016). I surveyed linear wetlands of the Oak Openings Region to evaluate these predictions and habitat suitability in general (e.g., vegetation cover, canopy cover, vegetation composition, etc.) in this unique environment.

Study area

This study was conducted in the Oak Openings Region of Northwest Ohio, an area of remnant glacial lakeshore-derived sandy soils covering 477 km^2 in Lucas, Fulton and Henry counties (41° 25’ to 41° 44’ N, 83° 34’ to 84° 2’ W) excluding the large portion in Michigan. Protected areas included multiple parcels each of Maumee State Forest, the Toledo Metroparks, Kitty Todd State Nature Preserve, Lou Campbell State Nature Preserve, and the Village of Swanton Reservoir (Figure 2.1).

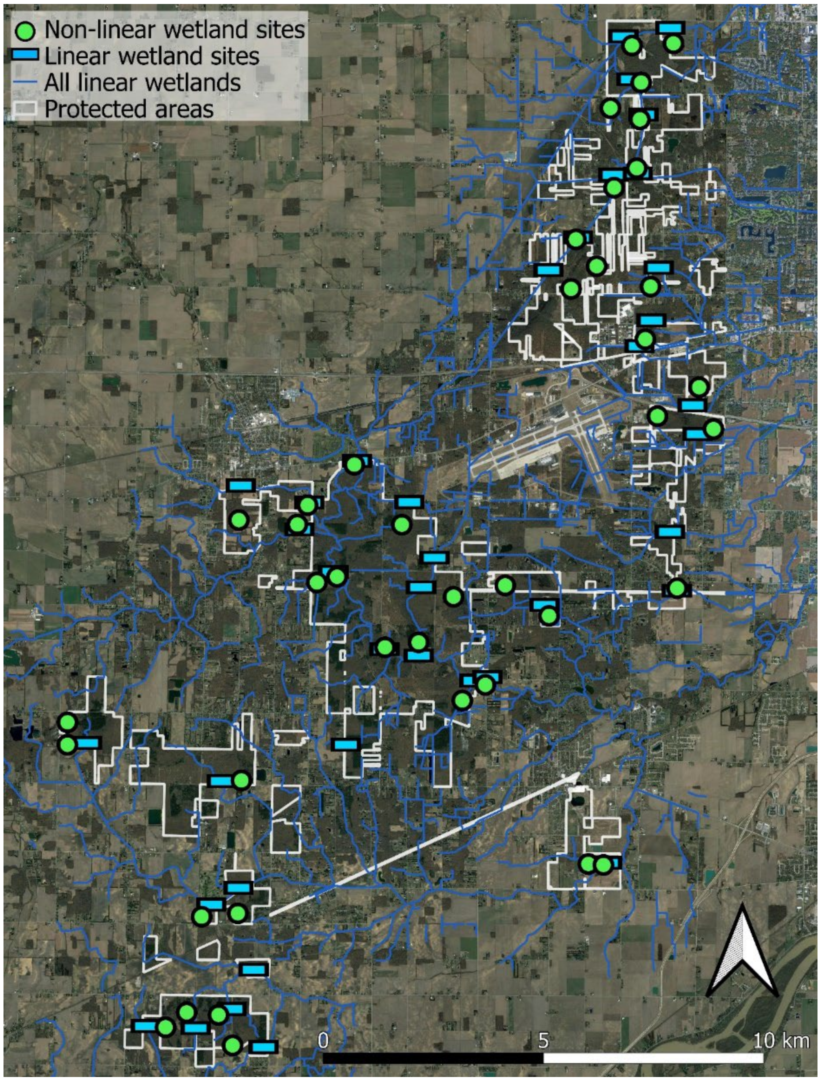

Figure 2.1. Study area in Northwest Ohio surveyed from May 19th through October 18th, 2021.

Methods

Site selection

Wetlands identified as linear were selected for inclusion in this study. Streams and ditches were referred to as linear rather than lotic because many ditches in the study area behaved similarly to lentic wetlands, i.e., their flow rates were very low. In contrast, wetlands referred to as nonlinear to contrast with the streams and ditches referred to as linear wetlands in a separate chapter of this thesis. Many ditches in the study area behaved similarly to lentic wetlands, i.e., their flow rates were very low. ‘Linear’ is therefore used to include lentic ditches and exclude wetlands with higher width-to-length ratios. Linear wetlands often maintained a direct surface water connection to the broader stream and ditch network and were consequently treated as continuous wetland habitat. Any given reach in these linear networks was considered to be more accessible to semiaquatic fauna than discrete wetlands isolated from these networks.

Surveys for animal tracks, scat, burrows and other sign were conducted at 40 linear wetland sites on at least one occasion of which 30 were surveyed on at least two consecutive occasions, from May 19th to October 18th 2021. Nocturnal spotlight surveys for crayfish and fish presence/activity were conducted at 30 linear wetland sites from June 12th to September 12th 2021. The linear site selection process was dependent on the nonlinear site selection process developed to investigate spatial questions in the latter part of this study. I systematically selected nonlinear sites within protected areas based on the following criteria in order of priority: (1) permanent or semi-permanent inundation and (2) high water surface area. These criteria were established to increase the likelihood of detecting minks and muskrats, which are not known to occur at high densities in the Oak Openings Region. I determined inundation regime of candidate wetlands using attribute data from the National Wetland Inventory (NWI) and the National

Hydrography Dataset (NHD) (USFWS 2020, USGS 2020). I evaluated surface area of candidate wetlands using Google Earth Engine aerial imagery from March 2021 when water levels were generally low (Google, Mountain View, CA, USA). For each nonlinear site that was selected, I additionally selected a nearby linear site for inclusion in the study. Where multiple linear wetlands occurred within approximately 750 meters of a particular nonlinear site, I chose the linear wetland that best met the two aforementioned nonlinear site selection criteria. After each nonlinear site was paired with a linear site, I then randomly selected additional linear sites to increase sample size while maintaining spatial independence (with respect to mink and muskrat home range sizes) within the confines of protected areas. Lotic sites consisted of a 200-meter reach defined using satellite imagery and established using a Garmin™ handheld GPS unit. This length approximately corresponded to the length of a muskrat core use area, a mink resource patch, and multiple crayfish home ranges, and has been used in studies of mink and muskrat habitat use in the Midwest (Schooley et al. 2012).

Sign searches

Linear wetland banks were searched within approximately two meters of the wetted area for sign of muskrats and minks and deployed one mink raft at each site to increase detection probability (Schooley et al. 2012). Sites were visited three times spaced over the course of approximately 14-28 days (separated by approximately 7-14 days); a mink raft was deployed on the first visit, the reach was searched and raft checked on the second visit, and the reach was searched and raft checked/retrieved on the last visit.

Spotlight surveys

Nocturnal spotlight surveys were utilized to increase detectability of crayfishes (Crandall 2016, Bonk et al. 2019) and obtain a measure of relative activity. Wetland littoral zones were scanned from their banks using handheld flashlights/spotlights, whereupon any crayfishes or other potential mink prey detected were recorded with respect to time spent scanning to account for survey effort (Allison and Destefano 2006). These nocturnal spotlight surveys were conducted for approximately 10-30 minutes per site or until the entire site was searched, once each month on nights closely approaching or following the new moon phase of the lunar cycle to reduce the visual interference posed by reflected moonlight. Surveys were conducted at least once at each linear site.

Habitat use and detection covariates

Maximum vegetation height in meters and dominant understory growth form (herbaceous or woody) within 4-meters of the wetted area were assessed at three equidistant points along each reach to estimate vegetation cover and composition. Percent cover of emergent vegetation within the channel was estimated based on reference images, canopy cover over the water's edge was ascertained with the smart phone application %Canopy, and maximum channel depth in meters was measured at these same three points (Mignanelli 2021). Presence/absence of a vegetated floodplain greater than or equal to the width of the channel was noted as ditches and highly-modified streams in the study area tended to lack discernable floodplains. These features were instead characterized by deeply incised channels with banks approximately level with the flat surrounding landscape.

I additionally recorded several covariates that could influence detection probability. I converted standard dates to Julian dates and calculated cumulative rainfall in centimeters within one week prior to each survey and daily mean temperature using National Oceanic and Atmospheric Administration (NOAA) Local Climatological Data (LCD) for the Kranz Toledo Express Airport weather station located approximately at the center of the study area (NOAA

2022). I similarly calculated proportion change in depth from the site mean for each survey, as large increases in water level tended to obscure or efface tracks. I also estimated sign detectability of sites to register sign as a three-level ordinal factor based on the degree of leaf litter cover over the substrate, as well as availability of structures (e.g. logs, riprap) for scat deposition. I classified fine-grained sandy substrates with few leaves that distinctly registered tracks as high detectability, substrates covered with an intermediate extent of partially degraded leaf litter as medium detectability, and substrates covered in mostly intact leaf litter as low detectability (Figure 2.2). In terms of scat deposition, I also classified banks covered in riprap or concrete/stone blocks as high detectability, banks with a high degree of large woody debris coverage as medium quality, and banks lacking substantial cover of either concrete or large woody debris as low quality. I similarly estimated benthic visibility as a three-level ordinal factor based on water clarity (clear, moderately turbid, turbid). I classified mostly clear water with little aquatic vegetation as high visibility, somewhat turbid water with intermediate coverage of aquatic vegetation as medium visibility, and highly turbid water or water with extensive aquatic vegetation cover as low visibility. Lastly, I recorded time of night for nocturnal surveys to account for potential diel activity patterns in crayfishes.

Figure 2.2. Images approximating substrates that were classified as (a) low, (b) medium and (c) high quality for track detectability in Northwest Ohio, USA, 2021.

Landscape variables

I calculated stream Strahler order as a measure of stream size using 1/9 arcsecond digital elevation models from the National Elevation Dataset (NED) and algorithms in SAGA (Strahler 1957, USGS 2010, Conrad et al. 2015). When calculated stream order differed from that reported in the National Hydrography Dataset (NHD) for a given reach, I manually determined stream order by inspection of satellite imagery (USGS 2020). I used GIS algorithms to calculate channel sinuosity within 500-meters (channel length in meters divided by the Euclidean distance between start and end vertices in meters) and number of vertices per digitized channel within a 500-meter buffer around study sites (digitized channel segments were simplified using a 5-meter tolerance to reduce bias from hand-digitization). I considered sinuosity and number of vertices potential negative correlates of channel modification or alteration, as smoothly meandering channels tended to be more sinuous and have more vertices than ditches in my study area (Figure 2.3). Although sinuosity has been tested as a covariate in studies of stream habitat use (e.g., Holland et al. 2019), I found that sinuosity failed to distinguish ditches or channelized streams with many abrupt angular turns from gently meandering natural streams. In my study area, channels with fewer vertices had longer stretches of straight channels but often intermediate to high degrees of sinuosity as a result of multiple abrupt angular turns over a relatively short distance. Number of vertices better differentiated modified channels, i.e., ditches or channelized streams. Channels with many vertices had shorter stretches of straight channels with a preponderance of gradual angles at their vertices; therefore, these features presumably represent less modified channels.

I calculated areal extent of each land cover class within buffers using a land cover raster developed for the Oak Openings Region in Martin and Root (2020). I aggregated land cover classes into anthropogenic (turf and pasture, residential mixed, Eurasian meadow, dense urban, and cropland) and natural (wet prairie, savanna, wet shrub, swamp forest, deciduous forest, sand barren, and upland prairie) groups for analysis. Furthermore, because vegetation structure is highly variable across the study area and understory vegetation is likely more relevant as habitat for these small focal organisms, I also aggregated land cover classes into open (turf and pasture, wet prairie, residential mixed, savanna, wetshrub, sand barren, Eurasian meadow, upland prairie, and cropland) and closed canopy (swamp forest, coniferous forest, deciduous forest) groups for analysis.

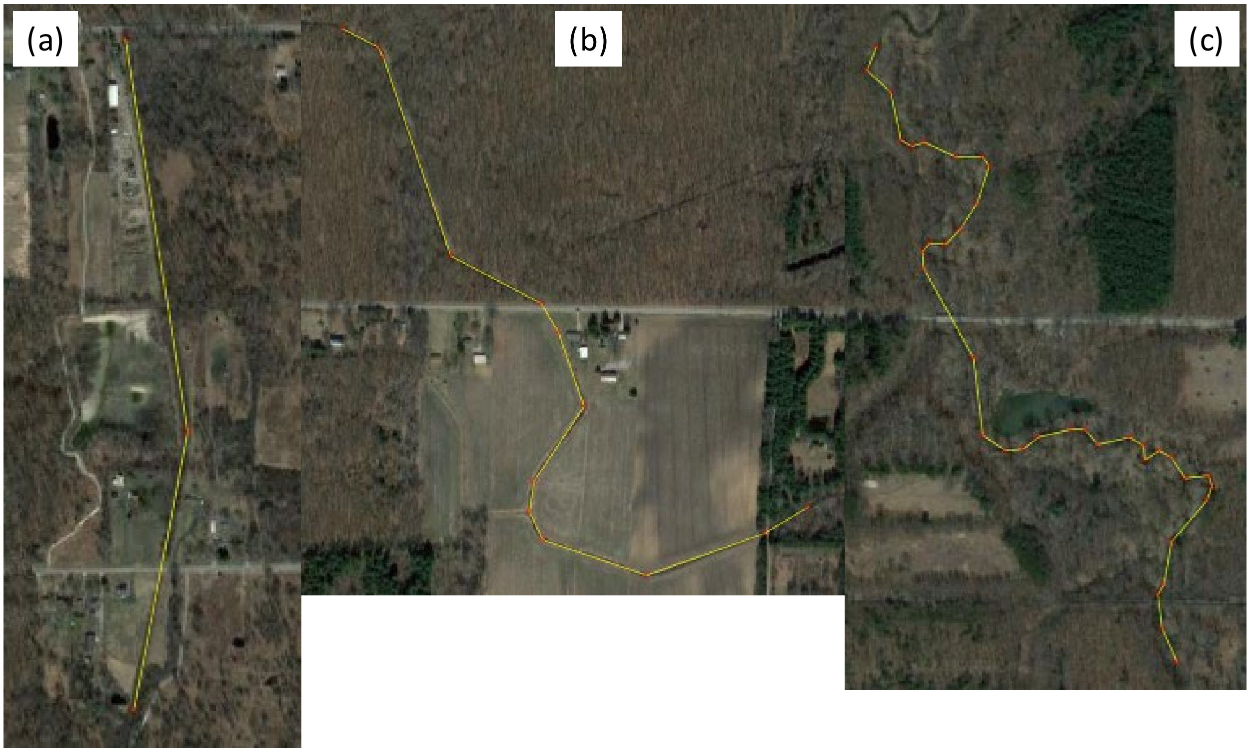

Figure 2.3. Images displaying channels with (a) low sinuosity and low number of vertices, (b) medium sinuosity and medium number of vertices, and (c) high sinuosity and high number of vertices identified in Northwest Ohio, USA, 2021.

Fauna variables

I recorded whether minks and/or muskrats were detected at least once over the sampling season, as well as the mean rate of crayfish and fish detection across nocturnal surveys, to determine whether habitat use by each focal organism was related to that of each other organism or to habitat use by fishes. For evaluating mink and muskrat habitat use, I also considered the survey-specific presence of one of the species as a correlate of the survey-specific presence or absence of the other species.

Analysis

I developed logistic regression models in R (R Core Team 2021). Although occupancy modeling produces unbiased parameter estimates by modeling both detection probability and occupancy hierarchically for repeat surveys (MacKenzie et al. 2018), I found that this approach demanded more replication than was possible in my study compared to regular logistic regression. Another likely consequence of limited sample size was that logistic regression models fit with more than two variables usually resulted in algorithm failure or non-convergence. I consequently constructed every possible subset of two or fewer variables out of all variables of interest and calculated Aikaike's Information Criterion corrected for small sample sizes (AICc) for each model (Ahmadi-Nedushan et al. 2006, McDonald et al. 2006, Ward and Hossie 2020). I removed models with highly correlated covariates as determined by Spearman's rank correlation coefficient ($\rho \geq 0.70$) from consideration and retained models with ΔAICc values less than or equal to 2. Because diurnally surveyed sites were surveyed twice in succession to increase survey period detectability, p represents the probability of detection over two successive surveys (one survey period). I averaged covariates that varied from survey to survey across both surveys in a survey period. Because several sites were surveyed in multiple survey periods, I repeated this process for all possible combinations of one survey period per site (128 possible combinations for diurnal surveys; 55296 possible combinations for nocturnal surveys). I used likelihood ratio tests (LRT) to determine whether top models were significantly more likely than the null intercept only model (Coates et al. 2014, Martinez et al. 2018, Ward and Hossie 2020), which models a constant probability of occurrence regardless of predictor variable values. I reported the resulting log of the likelihood of each model, improvement in AICc value of each model over the null model ($AICc_{null}$-$AICc_{candidate\ model}$), improvement in deviance from the saturated model of each model over the null model ($Deviance_{null}$-$Deviance_{candidate\ model}$) and P-value expressing the probability that the observed improvement of each model over the null model was due to chance.

Logistical constraints limited the number of sites at which vegetation variables could be measured, and some sites were not surveyed in both nocturnal and diurnal surveys; therefore, the model-fitting procedure differed for the full dataset (vegetation data omitted), the vegetation data subset (data from sites without vegetation measurements omitted), and the fauna data. I first fit best subsets models to the full dataset, then separately to the vegetation data subset. To investigate whether fauna variables were competitive with these models, I pooled all variables that appeared in the top 5 models for the full dataset and the top 5 models for the vegetation data with all fauna variables in a candidate variable set with which I fit best subset models a final time.

Results

Muskrats

Muskrat detections were recorded at 14/25 independent linear sites at least once over the sampling season. The top model for muskrat occurrence in all independent linear sites (N = 25), Order + Vertices, positively related Strahler order and number of vertices to muskrat occurrence (Table 2.1; Figure 2.4). This model fit the data significantly better than the null intercept-only model (ΔAICc = 16.06, LRT: ΔDeviance = 21.03, P=0.000047; Table 2.2). Other top models related muskrat occurrence positively to 500-meter buffer anthropogenic cover and Julian date and negatively to change in depth from site mean (Figure 2.4). Number of vertices occurred in each of the top five models whereas each other variable occurred once in the top five models.

The top model fit to the vegetation data subset (N = 17), Order + Herb_Dominance, positively related muskrat occurrence to both Strahler order and degree of herbaceous dominance (Figure 2.5). This model fit the data significantly better than the null intercept-only model (ΔAICc = 12.39, LRT: ΔDeviance = 17.97, P=0.00024; Table 2.2). Other top models introduced degree of woody dominance and change in depth from site mean as potential negative predictors and Strahler order, emergent aquatic vegetation cover and number of vertices as potential positive predictors of muskrat occurrence. Strahler order occurred in three of the top five models whereas change in depth from site mean and number of vertices each occurred in two of the top five models.

When the above top five models of muskrat occurrence fit to the full dataset were reconstructed while allowing for inclusion of fauna variables, Crayfish_Rate + Vertices ranked as the fourth top model, positively relating mean crayfish detection rate at each site and number of vertices to muskrat occurrence (Figure 2.5). This model was significantly more likely than the null intercept-only model (ΔAICc = 15.90, LRT: ΔDeviance = 21.10, P = 0.000043; Table 2.2).

When this process was repeated for the vegetation data subset, the same model ranked as the fifth top model.

Table 2.1. Top muskrat (*Ondatra zibethicus*) linear wetland occurrence models (ΔAICc ≤ 2) aggregated across all possible datasets (128), excluding models featuring correlated variables (Spearman rank correlation coefficient, ρ≥ 0.7). Each dataset represented a unique combination of a single survey period at each site, given that some sites were surveyed in multiple periods. The first column depicts the variable(s) incorporated in each model (only additive effects were considered). The second column depicts the proportion of datasets for which each model was within 2 ΔAICc units of the most supported (lowest AICc value) model for a given dataset. Models were fit to data collected in Northwest Ohio, USA, 2021.

Model terms	Proportion
Without vegetation variables (N = 25)	
Order + Vertices	0.875
Depth_Change + Vertices	0.445
Vertices	0.375
Vertices + Julian_Date	0.250
Anthro_500m + Vertices	0.125
Order + Open_500m	0.125
Open_500m + Vertices	0.125
Recent_Rain_CM + Vertices	0.125
Order + Open_500m	0.125
With vegetation variables (N = 17)	
Order + Herb_Dominance	0.875
Order + Woody_Dominance	0.656
Emergent_Cover + Vertices	0.250
Depth_Change + Vertices	0.219
Order + Depth_Change	0.188

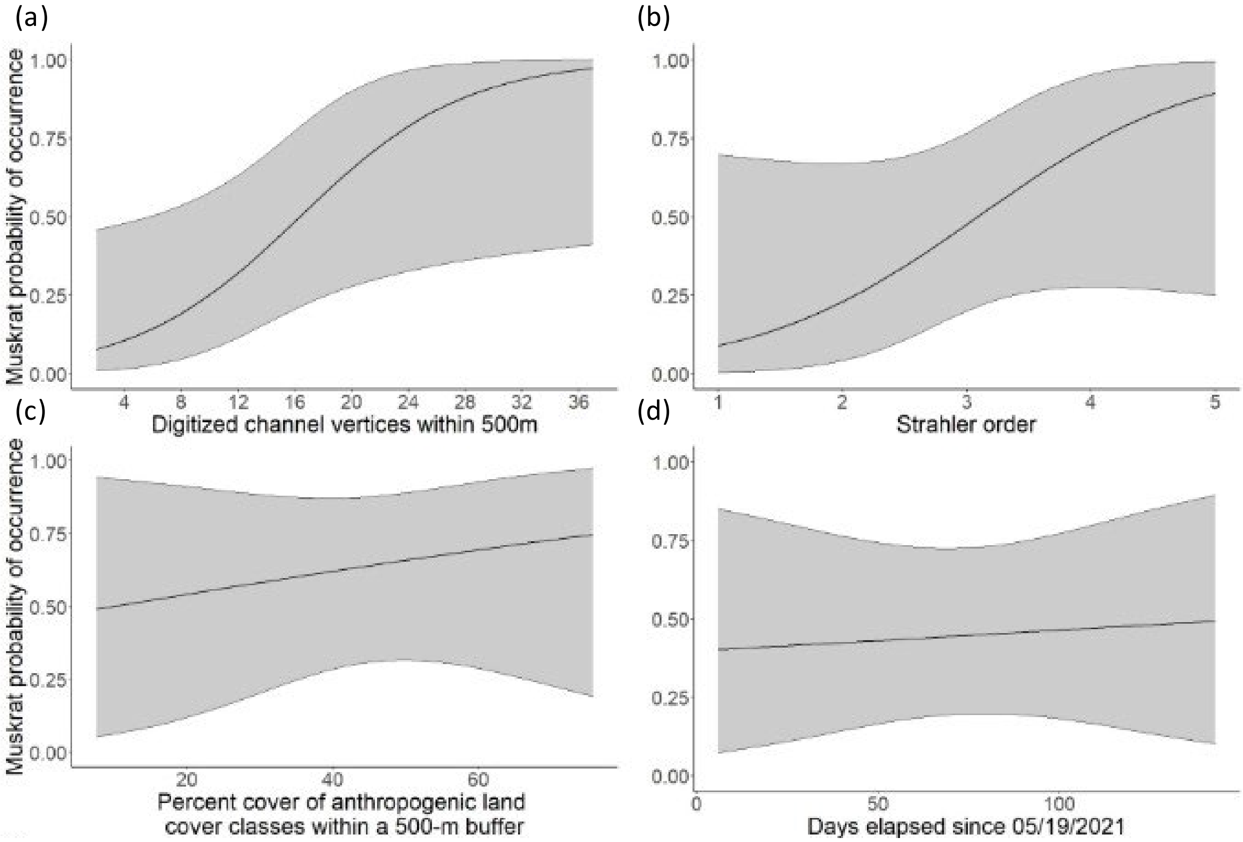

Figure 2.4. Modeled relationships between probability of muskrat (*Ondatra zibethicus*) occurrence and habitat use covariates in linear wetlands of Northwest Ohio, USA, 2021. Habitat use covariates: (a) number of vertices per simplified, digitized channel within a 500-meter site buffer, (b) channel Strahler order, (c) percent cover of anthropogenic land cover classes within a 500-meter site buffer, (d) days elapsed since the start of the sampling season (May 19th, 2021). For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Table 2.2. The most frequently supported models of muskrat (*Ondatra zibethicus*), crayfish (*Cambaridae spp.*) and mink (*Neovison vison*) occurrence in linear wetlands fit with the general dataset (base model), all variables in the vegetation data subset except fauna variables (vegetation variables model; only the top model featuring a vegetation variable), and all variables in the fauna data subset (fauna variables model). Also reported are model log likelihoods (LogLik), change in AICc values with respect to the null intercept-only model (ΔAICc), difference between the residual and null ΔDeviance from the saturated model (ΔDev.), and likelihood ratio test results P-value. Models were fit to data collected in Northwest Ohio, USA, 2021.

Focal organism	Variables considered	Model terms	LogLik	ΔAICc	ΔDev.	P-value
Muskrat	Base model	Order + Vertices	-6.75	16.06	21.03	4.7E-05
	Vegetation variables model	Order + Herbaceous	-2.71	12.39	17.97	2.4E-04
	Fauna variables model	Crayfish_Rate + Vertices	-3.93	15.90	21.10	4.3E-05
Crayfish	Base model	Order + Hour	-9.20	9.99	14.77	9.6E-04
	Vegetation variables model	Hour + Visibility	-5.32	4.69	9.97	7.3E-03
	Fauna variables model	Hour+Musk_Detected	-5.56	6.64	11.61	1.2E-02
Mink	Base model	Depth	-15.97	-0.17	2.20	2.0E-01
	Vegetation variables model	Canopy_Cover + Emergent_Cover	-8.30	1.10	6.68	6.2E-02
	Fauna variables model	Crayfish_Rate	-13.36	-0.69	1.77	4.0E-01

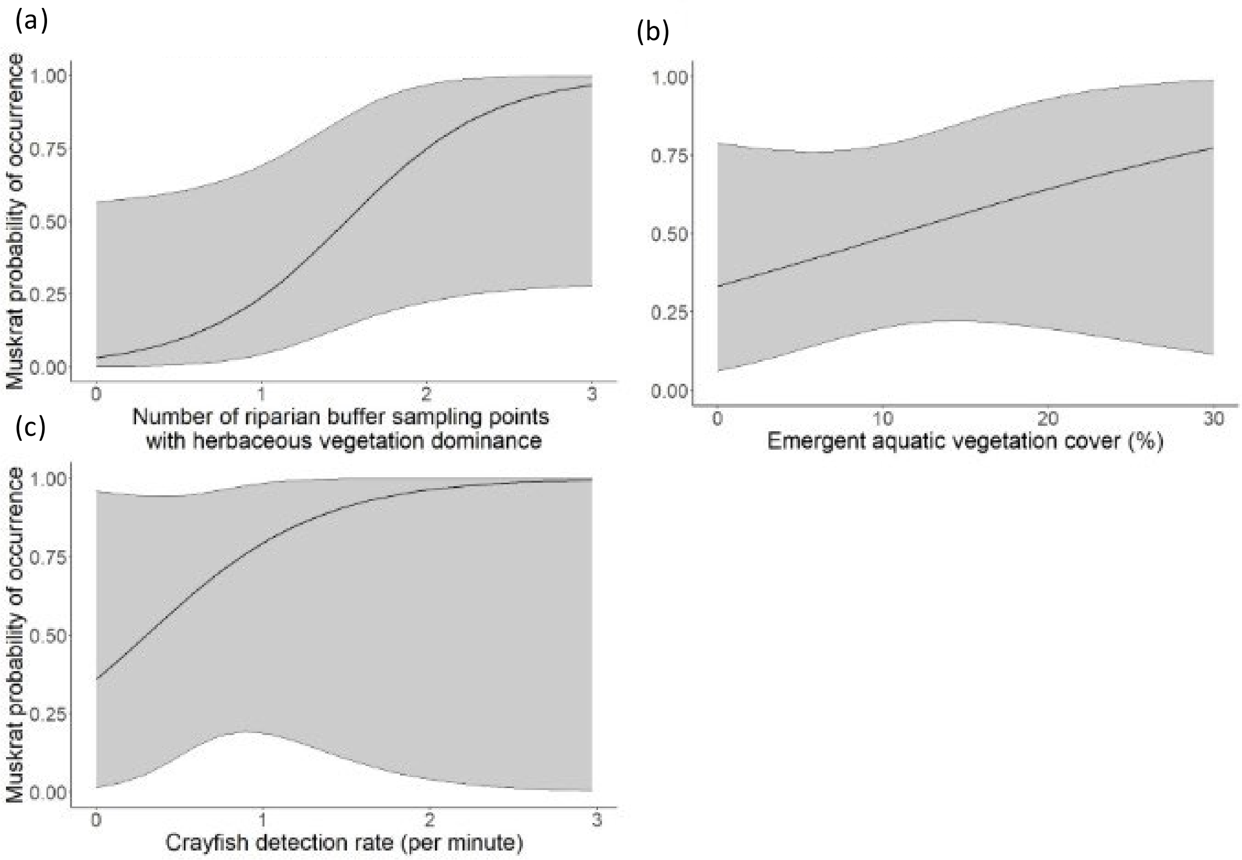

Figure 2.5. Modeled relationships between probability of muskrat (*Ondatra zibethicus*) occurrence and habitat use covariates in linear wetlands of Northwest Ohio, USA, 2021 continued. Habitat use covariates: (a) number of riparian buffer sampling points with herbaceous vegetation dominance, (b) percent cover of emergent aquatic vegetation within channel and (c) Average number of crayfishes detected per minute scanning during nocturnal survey(s). For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Crayfishes

Crayfish detections were recorded at least once at 23/30 independent linear sites over the sampling season. The top model for crayfish occurrence in all linear sites (N = 30), Order + Hour, related crayfish occurrence positively to Strahler order and negatively to hours elapsed since 22:00 EST (Table 2.3; Figure 2.6). This model fit the data significantly better than the null intercept-only model (ΔAICc = 9.99, LRT: ΔDeviance = 14.77, P = 0.00096; Table 2.2). Other top models related crayfish occurrence positively to DailyTemp and negatively to Julian date and benthic visibility. Strahler order appeared in four out of five top models whereas hours elapsed since 22:00 EST appeared in two.

When models were fit to the vegetation data subset (N = 20), no additional influential variables were identified. The top model for these sites, Hour + Visibility, fit the data significantly better than the null intercept-only model (ΔAICc = 4.69, LRT: ΔDeviance = 9.97, P = 0.0073; Table 2.2). Benthic visibility appeared in three out of five top models whereas Julian date, DailyTemp, and Strahler order appeared in two each.

When the above top five models of crayfish occurrence fit to the full dataset were reconstructed while allowing for inclusion of fauna variables, Musk_Detected + Hour and Daily_Temp + Musk_Detected ranked as the first and third top models respectively. Muskrat detection at least once at a site and daily temperature positively predicted crayfish occurrence whereas time elapsed since 22:00 EST negatively predicted crayfish occurrence (Figure 2.7). These models were significantly more likely than the null intercept-only model of crayfish occurrence (Musk_Detected + Hour: ΔAICc = 6.64, LRT: ΔDeviance = 11.61, P = 0.012; Table 2.2).

When this process was repeated for the vegetation data subset, Daily_Temperature + Fish_Rate, Order + Mink_Detected, and Mink_Detected + Musk_Detected ranked as the second, third and fifth top models. Fish detection rate and muskrat detection at least once at a site were positive predictors of crayfish occurrence, whereas mink detection at least once at a site was a negative predictor. These models were significantly more likely than the null intercept-only model; however, they failed to converge and are therefore likely to be imprecise.

Table 2.3. Top 5 crayfish (*Cambaridae* spp.) linear wetland occurrence models (ΔAICc ≤ 2) aggregated across 10000 possible datasets. Each dataset represented a unique combination of a single survey period at each site, given that some sites were surveyed in multiple periods. The first column depicts the variable(s) incorporated in each model (only additive effects were considered). The second column depicts the proportion of datasets for which each model was within 2 ΔAICc units of the most supported (lowest AICc value) model for a given dataset. Models were fit to data collected in Northwest Ohio, USA, 2021.

Model terms	Proportion
Without vegetation variables (N = 30)	
Order + Hour	0.749
DailyTemp + Order	0.611
Order + Julian_Date	0.555
Hour + Visibility	0.323
Order	0.536
With vegetation variables (N = 20)	
Hour + Visibility	1.000
Visibility + Julian_Date	0.543
Order + Julian_Date	0.526
DailyTemp + Visibility	0.369
DailyTemp + Order	0.154

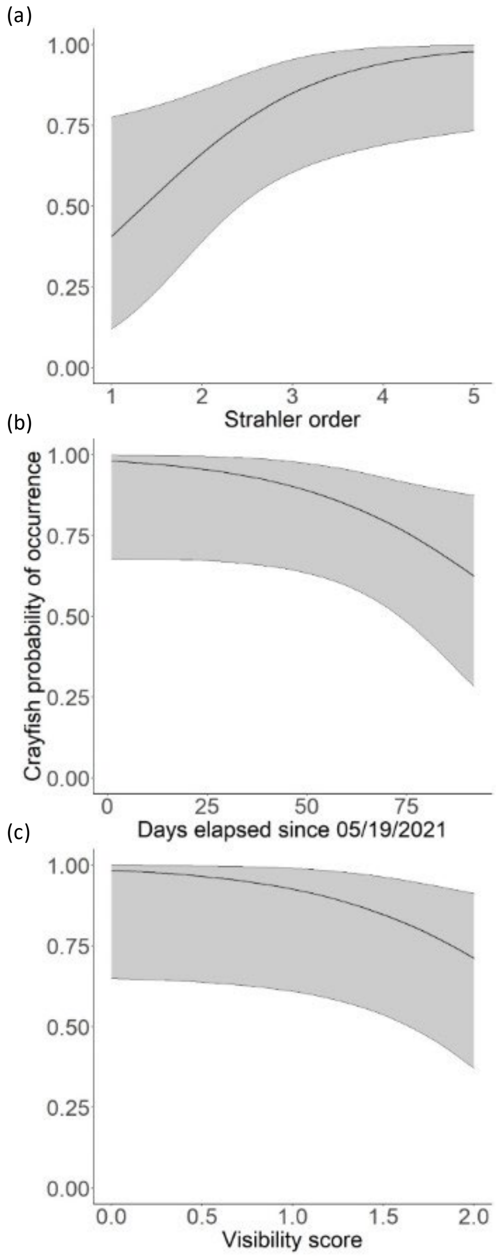

Figure 2.6. Modeled relationships between probability of crayfish (*Cambaridae* spp.) occurrence and habitat use covariates not including fauna variables in linear wetlands of Northwest Ohio, USA, 2021. Habitat use covariates: (a) channel Strahler order, (b) days elapsed since May 19th, 2021 (the beginning of the sampling season) and (c) average benthic visibility score. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

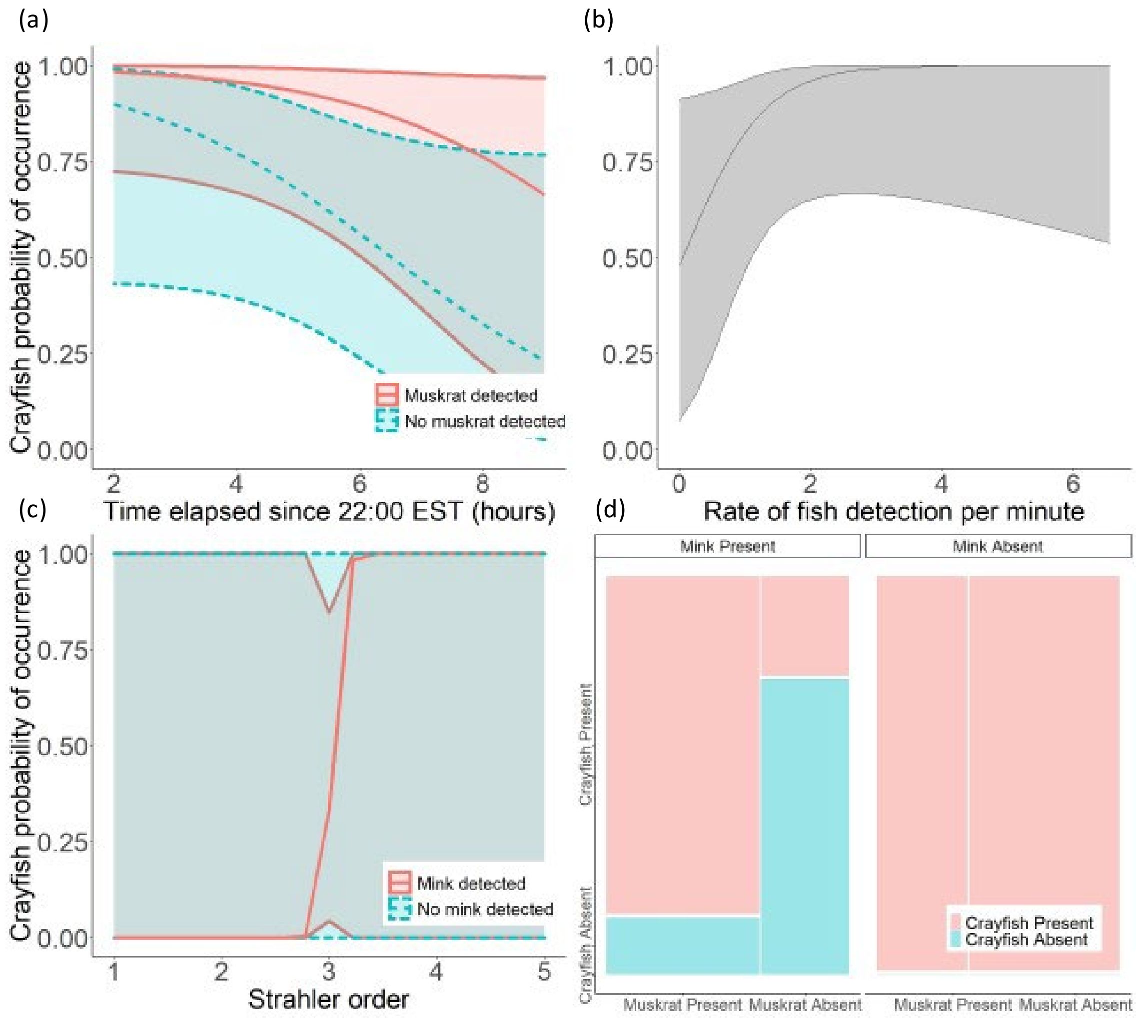

Figure 2.7. Modeled relationships between probability of crayfish (*Cambaridae* spp.) occurrence and habitat use covariates including fauna variables in linear wetlands of Northwest Ohio, USA, 2021. Habitat use covariates: (a) hours elapsed since 22:00 EST of the survey night for sites where muskrats were detected at least once during the sampling season and sites where muskrats were never detected, (b) number of fish detected per minute scanning during nocturnal surveys (c) channel Strahler order of sites where minks were detected at least once during the sampling season and sites where minks were never detected and (d) mink and muskrat detection at any time during the sampling season. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Minks

Mink detections were recorded at least once at 15/25 independent linear sites over the sampling season. The top model of mink occurrence in all linear sites (N = 25), Depth, negatively related survey period depth to mink occurrence (Table 2.4; Figure 2.8). This model did not fit the data significantly better than the null intercept-only model (ΔAICc = 0.17, LRT: ΔDeviance = 2.20, P = 0.20; Table 2.2). Other top models negatively related mink occurrence to amount of recent rain, sinuosity, and 500-meter buffer open canopy land cover. However, none of the other top models of mink linear wetland occurrence achieved significantly better fit than the null intercept-only model either.

The top model fit to the vegetation data subset (N = 17), Canopy_Cover + Emergent_Cover, positively related mink occurrence to both canopy cover and emergent aquatic vegetation cover. This model almost fit the data significantly better than the null intercept-only model (ΔAICc = 1.10, LRT: ΔDeviance = 6.68, P = 0.062; Table 2.2; Figure. 2.8). Canopy cover and emergent aquatic vegetation cover were the only additional influential variables identified in the top models fit to the vegetation data subset.

When the above top five models of mink occurrence fit to the full dataset were reconstructed while allowing for inclusion of fauna variables, Crayfish_Rate ranked as the fourth top model, negatively relating mean crayfish detection rate at each site to mink occurrence (Figure. 2.8). This model was not significantly more likely than the null intercept-only model (ΔAICc = 0.69, LRT: ΔDeviance = 1.77, P = 0.40; Table 2.2).

When this process was repeated for the vegetation data subset, Emergent_Cover + Crayfish_Rate, Crayfish_Rate + Fish_Rate, and Muskrat_Detected + Depth ranked as the third, fourth and fifth top models respectively. Percent cover of emergent aquatic vegetation, fish detection rate, and muskrat detection at least once at a site were positive predictors of mink occurrence whereas crayfish detection rate and depth were negative predictors of mink occurrence. However, none of these models were significantly more likely than the null intercept-only model of mink occurrence.

Table 2.4. Top 5 mink (*Neovison vison*) linear wetland occurrence models (ΔAICc ≤ 2) aggregated across all possible datasets (128). Each dataset represented a unique combination of a single survey period at each site, given that some sites were surveyed in multiple periods. The first column depicts the variable(s) incorporated in each model (only additive effects were considered). The second column depicts the proportion of datasets for which each model was within 2 ΔAICc units of the most supported (lowest AICc value) model for a given dataset. Models were fit to data collected in Northwest Ohio, USA, 2021.

Model terms	Proportion
Without vegetation variables (N = 25)	
Depth	0.969
Recent_Rain_CM	0.758
Sinuosity	0.539
Open_500m	0.422
Depth + Sinuosity	0.391
With vegetation variables (N = 17)	
Canopy_Cover + Emergent_Cover	0.703
Canopy_Cover + Depth	0.609
Depth	0.555
Canopy_Cover	0.328
Recent_Rain_CM	0.320

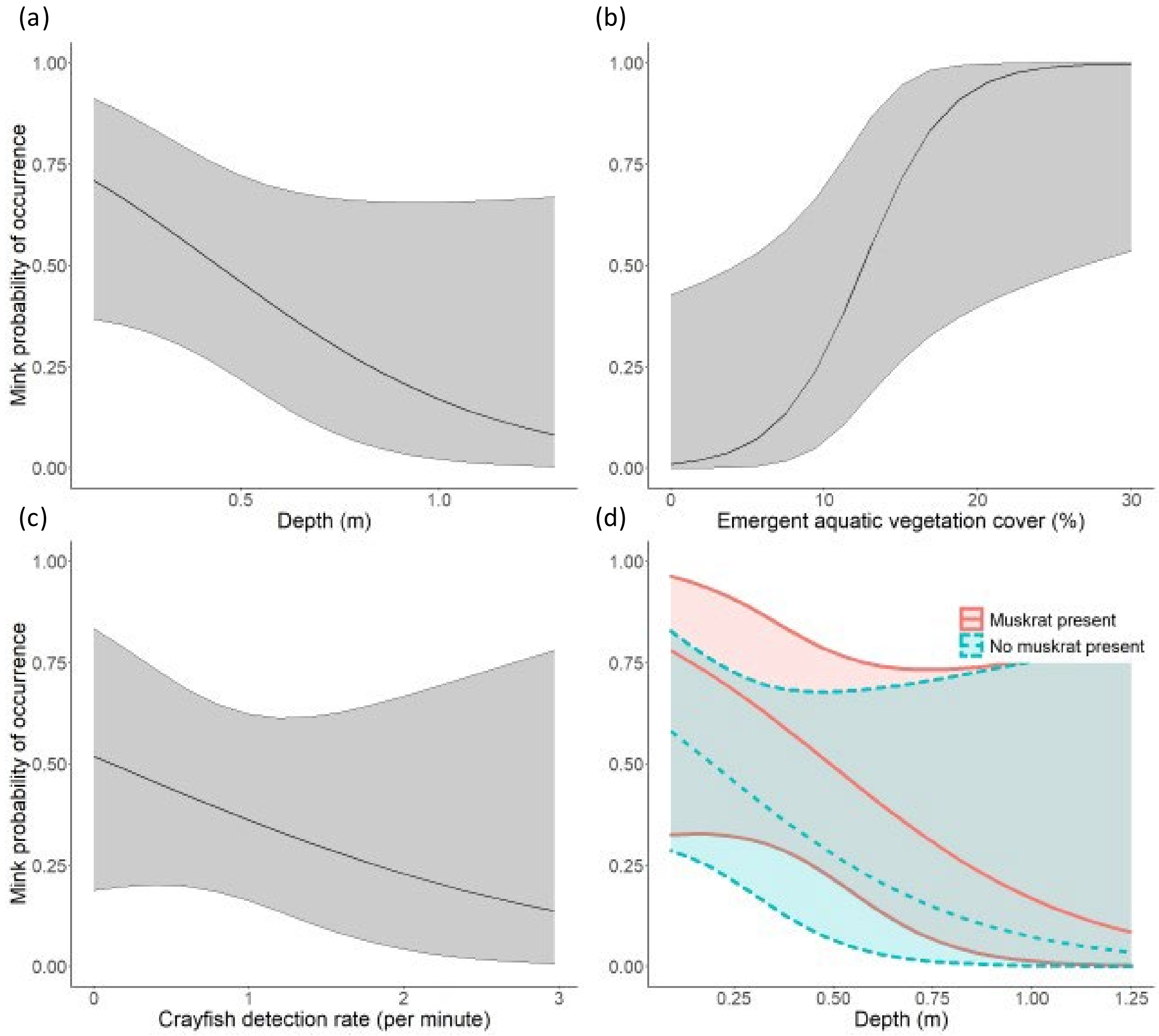

Figure 2.8. Relationships between probability of mink (*Neovison vison*) occurrence and habitat use covariates in linear wetlands of Northwest Ohio, 2021. Habitat use covariates: (a) channel depth, (b) percent cover of emergent aquatic vegetation within channel, (c) average number of crayfishes detected in the channel per minute scanning during nocturnal surveys and (d) water depth at sites where muskrats were concurrently detected and at sites where muskrats were not concurrently detected. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Discussion

Muskrats

The top model positively related muskrat occurrence to both stream order and number of vertices, suggesting that muskrats may prefer larger streams/ditches and smoothly meandering channels. Muskrats are thought to use larger, more perennial streams for their increased vegetation resources and reduced exposure to predation (Ahlers et al. 2015, Errington 1939). Furthermore, large streams in my study area may have constituted more suitable habitat for burrowing, as banks often consisted of rigid, clay-rich substrate presumably less resistant to collapse than the sandy soils found in shallower channels further up the watershed. Although muskrats are known to utilize ditches (Ahlers et al. 2010a), I expected less modified channels to be preferred because of their potential for well-developed riparian buffer vegetation, stable inundation regimes, and large size. The positive relationship between number of vertices and muskrat occurrence seems to indicate that muskrats were more likely to use less-modified, meandering streams relative to more-modified, highly linear ditches and channelized streams. As change in depth from site mean was negatively related to muskrat occurrence in a top model, it might be the case that increases in depth over the average for a given linear feature reduces occurrence of muskrats. However, I observed that increased water depth submerged substrate suitable for registering tracks at the edges of channels, which made detection of muskrat sign difficult even when animals were present. Furthermore, it is possible that any muskrat present at a site during periods of high flow simply reduced its activity to avoid displacement from these flows. It is therefore more likely that increased water depth reduced detectability of muskrats rather than occurrence. This highlights the importance of focusing surveys outside of large precipitation events. The positive relationship estimated between muskrat occurrence and Julian date in one top model may indicate an increase in detection probability due to increased survey experience, an increase in detection probability due to a temporal increase in muskrat activity, or a temporal increase in occurrence of muskrats across sites over the course of the field season (related to reproduction or recolonization of vacant habitats). I find that the latter two explanations are more likely, as several wetlands that lacked any muskrat sign earlier in the study eventually exhibited highly conspicuous muskrat sign towards the end. Muskrat breeding occurs in the spring and may be repeated multiple times in an asynchronous fashion until late Fall (Danell 1978); it is possible that increased detection of sign over time corresponded to increased muskrat family/social unit activity rates related to the maturation of successive muskrat litters.

In the top model fit to the vegetation data subset, the positive relationship between muskrat occurrence and stream order and degree of herbaceous dominance suggested that muskrats may prefer larger stream/ditches with a predominance of herbaceous vegetation in the riparian buffer. In my study sites, there was considerable variation in riparian buffer vegetation composition with herbaceous vegetation typically more dominant along channels in open canopy communities or otherwise with large canopy openings. Woody vegetation typically occurred around channels in heavily forested areas or shrub thickets. It is possible that muskrats selected for channels with riparian buffer herbaceous vegetation dominance for food and cover resources (Allen and Hoffman 1984, Nadeau et al. 1995). However, sites classified as woody dominant were often well shaded and sparsely vegetated in the understory. It is possible that reduced habitat use in woody dominant sites may relate more to low densities of understory vegetation in general rather than to inherent differences in resource value between herbaceous and woody vegetation. It is difficult to infer one way or another as to this possibility because maximum bank vegetation height, the variable designated as a measure of understory vegetation cover, did not occur in any top models. Future studies should take Robel pole measurements (Robel et al. 1970) of vegetation density and height parallel rather than perpendicular to linear wetland channels so that measurement bias due to variation in bank height and slope is minimized; vegetation density and height measurements will likely be more informative following this change. Nevertheless, the association of understory dominance and muskrat occurrence was reiterated in the next top model where degree of woody dominance featured as a negative predictor. In other top models, the positive relationship between emergent aquatic vegetation cover and muskrat occurrence may reflect habitat selection for emergent vegetation as food and shelter resources or selection for the perennial channels where emergent vegetation is more likely to grow (Allen and Hoffman 1984, Nadeau et al. 1995). Either factor could potentially influence the association between muskrat occurrence and emergent vegetation. Both possibilities are of interest in the context of the Oak Openings Region, where aquatic vegetation is often sparse as a result of unstable hydroperiods and excessive drainage (Brewer and Vankat 2004).

The most probable explanation for the finding that muskrats were more likely to use sites where crayfishes were detected at high rates is that these organisms share many habitat preferences. If muskrats and crayfishes both selected for similar habitat conditions, their occurrence could have been correlated without any direct trophic relationship between the two. Other models suggest some niche overlap as in the form of shared preferences for large linear wetlands with dense aquatic vegetation. Both organisms likely benefited from substrates suitable for burrowing.

Crayfishes

Strahler order emerged as a strong predictor of crayfish occurrence. This relationship is consistent with observed high densities of comparatively large crayfishes in large linear wetlands. This may relate to ranges of dissolved oxygen or nutrient concentrations, temperatures, flow velocities, substrate types (large streams in my study area tended to have clay-rich substrate in which crayfishes excavated large, sturdy burrows), and other factors associated with these wetlands (Flinders and Magoulick 2005, Fortino and Creed 2007). Given that different crayfish species select for or occur at higher densities in specific stream size ranges (Filipe et al. 2017, Flinders and Magoulick 2005, Fortino and Creed 2007), the reduced occurrence and activity of crayfishes in small streams may reflect a lack of small stream-adapted crayfish species in this study area. This could relate to the high rate of drying observed in small streams (Filipe et al. 2017) associated with hydromodification. Many small ditches in my study area exhibited little to no flow, rapid drying, and high leaf litter loads; therefore, they may have behaved similarly to vernal pools which often exhibit low dissolved oxygen and favor primary burrowing crayfishes that would not have been detected (Carrino-Kyker and Swanson 2007, Grow and Merchant 1980).

Other influential variables in crayfish occurrence models may have related more to observer detection probability than crayfish occurrence probability; e.g., some crayfishes become more active in warmer water whether that corresponds to seasonal or diurnal temperature change (Hamrin 1987). The apparent decrease in occurrence with respect to Julian date and hours elapsed since 22:00 EST could therefore have been a function of decreased detectability with decreasing seasonal and nightly temperatures. Models also suggested a negative effect of benthic visibility, although the opposite effect was expected (i.e., detection rate would be higher in clearer water). As many linear wetlands with low visibility were larger streams or streams with greater flow rates, this surprising result is likely a matter of linear wetland size confounding this detection variable (e.g., larger streams tend to be more turbid, thereby reducing visibility).

Interestingly, no other microhabitat or landscape-scale variables featured in the best models. This may be a result of limitations inherent in the spotlighting sampling method, as crayfishes could not be subclassified with any level of taxonomic confidence. Different families, genera or species could exhibit little overlap in habitat requirements, resulting in few identifiable microhabitat relationships of importance to crayfishes collectively. Furthermore, predictor variables I used may be of inappropriate scale or relevance, as crayfish habitat quality in streams can be a function of watershed-scale variables and streambed/bank structure-scale variables (Burksey and Simon, 2010). The 1000-meter and 500-meter buffers used to calculate my landscape scale variables may have been too small to capture upstream watershed-scale effects whereas my microhabitat variables may have failed to capture more relevant fine-scale physical characteristics of streams such as bank overhangs, riffle pools, debris, etc.

When top models were reconstructed with fauna variables included, all possible fauna variables featured in the top crayfish occurrence models either in those fitted to the full data set or the vegetation data subset. There are various potential explanations for these findings. That crayfishes were more likely to use linear sites with at least one muskrat detection is not surprising, as both organisms preferred larger linear wetlands and likely shared other habitat preferences. Similarly, crayfishes were more likely to use linear sites with high detection rates of fish. While large fish could limit crayfish populations, many crayfishes in streams with fish were quite large and likely less vulnerable to predation; they also tended to have shelters in stream banks and in woody debris accumulated in channels. Furthermore, both fish and muskrats require persistent water.

Interestingly, crayfishes were less likely to use linear sites with at least one mink detection. While minks may select for sites with abundant crayfishes (Wolff et al. 2015), it is also possible that crayfishes are behaviorally repressed in the presence of mink predators and thereby more difficult to detect in surveys. Alternatively, minks may have been using different habitats in the study area. For example, stream order tended to strongly influence crayfish and muskrat top models, whereas this relationship was not observed for minks. Minks may have segregated into smaller streams unoccupied by abundant crayfish populations, as their dietary and behavioral requirements may differ. These modeled fauna relationships are likely a function of many of these factors.

Minks

Models of mink occurrence exhibited poor fit (no models were significantly more likely than the null intercept-only model) likely due to sample size limitations required to maintain spatial independence of sites, probable non-negligible false detection as well as false absence rates, and potentially low densities of minks in the study area. I could not confidently differentiate between mink tracks and large, long-tailed weasel tracks in many cases, which may have resulted in misclassification of the latter as mink tracks. Models often featured depth and amount of recent rain, which likely reflects an imperfect detection process rather than an actual habitat use relationship; precipitation and high water levels were associated with reduced track detection. This was especially disruptive given that I almost never detected mink scats which could have signaled mink presence even when tracks were washed away. This may be indicative of low densities of minks in the study area, as other studies of mink habitat use have detected substantial quantities of scats in addition to tracks (Schooley et al. 2012). Furthermore, as cryptic predators, minks are thought to be sparsely distributed and elusive to begin with (Lariviere 1999). Notwithstanding, some variables appeared more frequently in top models than others.

Although I suspect that the support for survey period depth as a covariate reflects weasel detection in shallow linear wetlands or sign erasure, it is possible that increased mink occurrence with lower water levels instead relates to prey vulnerability. Fishes, crayfishes and other mink prey may be vulnerable to predation in shallow water. I find this unlikely however as findings from other studies indicate that mink occupancy is positively related to water depth (Schooley et al. 2012, Ahlers et al. 2015). The observed negative relationship between 500-meter buffer open canopy land cover and mink occurrence is consistent with evidence that minks select for dense forested areas in their native range under some circumstances (Hodder 2018), although the effect was small. Canopy cover and emergent aquatic vegetation cover ranked highly as positive predictors in models fit to the vegetation data subset; this may reflect selection for forested areas as described and more densely vegetated areas that offer more cover and prey resources.

There are several possible explanations for the findings that minks were more likely to use linear sites with muskrat detection at least once at a site and less likely to use sites with high rates of crayfish activity. Minks are more likely to abandon sites lacking muskrats, from which follows that minks likely select for habitat with available muskrat prey (Ahlers et al. 2016). My findings are consistent with minks selecting for sites with muskrats. Alternatively, sites where both minks and muskrats were detected may have had more suitable conditions for detecting both species. I expected that minks would be more likely to use sites with high rates of crayfish detection, as minks exhibit a documented preference for using sites with crayfish hotspots (Wolff et al. 2016). The opposite pattern was observed, potentially due to preferred habitat differences between the two organisms in the Oak Openings or potential behavioral suppression of crayfishes in the presence of minks that would have made detection of crayfishes more difficult.

Several factors are likely at play in these relationships, but the top models exhibited non-significant fit and are therefore less informative than models for other focal organisms.

Conservation implications

As has been discussed, the Oak Openings is naturally predisposed to seasonal drying. However, extensive ditching of the area exacerbates this drying while enabling wildlife like fish to migrate into seasonally dry water sources that historically would not have been so accessible. More mobile wetland fauna may be better able to track diminishing water, but others are not adapted to do so as readily and suffer substantial population-level mortality events with intensified drying associated with disturbed hydrological conditions (Acosta and Perry 2001). For example, I repeatedly observed juvenile fish trapped in rapidly drying ditches during this study. On the other hand, increased permeability of the landscape along ditches can facilitate species invasion (Maheu-Giroux and de Blois 2007). Furthermore, extensive ditching can increase severe flooding events downstream in watersheds (Poff et al. 1997). I observed rapid fluctuation from extremely low water levels to extremely high water levels in the highly downcut primary drainage of my study area. Although my study did not produce direct evidence of these deleterious effects of ditching and draining, the results do suggest that the muskrat, a native species in decline across its range (Ahlers and Heske 2017), is more likely to use streams than ditches in the area.

In light of these results and already documented impacts of hydromodification, land managers in the Oak Openings Region should increase efforts to mitigate the effects of ditching and draining on the landscape. My results suggest that restoring meandering channel morphology as opposed to that of highly linear ditches may benefit wildlife like the muskrat. Furthermore, blocking ditches to rewet sites can restore reference hydrological conditions and associated native plants (Maanavilja et al. 2014). Alternatively, reducing dredging may produce a similar effect in the long term. Reducing dredging or leaving some areas of vegetation intact when dredging ditches can promote aquatic vegetation and improve biodiversity (Whatley et al. 2014). Such efforts should increase residence time of water on the landscape and could promote muskrat habitat use, given that muskrats were more likely to use linear wetlands with greater cover of emergent vegetation. Emergent vegetation was generally rare in the linear wetlands surveyed in this study, likely due to the intermittent nature of most wetlands in the area and exacerbated by the legacy of hydromodification and continued dredging. While emergent aquatic vegetation may be naturally limited in the Oak Openings Region, upland herbaceous vegetation such as prairie grasses can be readily promoted through restoration techniques. Given that my models suggest that muskrats are more likely to use linear wetlands with herbaceous buffer vegetation, it is worth investigating whether this vegetation is of benefit to other wetland species and how such benefit varies between wet and upland prairie.

More research is needed as to the status of native crayfish in Oak Openings linear wetlands. While I observed higher probability of occurrence and substantial activity of crayfishes in large linear wetlands, it is unclear whether those observed were native or invasive due to insufficiency of the survey method used. Crayfishes using smaller streams and ditches may simply have been predominantly primary burrowers and consequently less detectable in nocturnal surveys. However, if this is not the case and crayfishes simply did not utilize these habitats, it is worth investigating whether or not this is due to impaired wetland function.

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CHAPTER III: HABITAT USE BY SEMIAQUATIC FAUNA IN NONLINEAR WETLANDS OF THE OAK OPENINGS REGION

Introduction

Wetlands in the lower forty-eight United States have been reduced in areal extent by more than 50% (as much as 90% in states such as Ohio) since the late 18th century (Dahl 1990). Ditching, tiling and draining, in addition to expansion of urban areas and associated impermeable surfaces, contributes to channelization, increased flooding, and reduced baseflow of waterways globally (Poff et al. 1997). Additionally, ponds constructed for flood control, water provisioning, nutrient and sediment retention, recreation and other purposes have proliferated such that ponds number more than 2.6 million in the contiguous United States (Renwick 2005). While construction of ditches and ponds can degrade aquatic ecosystems, these features can also create aquatic habitat, serve as refuges from wetland habitat loss and promote connectivity of wildlife populations (Gee et al. 1997, Akasaka and Takamura 2012, Chester and Robson 2013, Pryke et al. 2015, Kukkala and Moilanen 2016, Clifford and Hefferman 2018).

Habitat-use patterns by semiaquatic fauna of the Oak Openings Region of northwest Ohio are likely to reflect this hydromodification and associated altered hydrological and habitat conditions. Hydromodification following Anglo-American settlement of the Oak Openings Region has lowered its water table, reduced surface water residence time, and introduced many constructed ponds and ditches (Brewer and Vankat 2004, Grigore 2016). There are many protected areas in the region with diverse land cover types and wetland habitat characteristics (Abella et al. 2007).

Semiaquatic fauna that occur in this region include common muskrats (*Ondatra zibethicus*), cambarid crayfishes (*Cambaridae*) and American mink (*Neovison vison*). These focal organisms are common in wetlands of the American Midwest, fill a variety of niches, and use habitat across a range of scales. Therefore, differential habitat use by these organisms may reflect variable fine- and landscape-scale habitat suitability, accessibility and functioning of wetlands to a variety of fauna in the Oak Openings Region.

This study evaluated nonlinear wetland (pond, impoundment, scrape, vernal pool and similar wetlands) habitat use by focal semiaquatic organisms to explore the relationship between these factors and habitat use to inform conservation and management of modified wetlands and landscapes. Objectives included: (1) evaluate which fine- and landscape-scale habitat suitability factors most related to use of nonlinear wetlands in the semi-natural and hydrologically unique conditions of the Oak Openings Region, (2) evaluate the degree to which wetland size and isolation related to habitat use (3) evaluate the degree to which highly modified wetlands were used relative to less modified or restored wetlands.

I expected that muskrats, crayfishes and minks would likely utilize artificial or modified ponds given that ponds can exhibit disproportionate productivity and biodiversity (Dodson et al. 2000, Scheffer et al. 2006, Downing 2010), and that permanent water sources might perform drought refugia or landscape supplementation functions relative to wetlands subject to greater drying (Krapu et al. 2004, Ahlers et al. 2015). I also expected that anthropogenic land cover types would likely negatively influence crayfish and mink habitat use but positively influence muskrat habitat use.

Study area

This study was conducted in the Oak Openings Region of northwest Ohio, an area of remnant glacial lakeshore-derived sandy soils covering 477 km^2 in Lucas, Fulton and Henry counties (41° 25’ to 41° 44’ N, 83° 34’ to 84° 2’ W) excluding the large portion in Michigan.

Protected areas included multiple parcels each of Maumee State Forest, the Toledo Metroparks, Kitty Todd State Nature Preserve, Lou Campbell State Nature Preserve, and Village of Swanton Reservoir (Figure 3.1).

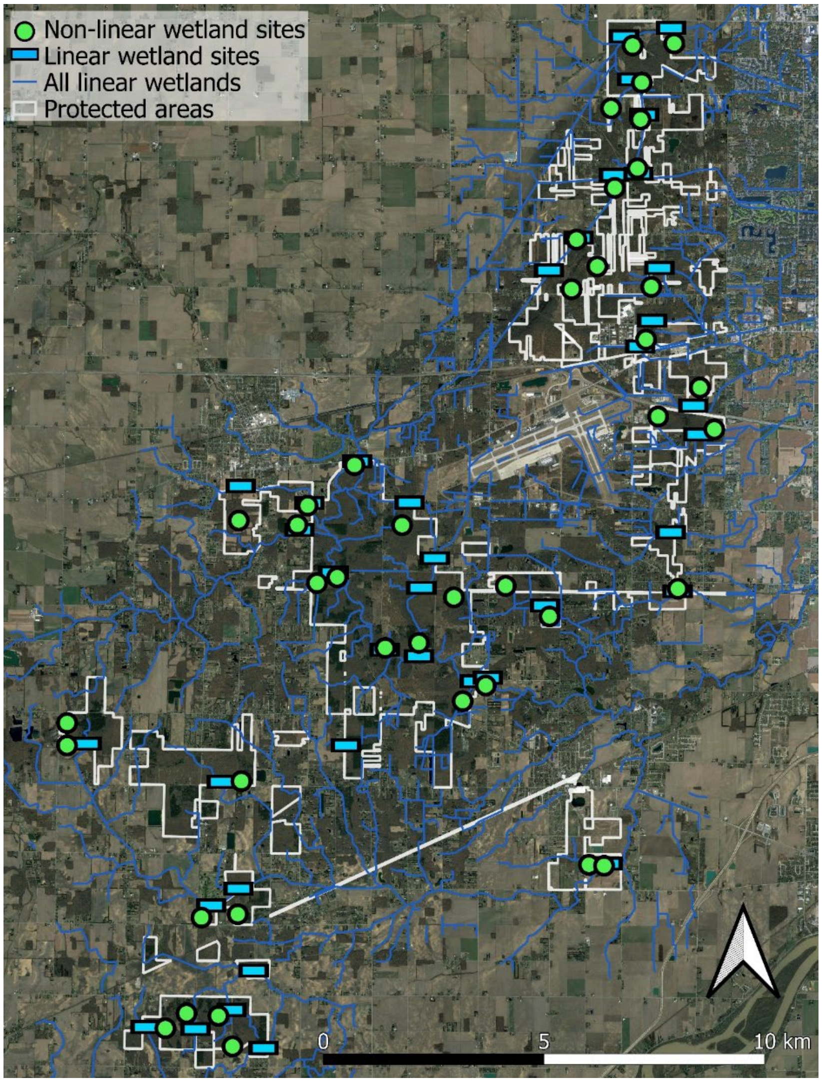

Figure 3.1. Study area in Northwest Ohio surveyed from May 19th through October 18th, 2021.

Methods

Site selection

Candidate wetland sites were categorized as either ‘linear’ or ‘nonlinear’. This chapter analyzed only nonlinear wetlands, which included lentic wetlands with higher width-to-length ratios and excluded lentic ditches. Nonlinear wetlands were treated as relatively discrete wetland habitat patches given that they lacked a surface water connection to the broader stream and ditch (‘linear’) network. Semiaquatic fauna would consequently have to travel over land to navigate to and from nonlinear wetlands. These wetlands therefore represented a unique opportunity to investigate spatial factors affecting habitat use. Furthermore, because lentic wetlands are primarily autochthonous ecosystems, a stronger connection between lentic wetland resources and their immediate habitat and landscape context could be postulated. Conversely, allochthonous wetland resources may relate more to upstream watershed-scale processes (Burskey and Simon 2010).

I selected nonlinear sites within protected areas based on the following criteria in order of priority: (1) permanent or semi-permanent inundation and (2) large water surface area. These criteria were established to increase the likelihood of detecting minks and muskrats, which are not known to occur at high densities in the Oak Openings Region. I determined inundation regime of candidate wetlands using attribute data from the National Wetland Inventory (NWI) and the National Hydrography Dataset (NHD) (USFWS 2020, USGS 2020). I evaluated surface area of candidate wetlands using Google Earth Engine aerial leaf-down imagery from March 2021 when water levels were generally low (Google, Mountain View, CA, USA). Sign surveys were conducted at 22 of the selected sites from May 19th to October 18th 2021. Nocturnal spotlight surveys were conducted at 27 of the selected sites June 12th to September 12th 2021.

Sign searches

Nonlinear wetland banks were searched within approximately two meters of the wetted area for sign of muskrats and minks. One mink raft was deployed at each site to increase detection probability (Schooley et al. 2012). Each site was visited three times spaced over the course of approximately 14-28 days (separated by approximately 7-14 days). A mink raft was deployed on the first visit, the reach was searched and raft checked on the second visit, and the reach was searched and raft checked/retrieved on the last visit.

Figure 3.2. Images approximating substrates that were classified as (a) low, (b) moderate and (c) high quality for registering tracks in Northwest Ohio, USA, 2021.

Spotlight surveys

Nocturnal spotlight surveys were utilized to increase detectability of crayfishes (Crandall 2016, Bonk et al. 2019) and obtain a measure of relative activity. Flashlights and headlamps were used to scan the littoral zone of wetlands from their banks, whereupon any crayfish or other potential mink prey detected were recorded with respect to time spent scanning to account for survey effort (Allison and Destefano 2006). These nocturnal spotlight surveys were conducted for approximately 10-30 minutes per site or until the entire site was searched, once each month on nights closely approaching or following the new moon phase of the lunar cycle to reduce the visual interference posed by reflected moonlight. Surveys were conducted at least once at each linear site.

Habitat use and detection covariates

Maximum vegetation height and dominant understory growth form (herbaceous or woody) within four meters of the water were recorded at three equidistant points along each nonlinear wetland perimeter to estimate vegetation cover and composition. Percent cover of emergent vegetation within the frequently inundated area was estimated based on reference images. Canopy cover over the edge of the frequently inundated area was measured using the smart phone application %Canopy (Mignanelli 2021). Lastly, as measuring depth at nonlinear sites was not logistically feasible, I designated a binary variable (yes/no) indicating whether each nonlinear site regularly underwent considerable intermittent drying (surface area change of 50% or more) based on field observations and inspection of sequential satellite/aerial imagery (Google, Mountain View, CA, USA).

I used Sentinel-2 multispectral 13-band imagery from 19 September 2021 USGS Earth Explorer to calculate 10-meter resolution Normalized Difference Vegetation Index (NDVI) and

Normalized Difference Water Index (NDWI) (Gao 1996, Wachid et al. 2017, USGS 2018). I used NDWI data to render nonlinear wetland features as binary rasters using NDWI threshold values that best produced agreement between wetland boundaries and those observed in satellite imagery. The mean NDVI value of each raster feature produced from this process served as another measure of canopy cover for the corresponding wetland (encompassing the entire surface area instead of just its edges as measured in the aforementioned canopy cover method).

To approximate the extent of modification of each water body, I recorded and summed presence of each of the following characteristics/features: 1) a cleared, mowed, or similarly maintained bank area; 2) a recreational trail within approximately 10-meters of the wetted area; 3) a recreational structure (e.g., bridge, bench, viewing platform, dock, etc.); 4) a bank area reinforced with riprap or concrete; 5) a ditch; 6) a culvert; 7) a dam (i.e., the wetland is impounded); 8) created by excavation; and 9) fish of size and density consistent with stocking (confirmed by land managers for most sites). Based on communications with land managers, I also designated a restored habitat binary variable which was coded as a 1 for sites created for wildlife or ecosystem services and a 0 for naturally occurring sites or sites created for other purposes.

I additionally recorded several covariates that could influence detection probability. I converted standard dates to days elapsed since the start of the survey season (May 19th, 2021), referred to hereafter as Julian date. Using National Oceanic and Atmospheric Administration (NOAA) Local Climatological Data (LCD) for the Kranz Toledo Express Airport weather station (located approximately at the center of the study area), I calculated cumulative rainfall (cm) within one week prior to each survey and joined daily mean temperature (° C) to survey data (NOAA 2022). I also estimated sign detectability as an ordinal factor based on quality and extent of substrate, as well as availability of structures (e.g. logs, riprap) for scat deposition. I classified Fine-grained sandy substrates with few leaves that distinctly registered tracks as high detectability, substrates covered with an intermediate extent of partially degraded leaf litter as medium detectability, and substrates covered in mostly intact leaf litter as low detectability (Figure 3.2.). In terms of scat deposition, I classified banks covered in riprap or concrete/stone blocks as high detectability, banks with a high degree of large woody debris coverage as medium detectability, and banks lacking substantial cover of either concrete or large woody debris as low detectability. I similarly estimated benthic visibility as a three-level ordinal factor based on water clarity (clear, moderately turbid, turbid). Further, I classified mostly clear water with little aquatic vegetation as high visibility, somewhat turbid water with intermediate coverage of aquatic vegetation as medium visibility, and highly turbid water or water with extensive aquatic vegetation cover as low visibility. Lastly, time of night of nocturnal surveys was recorded as a potential covariate of diel activity patterns in crayfishes.

Landscape variables

I used the geographic information system (GIS), QGIS version 3.22.3-Białowieża (https://qgis.org/en/site/, accessed 1 May 2022), to generate 500- and 1000-meter buffers to estimate percent cover of different land cover classes in the landscape neighborhood of each wetland. Using a land cover raster developed for the Oak Openings Region in Martin and Root (2020), I calculated areal extent of each land cover class within these buffers as a percentage. I aggregated land cover classes into anthropogenic (turf and pasture, residential mixed, Eurasian meadow, dense urban, and cropland) and natural (wet prairie, savanna, wet shrub, swamp forest, deciduous forest, sand barren, and upland prairie) groups for analysis. Furthermore, because vegetation structure is highly variable across the study area and understory vegetation is likely more relevant as habitat for these small focal organisms, I also aggregated land cover classes into open canopy (turf and pasture, wet prairie, residential mixed, savanna, wetshrub, sand barren, Eurasian meadow, upland prairie, and cropland) and closed canopy (swamp forest, coniferous forest, deciduous forest) groups for analysis.

Fauna variables

I recorded whether minks and/or muskrats were detected at least once over the sampling season, as well as the mean rate of crayfish and fish detection across nocturnal surveys, to determine whether habitat use by each focal organism was related to that of each other organism or to habitat use by fishes. For evaluating mink and muskrat habitat use, I also considered the survey-specific presence of one of the species as a correlate of the survey-specific presence or absence of the other species.

Analysis

I developed logistic regression models in R (R Core Team 2021). Although occupancy modeling produces unbiased parameter estimates by modeling both detection probability and occupancy hierarchically for repeat surveys (MacKenzie et al. 2018), I found that this approach demanded more replication than was possible in my study compared to regular logistic regression. Another likely consequence of limited sample size was that logistic regression models fit with more than two variables usually resulted in algorithm failure or non-convergence. I consequently constructed every possible subset of two or fewer variables out of all variables of interest and calculated Aikaike’s Information Criterion corrected for small sample sizes (AICc) for each model (Ahmadi-Nedushan et al. 2006, McDonald et al. 2006, Ward and Hossie 2020). I removed models with highly correlated covariates as determined by Spearman’s rank correlation coefficient ($\rho \geq 0.70$) from consideration and retained models with ΔAICc values less than or equal to 2. Because diurnally surveyed sites were surveyed twice in succession to increase survey period detectability, p represents the probability of detection over two successive surveys (one survey period). I averaged covariates that varied from survey to survey across both surveys in a period. Because several sites were surveyed in multiple survey periods, I repeated this process for all possible combinations of one survey period per site (256 possible combinations for diurnal surveys; 82944 possible combinations for nocturnal surveys). I used likelihood ratio tests (LRT) to determine whether top models were significantly more likely than the null intercept only model (Coates et al. 2014, Martinez et al. 2018, Ward and Hossie 2020), which models a constant probability of occurrence regardless of predictor variable values. I reported the resulting log of the likelihood of each model, improvement in AICc value of each model over the null model ($\text{AICc}_{\text{null}}$-$\text{AICc}_{\text{candidate model}}$), improvement in deviance from the saturated model of each model over the null model ($\text{Deviance}_{\text{null}}$-$\text{Deviance}_{\text{candidate model}}$) and P-value expressing the probability that the observed improvement of each model over the null model was due to chance.

Logistical constraints limited the number of sites at which vegetation variables could be measured, and some sites were not surveyed in both nocturnal and diurnal surveys; therefore, the model-fitting procedure differed for the full dataset (vegetation data omitted), the vegetation data subset (data from sites without vegetation measurements omitted), and the fauna data. I first fit best subsets models to the full dataset, then separately to the vegetation data subset. To investigate whether fauna variables were competitive with these models, I pooled all variables that appeared in the top 5 models for the full dataset and the top 5 models for the vegetation data with all fauna variables in a candidate variable set with which I fit best subset models a final time.

Results

Muskrats

Muskrats were detected at 14/22 independent nonlinear wetlands at least once over the sampling season. The top model of muskrat occurrence in all nonlinear sites (N = 22), Surface_Area + Area_Fluctuation (Table 3.1), related muskrat occurrence positively to surface area and negatively to substantial surface area fluctuation (Figure 3.3). This model fit the data significantly better than the null intercept-only model (ΔAICc = 10.97, LRT: ΔDeviance = 16.10, P=0.00094; Table 3.2). Other top models related muskrat occurrence negatively to distance to perennial linear wetland and distance to intermittent linear wetland, and positively to restoration. Surface area appeared in all top five models.

The top model of muskrat occurrence fit to the vegetation data subset, (N = 20), Surface_Area + Lowest_Robel (Table 3.1), related muskrat occurrence positively to Area and lowest visible Robel pole space (Figure 3.4). This model fit the data significantly better than the null intercept-only model (ΔAICc = 11.77, LRT: ΔDeviance = 17.04, P=0.00024; Table 3.2). Other top models introduced number of obstructed Robel pole spaces, maximum bank vegetation height and aquatic vegetation cover as positive predictors of muskrat occurrence. Surface area again appeared in all top five models.

When the above top five models of muskrat occurrence fit to the full data set were reconstructed while allowing for inclusion of fauna variables, Mink_Detected + Surface_Area ranked as the third top model, positively relating both mink detection at least once at a site and wetland surface area to muskrat occurrence. This model was significantly more likely than the null intercept-only model of muskrat occurrence (ΔAICc = 8.82, LRT: ΔDeviance = 13.95, P = 0.0019; Table 3.2).

When this process was repeated for the vegetation data subset, no models featuring fauna ranked over any of the pre-existing top five models.

Table 3.1. Top 5 muskrat (*Ondatra zibethicus*) nonlinear wetland occurrence models aggregated across all possible datasets (256). Each dataset represented a unique combination of a single survey period at each site, given that some sites were surveyed in multiple periods. The first column depicts the variable(s) incorporated in each model (only additive effects were considered). The second column depicts the proportion of datasets for which each model was within 2 ΔAICc units of the most supported (lowest AICc value) model for a given dataset. Models were fit to data collected in Northwest Ohio, USA, 2021.

Model terms	Proportion
Without vegetation variables (N=22)	
Surface_Area + Area_Fluctuation	1.000
Surface_Area + Perennial_Distance	0.750
Surface_Area	0.500
Surface_Area + Restored	0.500
Surface_Area + Intermittent_Distance	0.500
With vegetation variables (N = 20)	
Surface_Area + Lowest_Robel	0.750
Surface_Area + Height	0.500
Surface_Area + Robel_Obstructed	0.500
Aquatic_Cover + Surface_Area	0.250
Surface_Area + Area_Fluctuation	0.250

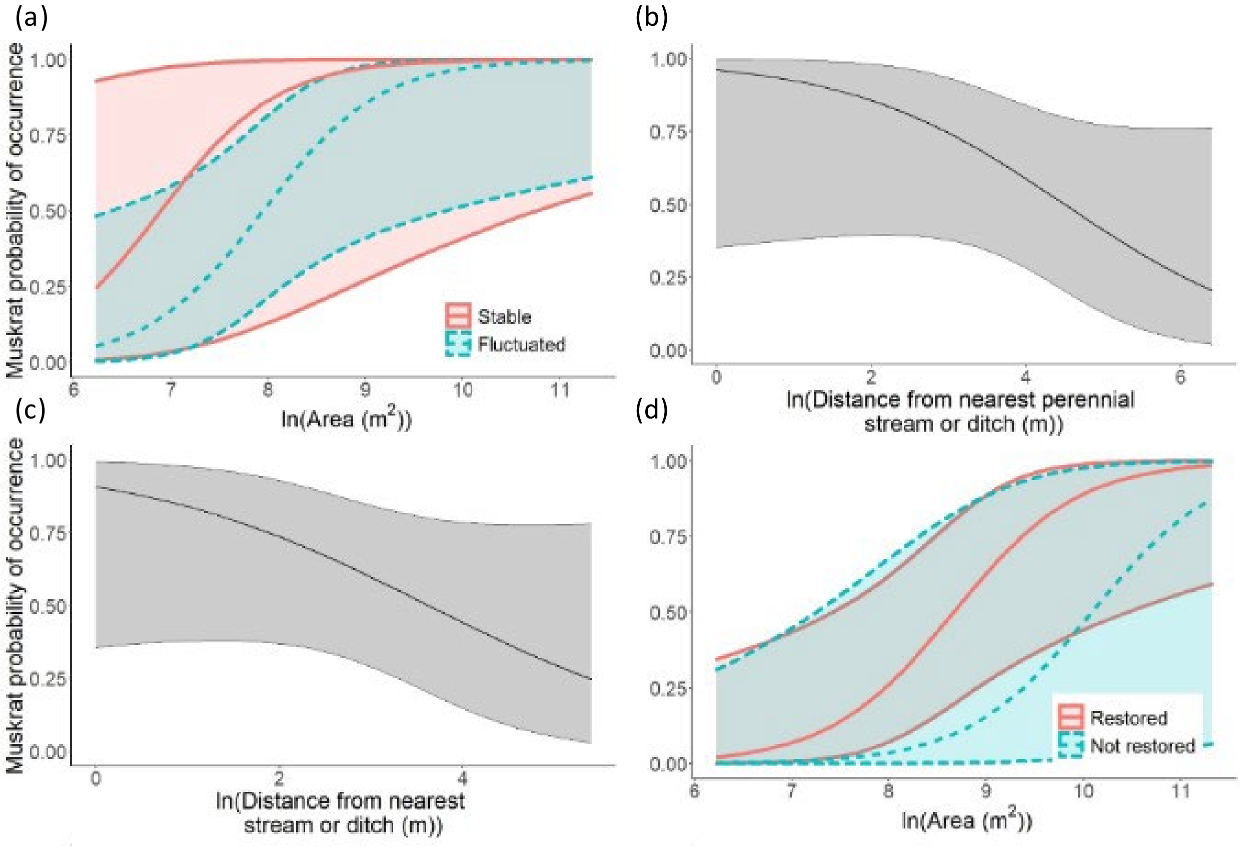

Figure 3.3. Modeled relationships between probability of muskrat (*Ondatra zibethicus*) occurrence and habitat use covariates in nonlinear wetlands of Northwest Ohio, USA, 2021. Habitat use covariates: (a) log of the surface area in square meters of sites that exhibited substantial annual surface area fluctuation compared with that of sites that did not exhibit substantial annual surface area fluctuation, (b) log of the distance in meters between the site and the nearest perennial linear wetland, (c) log of the distance in meters between the site and the nearest perennial or intermittent linear wetland, and (d) log of the surface area in square meters of sites that were created as restoration projects compared with that of other sites. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Table 3.2. The most frequently supported models of muskrat (*Ondatra zibethicus*), crayfish (*Cambaridae*) and mink (*Neovison vison*) occurrence in nonlinear wetlands fit with the general dataset (base model), all variables in the vegetation data subset except fauna variables (vegetation variables model) and all variables in the fauna data subset (fauna variables model). Also reported are model log likelihoods (LogLik), change in AICc values with respect to the null intercept-only model (ΔAICc), difference between the residual and null ΔDeviance from the saturated model (ΔDev.), and likelihood ratio test results P-value. Models were fit to data collected in Northwest Ohio, USA, 2021.

Focal organism	Variables considered	Model terms	LogLik	ΔAICc	ΔDev.	P-value
Muskrat	Base model	Area_Fluctuation + Surface_Area	-6.79	10.97	16.10	9.3E-04
	Vegetation variables model	Lowest_Robel + Surface_Area	-4.37	11.77	17.04	2.4E-04
	Fauna variables model	Mink_Detected + Surface_Area	-7.86	8.82	13.95	1.9E-03
Crayfish	Base model	NDVI + Restored	-13.68	1.75	6.64	5.3E-02
	Vegetation variables model[a]	Area_Fluctuation + Herb_Dominance	-7.37	3.95	9.42	2.9E-02
	Fauna variables model	Mink_Detected + Mod_Score	-6.99	7.76	13.04	5.4E-03
Mink	Base model	Anthro_1000m + Perennial_Distance	-5.99	3.23	8.60	8.4E-02
	Vegetation variables model[a]	Anthro_1000m + Woody_Dominance	-6.76	1.04	6.50	1.1E-01
	Fauna variables model	Muskrat_Detected + Perennial_Distance	-4.38	6.46	11.82	1.5E-02

[a] Although these models were not the respective top vegetation variables models, the actual top vegetation variables models did not incorporate vegetation variables. These models represent the next best models that actually incorporated vegetation variables.

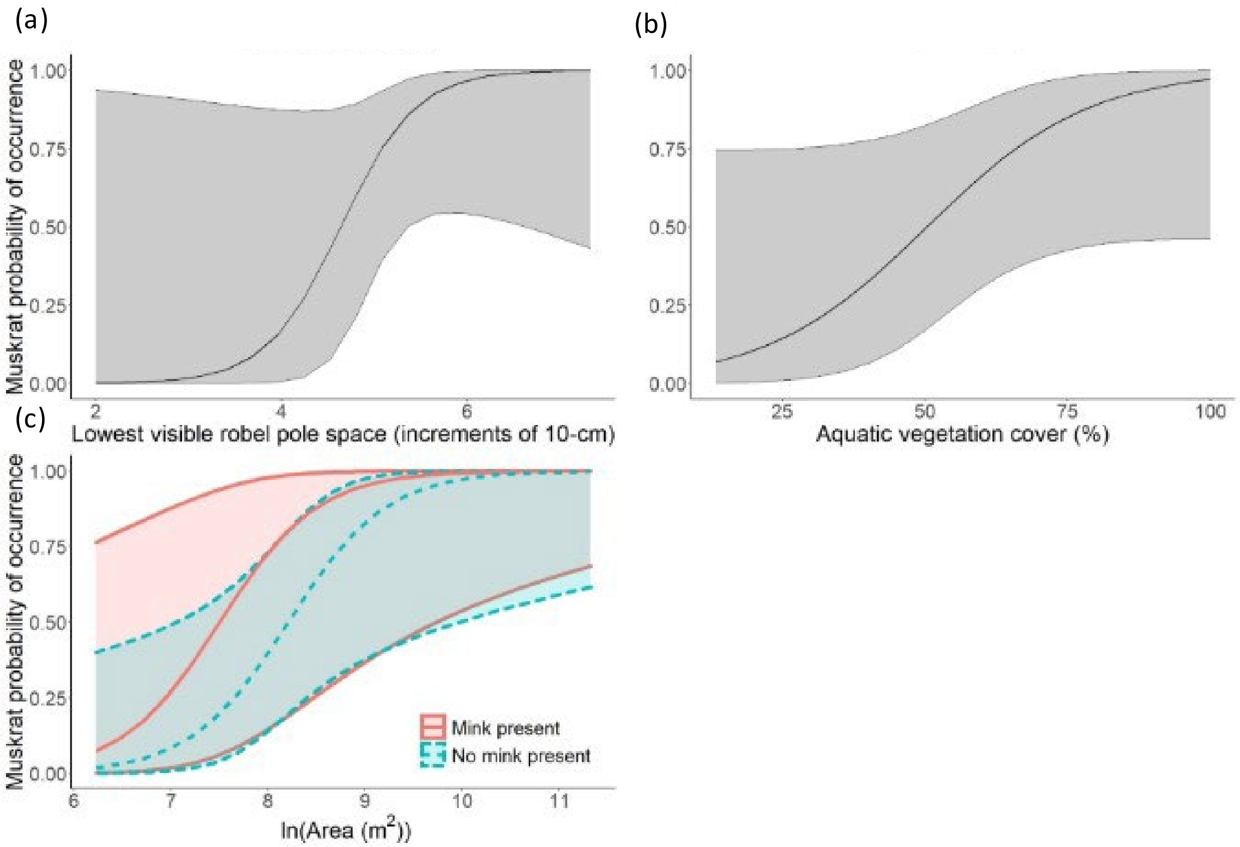

Figure 3.4. Modeled relationships between probability of muskrat (*Ondatra zibethicus*) occurrence and habitat use covariates in nonlinear wetlands of Northwest Ohio, USA, 2021 continued. Habitat use covariates: (a) riparian buffer understory vegetation density as measured by the lowest space visible on a Robel pole erected four meters from the water viewed from the edge of the water, (b) percent cover of aquatic vegetation within site channel and (c) log of the surface area in square meters of sites where minks were and were not concurrently detected. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Crayfishes

Crayfishes were detected at 12/27 independent nonlinear wetlands at least once over the sampling season. The top model for crayfish occurrence in all nonlinear sites (N = 27), NDVI + Restored (Table 3.3), positively related crayfish occurrence to restoration and NDVI (Figure 3.5). This model nearly fit the data significantly better than the null intercept-only model (ΔAICc = 1.75, LRT: ΔDeviance = 6.62, P = 0.053; Table 3.2). Other top models related crayfish occurrence negatively to modification score and positively to distance to perennial linear wetland (Figure 3.5).

The top model fit to the vegetation data subset (N = 18 Restored + Perennial_Distance (Table 3.3), related crayfish occurrence positively to restoration and Distance to perennial linear wetland (Figure 3.5). Another top model introduced degree of herbaceous dominance as a positive predictor of crayfish occurrence (Figure 3.5). These models fit the data significantly better than the null intercept-only model (Area_Fluctuation + Herb_Dominance: ΔAICc = 3.95, LRT: ΔDeviance = 9.42, P = 0.029; Table 3.2). Distance to perennial linear wetland and Substantial surface area fluctuation each appeared in three out of five top models.

When the above top five models of crayfish occurrence fit to the full dataset were reconstructed while allowing for inclusion of fauna variables, Mink_Detected + Mod_Score ranked as the second top model, positively relating mink detection at least once at a site and negatively relating modification score to crayfish occurrence. This model was significantly more likely than the null intercept-only model of crayfish occurrence (ΔAICc = 7.76, LRT: ΔDeviance = 13.04, P = 0.0054; Table 3.2).

When this process was repeated with the vegetation data subset, Mink_Detected + Mod_Score and Mink_Detected + Area_Fluctuation ranked as the first and fourth top models respectively. Mink detection at least once at a site and substantial fluctuation of water levels were positive predictors of crayfish occurrence whereas modification score was again a negative predictor. Both models were significantly more likely than the null intercept-only model of crayfish occurrence.

Table 3.3. Top 5 crayfish (*Cambaridae* spp.) nonlinear wetland occurrence models for sites aggregated across 10000 possible datasets, excluding models featuring correlated variables (Spearman rank correlation coefficient, $\rho \geq 0.7$). Each dataset represented a unique combination of a single survey period at each site, given that some sites were surveyed in multiple periods. The first column depicts the variable(s) incorporated in each model (only additive effects were considered). The second column depicts the proportion of datasets for which each model was within 2 ΔAICc units of the most supported (lowest AICc value) model for a given dataset. Models were fit to data collected in Northwest Ohio, USA, 2021.

Model terms	Proportion
Without vegetation variables (N=27)	
Restored + NDVI	0.665
Mod_Score + Restored	0.555
Restored	0.514
Mod_Score + Month	0.508
Restored + Perennial_Distance	0.428
With vegetation variables (N = 18)	
Restored + Perennial_Distance	0.172
Herb_Dominance + Area_Fluctuation	0.158
Mod_Score + Perennial_Distance	0.148
Area_Fluctuation + Woody_Dominance	0.141
Perennial_Distance + Area_Fluctuation	0.120

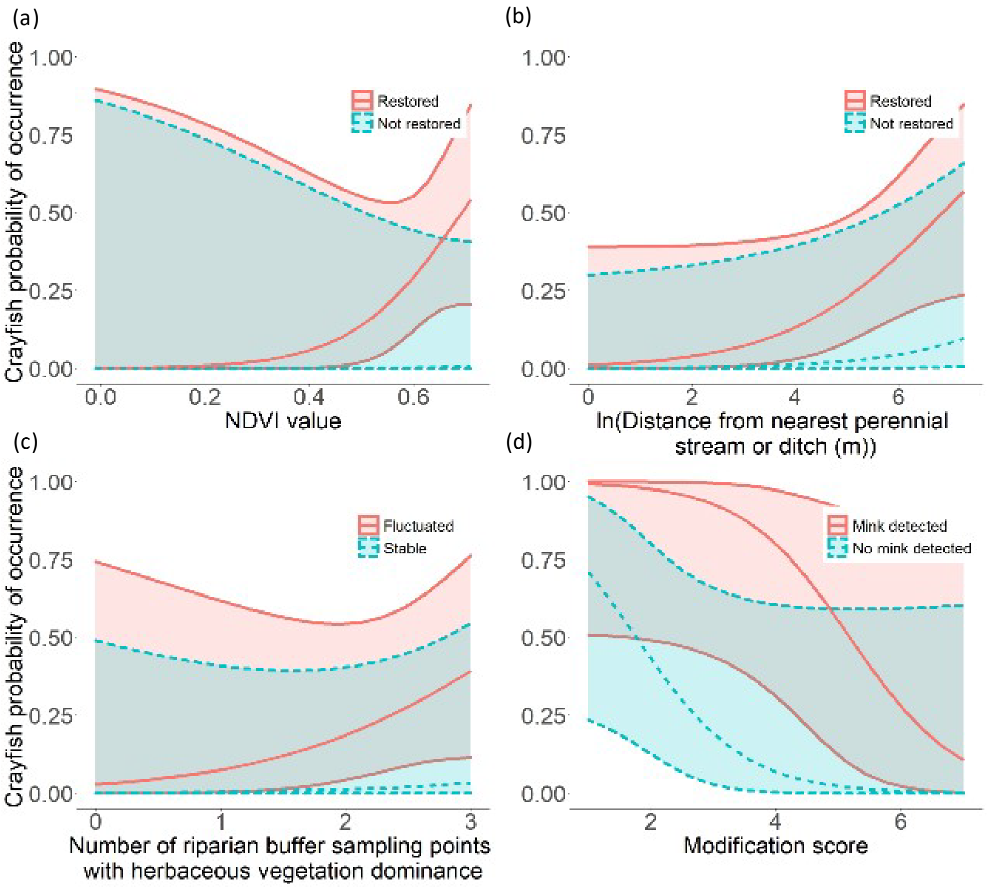

Figure 3.5. Modeled relationships between probability of crayfish (*Cambaridae* spp.) occurrence and habitat use covariates in nonlinear wetlands of Northwest Ohio, USA, 2021. Habitat use covariates: (a) mean Normalized Difference Vegetation Index (NDVI) value of the site over its surface area for sites that were created as restoration projects compared with that of other sites, (b) log of the distance in meters between the site and the nearest perennial linear wetland for sites that were created as restoration projects compared with that of other sites, (c) number of riparian buffer sampling points out of three that exhibited herbaceous vegetation dominance, and (d) modification score of sites where minks were detected at least once during the sampling season compared with that of sites where minks were never detected. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Minks

Minks were detected at 7/19 independent nonlinear wetlands at least once over the sampling season. The top model for mink occurrence in all nonlinear sites (N=19), Anthro_1000m + Perennial_Distance (Table 3.4), related mink occurrence positively to both 1000-meter buffer anthropogenic cover and distance to perennial linear wetland (Figure 3.6). This model nearly fit the data significantly better than the null intercept-only model (ΔAICc = 3.23, LRT: ΔDeviance = 8.60, P = 0.084; Table 3.2). However, the fitting algorithm failed to converge on parameter estimates for this model and produced unusually high magnitude coefficients that were likely inflated. Other top models related mink occurrence positively to surface area and negatively to Julian date and NDVI (Figure. 3.6). Both 1000-meter buffer anthropogenic cover and distance to perennial linear wetland appeared in three out of five top models.

The top model for mink occurrence fit to the vegetation data subset (N = 18), Anthro_1000m + Julian_Date, related mink occurrence positively to 1000-meter buffer anthropogenic cover and negatively to Julian date. However, the fitting algorithm also failed to converge on parameter estimates for this model and produced unusually high magnitude coefficients that are likely inflated. Another top model introduced degree of woody dominance as a positive predictor of mink occurrence (Figure 3.6). This model did not fit the data significantly better than the null intercept-only model (ΔAICc =1.04, LRT: ΔDeviance = 6.50, P = 0.11; Table 3.2). 1000-meter buffer anthropogenic cover appeared in four out of five top models whereas Julian date appeared in two.

When the above top five models of mink occurrence fit to the full dataset were reconstructed while allowing for inclusion of fauna variables, Muskrat_Detected +

Perennial_Distance, Muskrat_Detected, and Muskrat_Detected + Julian_Date ranked as the top three models (Table 3.2). Muskrat detection at least once at a site and distance to nearest perennial linear wetland were positive predictors of mink occurrence whereas Julian date was a negative predictor (Figure 3.6). Each model was significantly more likely than the null intercept-only model of mink occurrence (Muskrat_Detected + Perennial_Distance: ΔAICc = 6.46, LRT: ΔDeviance = 11.82, P = 0.015; Table 3.2).

When this process was repeated with the vegetation data subset, the same models ranked as the first, fourth and fifth ranked models.

Table 3.4. Top 5 mink (*Neovison vison*) nonlinear wetland occurrence models (ΔAICc ≤ 2) aggregated across all possible datasets (256), excluding models featuring correlated variables (Spearman rank correlation coefficient, ρ ≥ 0.7). Each dataset represented a unique combination of a single survey period at each site, given that some sites were surveyed in multiple periods. The first column depicts the variable(s) incorporated in each model (only additive effects were considered). The second column depicts the proportion of datasets for which each model was within 2 ΔAICc units of the most supported (lowest AICc value) model for a given dataset. Models were fit to data collected in Northwest Ohio, USA, 2021.

Model terms	Proportion
Without vegetation variables (N=19)	
Anthro_1000m + Perennial_Distance	0.539
Anthro_1000m + Julian_Date	0.520
Surface_Area + Perennial_Distance	0.445
Anthro_1000m	0.391
NDVI + Perennial_Distance	0.250
With vegetation variables (N=18)	
Anthro_1000m + Julian_Date	0.652
Anthro_1000m + Perennial_Distance	0.516
Anthro_1000m + Woody_Dominance	0.332
Anthro_1000m	0.285
Julian_Date	0.285

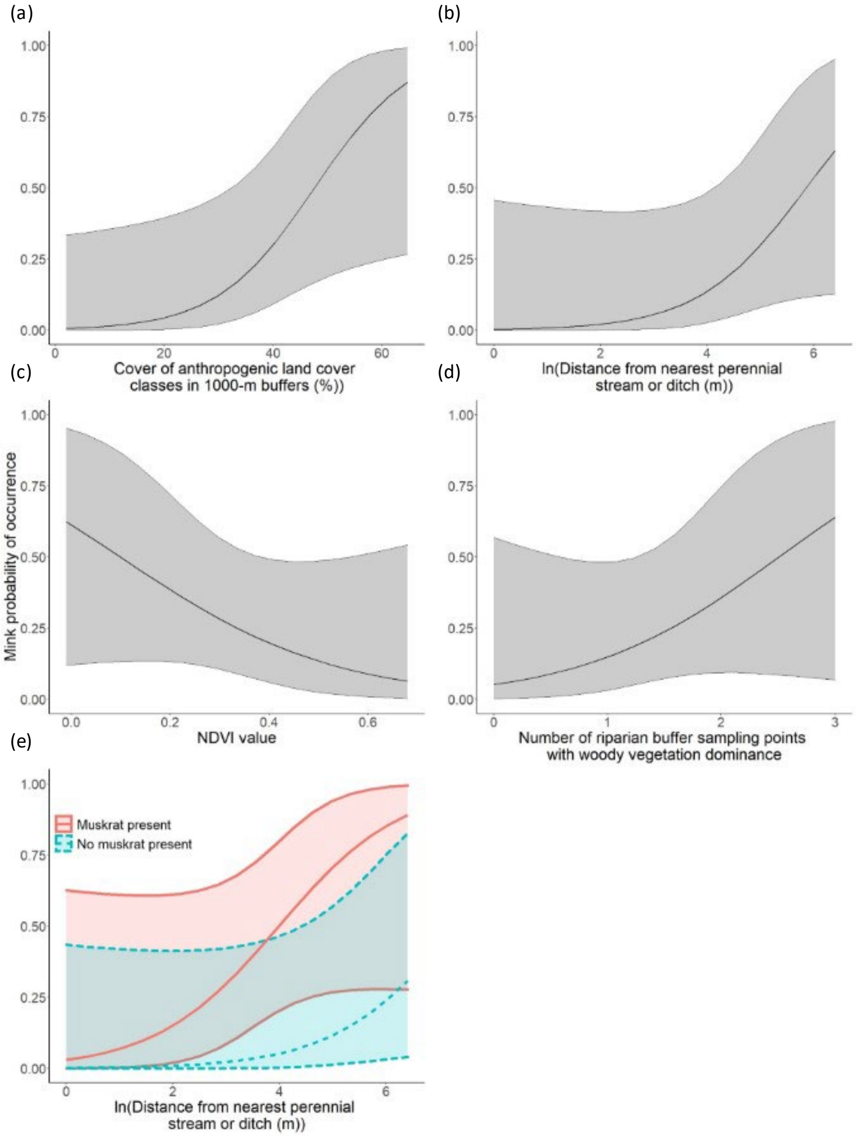

Figure 3.6. Modeled relationships between probability of mink (*Neovison vison*) occurrence and habitat use covariates in nonlinear wetlands of Northwest Ohio, USA, 2021. Habitat use covariates: (a) percent cover of anthropogenic land cover classes within a 1000-meter buffer, (b) log of the distance in meters between the site and the nearest perennial linear wetland, (c) mean Normalized Difference Vegetation Index (NDVI) value of the site over its surface area, (d) number of riparian buffer sampling points out of three that exhibited woody vegetation dominance and (e) log of the distance in meters between the site and the nearest perennial linear wetland with and without concurrent muskrat detections. For models with two covariates, only one variable was displayed in a single figure while the other variable was held at its mean value.

Discussion

Muskrats

The metapopulation theory area-isolation paradigm predicts that, assuming similar habitat quality, larger patches less functionally isolated from source populations should exhibit higher rates of muskrat colonization, lower rates of extinction and consequently higher rates of occupancy (Schooley and Branch 2009). Although streams and ditches are not large in terms of width alone, they may constitute continuous habitat patches and/or movement corridors of great length along which semiaquatic animals can more readily disperse (Mauritzen et al. 1999, Schooley and Branch 2009); consequently, these linear features may function as source habitats or corridors for source populations. Given this possibility, and that muskrats are less likely to disperse through upland habitat where they are exposed to greater predation risk (Errington 1939; 1943, Ahlers et al. 2015), I expected that muskrats would occur more frequently in large, nonlinear wetlands close to perennial linear wetlands from which they presumably disperse regularly. Consistent with this expectation, the top muskrat occurrence model predicted high probability of occurrence for large nonlinear wetlands close to perennial linear wetlands. The surface area variable indeed appeared in each of the top five models fit to both the full dataset and the vegetation data subset. Wetland area may consequently be an especially important habitat use variable for muskrats in the Oak Openings Region.

Fine-scale habitat variables were also highly influential. Models fit to the vegetation data subset demonstrated the association of vegetation variables with muskrat habitat quality. Both aquatic vegetation and understory vegetation density were positive predictors in top models; however, understory vegetation density appeared in the highest ranked models and exhibited larger coefficients. Even though aquatic vegetation is a commonly referenced correlate of muskrat habitat use as a forage resource, bank riparian vegetation is also important either as cover from predation or as forage (Allen and Hoffman 1984, Ahlers et al. 2010, Cotner and Schooley 2011).

The higher occurrence rates observed in restored wetlands may relate to vegetation variables. While restoration favors wetlands with the more natural ephemeral hydroperiod of the region that may not be conducive to muskrat habitat use, restored sites also had more dense riparian buffer understory vegetation and greater cover of aquatic vegetation. The negative effects of greater drying in restored wetlands could also have been offset by potential greater retention of water in their deeper sections compared to those of natural wetlands; however, this speculation is based on anecdote as I did not actually quantify water depth in nonlinear wetlands.

There are several possible explanations for the finding that muskrats were more likely to use sites with at least one mink detection. Minks may abandon stream sites that lack muskrats at higher rates, suggesting selection by minks for habitat where muskrat prey are more available (Ahlers et al. 2016). While this is the reverse of the causal relationship suggested by the model, mink selection for habitats with muskrats could have produced this association. Alternatively, sites where both minks and muskrats were detected may have had more suitable substrates for registering their tracks or scat, increasing the likelihood of detecting both species. Lastly, if muskrats and minks both selected for similar habitat conditions, their occurrence could have been correlated without influence of the direct trophic relationship between the two. The modeled relationship is likely a function of all of these factors.

Crayfishes

Restored wetlands exhibited higher probability of occurrence of crayfishes than un-restored wetlands. This likely relates to the lack of fish, the presence of aquatic vegetation, and the intermediate depths and hydroperiods observed in restored wetlands of my study area, as crayfishes can be more vulnerable to predation by fish in deep water lacking aquatic vegetation and more vulnerable to predation by terrestrial predators when water is low (Wolff et al. 2016). In contrast, excavated ponds in my study area often lacked emergent vegetation and associated gently sloping shallow zones; instead, slopes at pond edges often dropped steeply to deep waters. These ponds also tended to host large fish populations. In the presence of these fishes, crayfishes are likely unable to avoid predation without aquatic vegetation cover and shallow water refugia. The same inferences apply for the models featuring the modification score variable, as more modified wetlands exhibited lower crayfish occurrence probability. Other top models interestingly featured positive coefficients for NDVI and Distance to perennial linear wetland. Both variables were positively associated with closed-canopy vernal pools. Unsurprisingly, these sites tended to lack fish compared to many large, open-canopy, impounded sites. Impounded sites are more likely to contain fish either by colonization by fish in contiguous streams or stocking for recreational purposes. Furthermore, sites with high NDVI and therefore high volumes of vegetation contained substantial woody debris, floating or submerged aquatic vegetation, and leaf litter. These features can provide crayfishes with both shelter and food.

Interestingly, when models were fit to the vegetation data subset, substantial surface area fluctuation, degree of herbaceous dominance and degree of woody dominance were important predictors. Although sites with high herbaceous dominance often contained fishes, those that did not tended to exhibit high densities of crayfishes and substantial surface area fluctuation. High herbaceous dominance was associated with canopy openness, which has previously been related to wetland productivity and biodiversity in the study area (Plenzler and Michaels 2015). Furthermore, herbaceous leaf litter content often exhibits higher nutrient content and decomposition rates than that of woody leaf litter (Gilliam 2007); accumulation of herbaceous leaf litter may therefore further facilitate secondary productivity of wetland ecosystems and a labile food source for crayfishes.

There are several possible explanations for the finding that crayfishes were more likely to use linear sites with at least one mink detection. A likely possibility is that minks selected for sites with more crayfishes, as has been documented in the Midwest (Wolff et al. 2015). While this is the reverse of the causal relationship indicated by the model, mink selection for habitats with crayfishes could have produced this association. Alternatively, sites where both minks and crayfishes were detected may have had more suitable conditions for detecting both species. Lastly, if muskrats and minks both selected for similar habitat conditions, their occurrence could have been correlated without influence of the direct trophic relationship between the two. The modeled relationship is likely a function of each of these factors.

Minks

Models of mink occurrence exhibited low rates of convergence likely due to sample size limitations required to maintain spatial independence of sites, low detectability in nonlinear sites, probable non-negligible false detection rates, and possible low densities of minks in the study area. Nonlinear sites typically lacked extensive coverage of substrate suitable for registering tracks that was characteristic of stream sites. Furthermore, I detected almost no mink scats in the study area, which have yielded valuable information in other studies (e.g., Schooley et al. 2012). I could not confidently differentiate between mink tracks and large long-tailed weasel tracks in many cases, which may have resulted in misclassification of the latter as mink tracks. Lastly, it is possible that minks simply do not use habitats of the Ohio Oak Openings Region at high rates. In any case, I only recorded mink detections at three to six nonlinear sites depending on the dataset.

Given that logistic regression models fit to data with few events in the less frequent outcome category (i.e., presence in this case) are characterized by considerable bias, low confidence, and spurious variable effects (Peduzzi et al. 1996), low detection rates of minks in nonlinear sites likely contributed to poor model fit and low convergence.

Notwithstanding the above qualifications, the models did suggest some relationships. The consistent positive relationship between 1000-meter buffer anthropogenic cover and mink occurrence across top models was unexpected, as several studies have suggested that site proximity to urban areas may reduce mink occurrence (e.g., Burksey and Simon 2010, Ahlers et al. 2015, Holland et al. 2019). However, most my study area was substantially less developed than true urban areas. Sites where minks occurred were all relatively large wetlands surrounded by rural land. Occurrence of agricultural fields and roads in close proximity to these sites likely accounted for their higher proportion of 1000-meter buffer anthropogenic cover. Minks dispersing from nearby linear wetlands would not have to cross over roads or through adjacent dense urban land cover to access any of these isolated wetlands. This modeled relationship may therefore be exaggerated by the method of lumping anthropogenic land cover classes used here. The positive relationship between Distance to perennial linear wetland and mink occurrence in nonlinear sites was similarly unexpected, as minks tend to stay near stream and ditch habitat and experience higher mortality risks away from these features (Ahlers et al. 2015). I expected that nonlinear wetlands nearer to streams and ditches would therefore be used at higher rates assuming that nonlinear wetland networks would constitute both source habitats and dispersal corridors. This modeled effect may reflect the aforementioned replication and detection inadequacies. The effects of Surface area and NDVI are likely related, as minks used larger wetlands with open canopies at higher rates; these wetlands also tended to exhibit lower NDVI as lower proportions of open water were obscured by canopy cover. As mentioned, large wetlands with open canopies were likely to contain more resources and exhibit higher primary productivity (Plenzler and Michaels, 2015). The negative relationship between mink occurrence and Julian date may relate to increased water levels from summer precipitation later in the sampling season. Degree of woody dominance became an influential positive predictor of mink occurrence when models were fit to the vegetation data subset. This may relate to a preference for forested environments with shrubby cover to avoid predation or to rest (Mason and MacDonald 1983, Racey and Euler 1983, Yamaguchi et al. 2003, Haan and Halbrook 2014).

There are several possible explanations for the finding that minks were more likely to use linear sites with at least one muskrat detection. Minks are more likely to abandon sites lacking muskrats, from which follows that minks likely select for habitat with available muskrat prey (Ahlers et al. 2016). My findings are consistent with minks selecting for sites with muskrats. Alternatively, sites where both minks and muskrats were detected may have had more suitable conditions for detecting both species. Lastly, if muskrats and minks both selected for similar habitat conditions, their occurrence could have been correlated without influence of the direct trophic relationship between the two. The modeled relationship is likely a function of each of these factors.

Conservation implications

As has been discussed, the Oak Openings is naturally predisposed to seasonal drying and likely exhibits comparatively low establishment of aquatic vegetation as a result (Brewer and Vankat 2004). However, extensive ditching of the area exacerbates this drying. This poses challenges to wildlife as although more mobile wetland fauna may be better able to track diminishing water, others are not adapted to do so as readily and suffer substantial population-level mortality events with intensified drying associated with disturbed hydrological conditions (Acosta and Perry 2001). Although my study did not produce direct evidence of these deleterious effects of ditching, draining and pond construction, general mitigation strategies are still advised. Blocking ditches to rewet sites can restore reference hydrological conditions and associated native plants (Maanavilja et al. 2014). Such efforts should increase residence time of water on a landscape already prone to seasonal drying. While excavated ponds can provide a buffer from this drying for wildlife that use lentic wetlands, the ponds in my study area tended to lack many of the characteristics of many of the natural wetlands of the region.

My results support restoration of more of the natural wetlands of the region, as muskrats and crayfishes used restored wetlands at least as much as excavated recreational ponds, despite the unstable water levels of the former. However, it should be qualified that many of these restored wetlands are recent additions to the landscape and may only structurally replicate reference wetlands at this stage (Swartz et al. 2019). If created wetlands only structurally replicate reference wetlands and fail to consider the consumptive and utility requirements of a species of conservation concern across its life history stages, as well as the perceptual cues it follows, these wetlands could become ecological traps (Hale and Swearer 2016). However, given the historical loss of reference wetlands in this region, more wetland habitat is urgently needed. Creating scrapes, wet prairies and kettles closer to the lowered water table with heterogeneous topography to promote shallow and deep-water refugia could reduce the effects of drying while promoting coexistence of crayfishes, fishes and other wildlife with a variety of habitat requirements. Post-creation monitoring should not be neglected to ensure that created wetlands are benefiting populations of native species rather than hindering them. I recommend promoting greater cover of aquatic vegetation and dense bank vegetation for similar reasons. These recommendations likely also apply to improving existing excavated ponds and impoundments. Furthermore, while clear and unobstructed water may be preferable for recreational purposes, allowing for some establishment of open water and littoral zone aquatic vegetation as well as accumulation of woody debris is likely to benefit many species. Investing in restoration techniques higher in the watershed and promoting sustainable agricultural, wastewater treatment, gardening, and lawncare practices should be prioritized over chemically treating waters to reduce algae as much as possible.

Spatial considerations in conservation prioritization for the region are also important depending on the species of interest. Muskrats and crayfishes used habitat very differently with respect to wetland size and isolation. If muskrat conservation is prioritized, nonlinear wetlands closer to perennial linear wetlands might be more fruitful, although there was some evidence that proximity to intermittent ditches was also important. Crayfishes may retain the ability to access vernal pools and scrapes distant from perennial water sources because of their adaptations to drying and their dispersal ability, although it is unclear to what degree they are doing so from intermittent ditches. However, unlike crayfishes, some other native fauna may disperse passively or generally have more limited dispersal capacities. For these taxa, spatial isolation may be a more critical factor influencing accessibility of nonlinear wetlands (Swartz et al. 2019). More dedicated research as to the effects of spatial isolation of wetlands, as well as the spatial pattern of ditches, on dispersing native wildlife of concern as compared to invasive species in the region would be valuable.

More research is needed as to the status of native crayfishes in Oak Openings linear wetlands. While I observed higher probability of occurrence and substantial activity of crayfishes in large linear wetlands, it is unclear whether those observed were native or invasive due to insufficiency of the survey method used. Crayfishes using smaller streams and ditches may simply have been predominantly primary burrowers and consequently less detectable in nocturnal surveys. However, if this is not the case and crayfishes simply did not utilize these habitats, it is worth investigating whether and how wetland function is impaired.

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APPENDIX A: LISTS OF HABITAT USE AND DETECTION VARIABLES/COVARIATES AND THEIR DEFINITIONS

Table A.1. List of linear wetland habitat use and detection variables/covariates, their descriptions grouped according to category (channel structure/hydrology, landscape variables, vegetation variables, detection covariates and fauna variables) Associated term/variable name(s) in logistic regression models are reported in the last column. All variables were measured in Northwest Ohio, USA, 2021.

Variable	Description/measure(s)	Model term name(s)
Channel structure/hydrology		
Water depth	Average of maximum depth in meters at three equidistant points along reach.	Depth
Channel size	Strahler order.	Order
Channel curvature	Sinuosity and number of vertices per digitized and simplified reach within 500-meter buffers of sites.	Sinuosity, Vertices
Floodplain development	Presence/absence of a vegetated floodplain greater than or equal in width to the width of the channel.	Floodplain

Continued

Table A.1 Continued.

Variable	Description/measure(s)	Model term name(s)
Landscape variables		
Anthropogenic land cover extent	Areal extent of all anthropogenic land cover classes combined within 500- and 1000-meter buffers.	Anthropo_500, Anthropo_1000
Natural land cover extent	Areal extent of all natural land cover classes combined within 500- and 1000-meter buffers.	Natural_500, Natural_1000
Open canopy land cover extent	Areal extent of all non-urban open canopy land cover classes combined within 500- and 1000-meter buffers.	Open_500, Open_1000
Closed canopy land cover extent	Areal extent of all closed canopy land cover classes combined within 500- and 1000-meter buffers.	Closed_500, Closed_1000

Continued

Table A.1 Continued.

Variable	Description/measure(s)	Model term name(s)
Vegetation variables		
Riparian buffer understory vegetation structure	Mean maximum vegetation height in meters within 4-meters of the channel at three equidistant points along each reach.	Height
Riparian buffer understory vegetation composition	Dominant understory vegetation growth form (herbaceous or woody) within 4-meters of the channel summed across three equidistant points along each reach.	Herb_Dominance, Woody_Dominance
Aquatic vegetation cover	Visually estimated percent cover of aquatic vegetation within the channel. Sub-categorized aquatic vegetation as floating, submerged, or emergent.	Aquatic_Cover, Floating_Cover, Submerged_Cover, Emergent_Cover,
Canopy structure	Canopy cover measured at three equidistant points along each reach.	Canopy

Continued

Table A.1 Continued.

Variable	Description/measure(s)	Model term name(s)
Detection covariates		
Date	Days elapsed between each survey and the beginning of the sampling season.	Julian_Date
Precipitation	Cumulative rainfall in centimeters within one week prior to each survey.	Precipitation
Temperature	Daily mean temperature at the center of the study area.	Temperature
Change in depth	Survey-specific proportion change in depth from the site mean.	Depth_Change
Sign detectability	Quality of substrates and structures at sites for registering sign as a three-level ordinal factor; high, medium, and low quality.	Sign_Detectability
Benthic visibility	Visually-estimated turbidity classified as a three-level ordinal factor (clear, moderately turbid, turbid).	Visibility
Nocturnal survey time	Time of night as measured in hours elapsed since 22:00 EST.	Hour

Continued

Table A.1 Continued.

Variable	Description/measure(s)	Model term name(s)
Fauna variables		
Muskrat habitat use	For crayfishes: muskrat detection at least once over the sampling season; for minks: muskrat detection during the concurrent survey period.	Musk_Detected, Musk_Present
Crayfish habitat use	Mean rate of crayfish detection across all surveys at each site.	Crayfish_Rate
Mink habitat use	For muskrats: mink detection during the concurrent survey period; for crayfishes: mink detection least once over the sampling season.	Mink_Present, Mink_Detected
Fish habitat use	Mean rate of fish detection across all surveys at each site.	Fish_Rate

Table A.2. List of nonlinear wetland habitat use and detection variables/covariates and their descriptions grouped according to category (channel structure/hydrology, landscape variables, vegetation variables, detection covariates and fauna variables). Associated term/variable name(s) in logistic regression models are reported in the last column. All variables were measured in Northwest Ohio, USA, 2021.

Variable	Description/measure(s)	Model term name(s)
Wetland structure/ hydrology		
Surface area	Inundated area as digitized from March 2021 aerial imagery.	Surface_Area
Degree of surface area fluctuation	Binary variable (yes/no) indicating whether each wetland underwent regular seasonal drying (surface area change of 50% or more) in recent years.	Area_Fluctuation
Degree of modification	Score (1-9) based on presence or absence of 9 qualitative attributes related to wetland modification/anthropogenic influence.	Mod_Score
Restoration status	Binary variable (yes/no) indicating whether each wetland was created according to restoration principles.	Restored

Continued

Table A.2 Continued.

Variable	Description/measure(s)	Model term name(s)
Landscape variables		
Anthropogenic land cover extent	Areal extent of all anthropogenic land cover classes combined within 500- and 1000-meter buffers.	Anthropo_500, Anthropo_1000
Natural land cover extent	Areal extent of all natural land cover classes combined within 500- and 1000-meter buffers.	Natural_500, Natural_1000
Open canopy land cover extent	Areal extent of all non-urban open canopy land cover classes combined within 500- and 1000-meter buffers.	Open_500, Open_1000
Closed canopy land cover extent	Areal extent of all closed canopy land cover classes combined within 500- and 1000-meter buffers.	Closed_500, Closed_1000
Distance to nearest nonlinear wetland	Distance in meters between each wetland and the nearest stream or ditch; distance to nearest perennial stream or ditch.	Intermittent_Distance, Perennial_Distance

Continued

Table A.2 Continued.

Variable	Description/measure(s)	Model term name(s)
Vegetation variables		
Riparian buffer understory vegetation structure	Mean maximum vegetation height in meters, as well as understory visual obstruction in terms of the lowest visible Robel pole space and the number of Robel pole spaces obstructed, within 4-meters of the wetland edge measured at three equidistant points along the perimeter.	Height, Lowest_Robel, Robel_Obstructed
Riparian buffer understory vegetation composition	Dominant vegetation growth form (herbaceous or woody) within 4-meters of the wetland edge at three equidistant points along the perimeter.	Herb_Dominance, Woody_Dominance
Aquatic vegetation cover	Visually estimated percent cover of aquatic vegetation within the channel. Sub-categorized aquatic vegetation as floating, submerged, or emergent.	Aquatic_Cover, Floating_Cover, Submerged_Cover, Emergent_Cover
Canopy structure	Canopy cover measured at three equidistant points along each reach.	Canopy
Normalized Difference Vegetation Index (NDVI)	Mean NDVI value calculated for the rasterized surface area of each wetland. Rasterized wetland surface area was rendered using a Normalized Difference Water Index (NDWI) thresholding procedure.	NDVI

Continued

Table A.2 Continued.

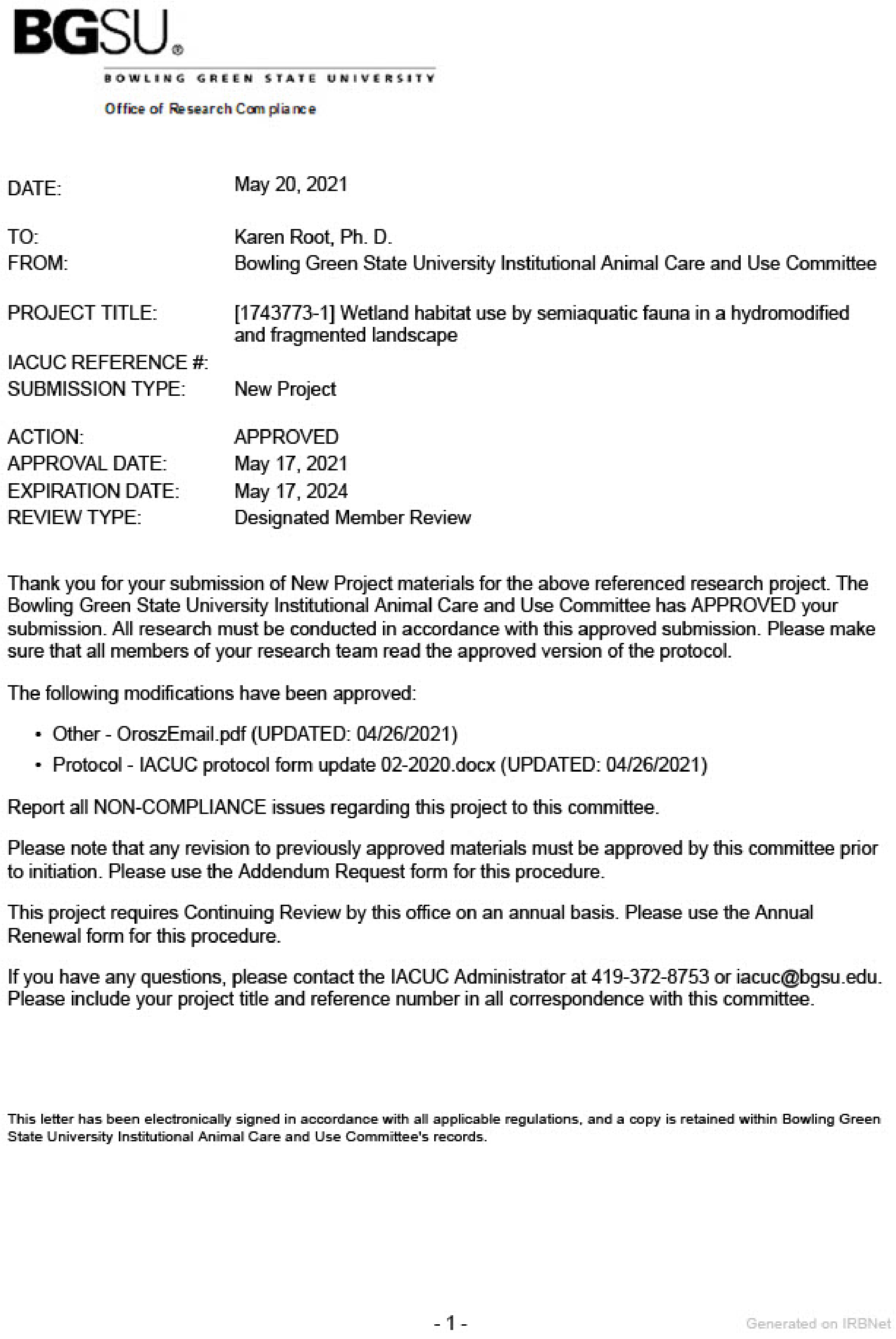
Variable	Description/measure(s)	Model term name(s)
Detection covariates		
Date	Days elapsed between each survey and the beginning of the sampling season.	Julian_Date
Precipitation	Cumulative rainfall in centimeters within one week prior to each survey.	Precipitation
Temperature	Daily mean temperature at the center of the study area.	Temperature
Sign detectability	Quality of substrates and structures at sites for registering sign as a three-level ordinal factor; high, medium, and low quality.	Sign_Detectability
Benthic visibility	Visually-estimated turbidity classified as a three-level ordinal factor (clear, moderately turbid, turbid).	Visibility
Nocturnal survey time	Time of night as measured in hours elapsed since 22:00 EST.	Hour

Continued

Table A.2 Continued.

Variable	Description/measure(s)	Model term name(s)
Fauna variables		
Muskrat habitat use	For crayfishes: muskrat detection at least once over the sampling season; for minks: muskrat detection during the concurrent survey period.	Musk_Detection, Musk_Present
Crayfish habitat use	Mean rate of crayfish detection across all surveys at each site.	Crayfish_Rate
Mink habitat use	For muskrats: mink detection during the concurrent survey period; for crayfishes: mink detection least once over the sampling season.	Mink_Present, Mink_Detected
Fish habitat use	Mean rate of fish detection across all surveys at each site.	Fish_Rate

APPENDIX B: INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL



BGSU®
BOWLING GREEN STATE UNIVERSITY
Office of Research Compliance

DATE: May 20, 2021

TO: Karen Root, Ph. D.
FROM: Bowling Green State University Institutional Animal Care and Use Committee

PROJECT TITLE: [1743773-1] Wetland habitat use by semiaquatic fauna in a hydromodified and fragmented landscape
IACUC REFERENCE #:
SUBMISSION TYPE: New Project

ACTION: APPROVED
APPROVAL DATE: May 17, 2021
EXPIRATION DATE: May 17, 2024
REVIEW TYPE: Designated Member Review

Thank you for your submission of New Project materials for the above referenced research project. The Bowling Green State University Institutional Animal Care and Use Committee has APPROVED your submission. All research must be conducted in accordance with this approved submission. Please make sure that all members of your research team read the approved version of the protocol.

The following modifications have been approved:

- Other - OroszEmail.pdf (UPDATED: 04/26/2021)
- Protocol - IACUC protocol form update 02-2020.docx (UPDATED: 04/26/2021)

Report all NON-COMPLIANCE issues regarding this project to this committee.

Please note that any revision to previously approved materials must be approved by this committee prior to initiation. Please use the Addendum Request form for this procedure.

This project requires Continuing Review by this office on an annual basis. Please use the Annual Renewal form for this procedure.

If you have any questions, please contact the IACUC Administrator at 419-372-8753 or iacuc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Bowling Green State University Institutional Animal Care and Use Committee's records.