Upland–wetland linkages: relationship of upland and wetland characteristics with watersnake abundance

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Abstract

Land-use practices surrounding a wetland may be as important for maintaining wildlife populations as the wetland itself. Although imperiled species may appear to be more impacted than ubiquitous species from changes in the landscape surrounding wetlands, studies of common wetland species are useful for conservation because they provide insight into why some species persist despite landscape changes. We therefore investigated the relationship between connectivity, measured as the wetland distance to other wetlands; connectivity quality, implied by wetland distance to roads and forest area within 30, 125, 250, 500 and 1000 m buffer zones around the wetland; and patch size as indicated by wetland size with northern watersnake Nerodia sipedon sipedon abundance. Our results suggest that both upland and wetland characteristics influence the abundance of N. s. sipedon, as wetland size and wetland connectivity to other wetlands were significantly associated with abundance. Abundance was positively correlated with increasing wetland size and wetland connectivity. We were not able to find a significant relationship between abundance and connectivity quality, and wetland distance to road or forest area within 30, 125, 250, 500 and 1000 m buffer zones. We conclude that wetland conservation should focus on wetland complexes as well as individual wetlands. In addition, common wetland species such as the northern watersnake do not appear to be negatively impacted by modifications to nearby terrestrial habitats, such as deforestation and roads, and may benefit from the creation of larger, permanent wetlands.

Introduction

Wetland conservation typically focuses on the wetland as an individual unit, with little consideration for the surrounding landscape (Amezaga, Santamaria & Green, 2002). However, land-use practices surrounding a wetland may be as important for maintaining wildlife populations as the management of the wetland itself (Findley & Houlahan, 1997; Gibbons, 2003). For example, loss of wetlands surrounding a wetland reduces connectivity to other wetlands, thereby isolating populations (Semlitsch & Bodie, 1998; Roe, Kingsbury & Herbert, 2003). The value of connectivity is a fundamental concept in metapopulation theory, and we predict that wetlands in close proximity to other wetlands would have higher abundances than isolated wetlands (Hanski, 1999; Houlahan & Findley, 2003; Marchand & Litvaitis, 2004).

Land management that reduces forest area could negatively impact wetland wildlife because many species spend a significant proportion of their life outside wetlands (Buhlmann & Gibbons, 2001; Joyal, McCollough & Hunter, 2001; Roe et al., 2003; Semlitsch & Bodie, 2003). For example, wetland herpetofauna use terrestrial habitats for nesting and parturition (Buhlmann & Gibbons, 2001; Roth, 2005), hibernation and aestivation (Burke & Gibbons, 1995; Joyal et al., 2001), and terrestrial residence (Semlitsch, 1998). In addition, forest loss could affect connectivity quality, that is the degree to which the landscape structure helps or hinders movement because wetland species use forest as dispersal corridors to other wetlands (Taylor et al., 1993; Moilanen & Hanski, 2001; Roe, Kingsbury & Herbert, 2004). Roads can disrupt connectivity because they fragment upland forest, act as barriers to movement and cause mortality (Merrian et al., 1989; Ashley & Robinson, 1996; Kramer-Schadt et al., 2004).

Wetland protection often focuses on characteristics such as wetland size and quality. Theory predicts that larger patches should sustain larger populations and these populations would be less vulnerable to extirpation (Hanski, 1999). Consequently, smaller patches are less likely to be occupied because small populations have a higher probability of extinction. Some studies have shown that larger wetlands have greater wildlife abundances, suggesting that ‘bigger is better’ (Findley & Houlahan, 1997; Knutson et al., 1999;
Houlahan & Findley, 2003). However, other studies have shown that small wetlands are important for maintaining regional diversity as species composition and abundance may be different than larger, permanent wetlands (Semlitsch & Bodie, 1998; Snodgrass et al., 2000; Joly et al., 2001; Gibbons, 2003; Roe et al., 2004).

In some cases, imperiled species appear to be more impacted by landscape changes surrounding wetlands than ubiquitous species (Roe et al., 2003, 2004; Roe, Gibson & Kingsbury, 2006). Studies often investigate reasons behind the decline of an imperiled species, but studies examining ubiquitous wetland species could be useful for conservation as they provide insight into why some species persist despite landscape changes. The northern watersnake *Nerodia sipedon* is an example of a model species that is widespread and common in the midwestern United States despite wetland losses and landscape changes that have negatively affected other closely related aquatic snakes (Dahl, 1990; Dahl & Johnson, 1991; Laurent & Kingsbury, 2003; Roe et al., 2003, 2004). We therefore investigated the relationship between connectivity, measured as the wetland distance to other wetlands; connectivity quality, implied by wetland distance to roads and forest area within 30, 125, 250, 500 and 1000 m buffer zones around the wetland; and patch size as indicated by wetland size with northern watersnake abundance. We predicted that wetlands that were larger, less isolated from other wetlands, farther away from roads and had more forest area within their buffer zone would have higher abundance.

**Methods**

This study took place in north-western Ohio and southern Michigan, USA, on public and private land. The study site contained a variety of wetland sizes and types including small, ephemeral wetlands and large, permanent wetlands. Some of the larger, permanent wetlands were artificially created, with water levels controlled for game fish and bird management. Some wetlands were fed by a spring, river, lake or local runoff. The St Joseph River also flows through the study site. The upland landscape consists of a matrix of forest, shrub-scrub, old field, roads and agricultural and residential habitats.

We surveyed 111 wetlands between 15 April and 15 June 2005. Focal surveys consisted of walking along the wetland’s perimeter and wading through the water when necessary by a team of two to three individuals. When it was not possible to walk around a portion of a wetland, we used binoculars to survey that area. Each wetland was surveyed three times during the study period. Relative abundance was the number of observed snakes, calculated using the mean of the two surveys with the highest snake observations. When snakes escaped into the water, their escape route was observed in order to minimize double counting individuals.

Wetland and upland habitat characteristics were obtained post hoc using ArcView 3.2 GIS software. Most of the wetlands were mapped during previous studies by digitizing wetlands from aerial photographs (digital ortho-photo quarter-quadrangles images) and ground truthing (Roe et al., 2003, 2004). Additional wetlands and forested habitat were mapped as needed, using methods from previous studies. We did not consider other land-use categories, such as old field, pasture, residential and grassland, because of the difficulty in accurately distinguishing between them using aerial photographs. Wetland boundaries were defined following Cowardin et al. (1979) guidelines. On the basis of aerial photographs, forests were defined as areas with nearly complete or complete canopy. Wetland size (surface area) and forest area within a wetland buffer zone were calculated using the X-tools extension for ArcView GIS. We calculated forest area within several buffer-zone sizes. We used a buffer zone of 30 m because this was the recommended buffer size for northern watersnakes (Roe et al., 2003). We also used a 125 m buffer zone because this is the recommended size for the sympatric and state-endangered copperbelly watersnake *Nerodia erythrogaster neglecta* (Roe et al., 2003), and 250, 500 and 1000 m buffer zones because these sizes were recommended for other wetland species and have often been used in past studies (Findlay & Houlahan, 1997; Semlitsch, 1998; Herrmann et al., 2005). Wetland distance to the nearest wetland and wetland distance to a paved, two-lane road was measured using the Nearest Features v3.8 extension for ArcView GIS (Jenness, 2005).

**Statistical analysis**

We used a stepwise regression to analyze which landscape and wetland characteristics had a significant relationship with northern watersnake abundance. Variables were included in the model if *P* < 0.05 and excluded if *P* > 0.10. The independent variables were attributes of the surrounding uplands and wetlands: distance to a road, wetland size and distance to nearest wetland. The area of forest within wetland buffer zones was not included in the stepwise regression because of significant correlations with wetland size (see Table 1 for a description of correlations among all variables). Larger wetlands have more forest area within their buffer zone because their buffer zones are larger. In order to test whether forest area within a buffer zone had an effect on abundance while accounting for wetland size, we first performed a linear regression of wetland size versus buffer-zone forest area. Residuals with a positive value would indicate more forest area within the buffer zone than predicted for a given wetland size. We then regressed the residual values with abundance. All data were log(*y* + 1) transformed before analysis to normalize the data, with the exception of the residuals.

**Results**

A mean ± se (range) summary of terrestrial landscape characteristics is as follows: wetland distance to the road 368.0 ± 20.6 m (3.8–760.1), distance to nearest wetland 59.3 ± 3.8 m (2.6–197.7); and forest area within 30 m buffer zones 1.22 ± 0.14 ha (0.0–11.78), forest area within 125 m
buffer zones 6.47 ± 0.45 ha (0.37–34.48), forest area within 250 m buffer zones 17.22 ± 0.98 ha (2.46–68.72), forest area within 500 m buffer zones 49.92 ± 1.95 ha (12.27–146.95), forest area within 1000 m buffer zones 154.03 ± 5.06 ha (65.4–333.80). The mean size of the wetlands was 1.1 ± 0.3 ha (0.01–31.9).

Wetland distance to a road did not have a significant relationship with abundance ($t = -0.678$, $P = 0.50$) and was dropped from the final stepwise regression model. The first regression model consisted only of wetland size, describing an additional 4% ($r^2 = 0.33$). Wetland size and distance to nearest wetland remained in the final stepwise regression model ($F_{2,110} = 31.6, P < 0.0001$), with distance to nearest wetland describing an additional 4% ($r^2 = 0.04$) of abundance. Northern watersnakes were found within a wide range of wetland sizes from 0.03 to 31.9 ha. However, abundance was significantly related to wetland size ($B = 0.68 ± SE 0.10, t = 6.73, P < 0.0001$), with larger wetlands having more snakes (Fig. 1a). Northern watersnakes were also found within the entire range of wetland distances to other wetlands, with abundance significantly increasing as the distance between wetlands decreased ($B = -0.17 ± SE 0.06, t = -2.61, P = 0.01$; Fig. 1b).

When accounting for wetland size, there was no significant relationship between abundance and forest area within any of the buffer zones (30 m: $F_{1,110} = 0.998, P = 0.75$; 125 m: $F_{1,110} = 0.15, P = 0.70$; 250 m: $F_{1,110} = 0.16, P = 0.69$; 500 m: $F_{1,110} = 0.033, P = 0.86$; 1000 m: $F_{1,111} = 0.04, P = 0.84$).

**Discussion**

Wetland and upland characteristics significantly influenced northern watersnake abundance. Larger wetlands had higher abundance, suggesting ‘bigger is better’ does apply to northern watersnakes and supports metapopulation theory that patch size is an indication of population size (Hanski, 1999). Larger wetlands presumably have higher carrying capacity because they have more shoreline, the microhabitat most used by watersnakes, are more likely to have fish, an important component of the diet of northern watersnakes, and are more likely to be permanent (Laurent & Kingsbury, 2003; Roe et al., 2004). Our results corroborate past habitat-use studies that have shown that northern watersnakes prefer larger and more permanent wetlands (Roe et al., 2003). Despite northern watersnakes being less abundant in smaller wetlands, these wetlands may still be important to this species because small wetlands may be visited between excursions to larger wetlands and are often critical landscape elements that influence the suitability of larger wetlands (Naugle et al., 2001; Roe et al., 2003, 2004).

Many studies have suggested that wetland conservation should focus on protecting wetland complexes versus individual wetlands (Semlitich & Bodie, 1998; Joyal et al., 2001; Naugle et al., 2001; Roe et al., 2003). Our results support the importance of maintaining wetland connectivity and conserving wetland complexes as isolated wetlands had lower northern watersnake abundance. Patch connectivity increases colonization by dispersing individuals and promotes an exchange of individuals between populations, which is important in preventing local extinctions (Hanski, 1999; Thomas et al., 2001). Thus, wetland losses would disrupt this connectivity by increasing distances between wetlands and cause population declines. Northern watersnakes in our study site have been found to use two wetlands over the course of a year, and wetland proximity may be important for finding mates and alternate foraging sites (Roe et al.,
watersnakes are not able to disperse to that wetland because of their poor dispersal capabilities, regardless of barriers (Roe et al., 2003, 2006). In addition, northern watersnakes may not need large areas of forest because they do not travel between wetlands as much as other wetland species, they are rarely found in upland habitats, and their use of larger wetlands ensures that they have access to some forest, given that larger wetlands in our study have more forest area within buffer zones of any size. Furthermore, other upland habitats, such as old field, or small forest patches may not be barriers to movement and may be adequate for northern watersnake terrestrial activities (Herbert, 2003; Roe et al., 2003). Habitat resistance to movement often differs among species, and upland characteristics have generally been found to have poor predictive power on the distribution and abundance of other common wetland species (Houlahan & Findlay, 2003; Dunford & Freemark, 2004, Herrmann et al., 2005).

Sedentary species, such as the northern watersnake, are generally less susceptible to road mortality than vagile species (Gibbs, 1998; Bonnet, Naulleau & Shine, 1999; Carr & Fahrig, 2001; Roe et al., 2006). Roads may not routinely serve as barriers or cause high mortality in northern watersnakes because they do not travel long distances. Their use of permanent wetlands may reduce the need to disperse to other wetlands, and most individuals occur <30 m from a wetland (Houlahan & Findlay, 2003; Roe et al., 2003, 2004). This is supported by models that predict a low annual road mortality of 3–5% in northern watersnakes because of their aquatic and sedentary lifestyle (Roe et al., 2006). Although abundance was not affected by wetland distance to roads, roads nevertheless could potentially affect population demographics especially given intraspecific differences in northern watersnake movement (Roe et al., 2003). For example, road density negatively altered the demographics but not abundance of two common wetland species, painted turtles Chrysemys picta and common snapping turtles Chelydra serpentina, with females being more susceptible to road mortality because of their aquatic and sedentary lifestyle (Roe et al., 2006). Male northern watersnakes could also be more susceptible to road mortality because of greater terrestrial movement in search of parturition sites, and they typically move more frequently among a larger set of wetlands than males (Herbert, 2003; Roe et al., 2003).

A benefit of studying common species is that they provide insight into why a species persists or remains common, despite landscape and wetland changes. Our results suggest why northern watersnakes are able to persist in regions that have been largely deforested and fragmented by roads and have had small wetlands replaced with larger, more permanent ones. Small wetlands are often enlarged, with new larger, permanent wetlands being created for human recreation such as fishing (Richter et al., 1997; Rubbo & Kiesecker, 2005). Common wetland species, such as northern watersnakes, are not negatively impacted from the creation of large, permanent wetlands, whereas rarer wetland species may experience declines by the loss of small and less

Figure 1 Relationship between wetland characteristics and abundance for northern watersnakes Nerodia sipedon sipedon. (a) Relationship between wetland size (ha) and abundance. (b) Relationship between wetland distance to nearest wetland (m) and abundance.

2003, 2004). Wetland proximity may also allow snakes to find new wetlands when environmental conditions have changed, such as the drying of a wetland as a result of drought (Seigel, Gibbons & Lynch, 1995). For example, Australian turtles that used permanent wetlands were more likely to migrate to another wetland during times of drought (Kennett et al., 1992). However, wetland size and connectivity only explained 37% of the variation ($r^2 = 0.37$), suggesting that other factors such as water quality, aquatic vegetation structure, prey abundance, predator pressure and surrounding land-use patterns not tested in our analysis may also influence abundance (Joly et al., 2001; Thomas et al., 2001; Fleshman et al., 2002; Dunford & Freemark, 2004; Franken & Hik, 2004).

Our results suggest that connectivity quality, as indicated by forest area and roads, does not impact abundance, in contrast to previous studies (Knutson et al., 1999; Carr & Fahrig, 2001; Moilanen & Hanski, 2001; Ricketts, 2001; Moilanen & Nieminen, 2002; Houlahan & Findley, 2003; Kramer-Schadt et al., 2004). This may be because when a wetland is beyond a certain threshold distance, northern
permanent wetlands (Semlitsch & Bodie, 1998; Adams, 1999; Joyal et al., 2001; Roe et al., 2004; Rubbo & Kiesecker, 2005). However, while northern watersnakes may be minimally impacted by many anthropogenic landscape modifications to both terrestrial and wetland habitats, our analysis indicates that availability of other nearby wetlands increases abundance. This finding demonstrates that the landscape is an important factor for northern watersnake populations and suggests that conservation should focus on wetland complexes as well as single wetlands.

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References


