# DISTRIBUTION OF AMPHIBIANS IN TERRESTRIAL HABITAT SURROUNDING WETLANDS

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Abstract: Estimating the distribution of amphibians in terrestrial habitats surrounding wetlands is essential for determining how much habitat is required to maintain viable amphibian populations and how much habitat may be allocated to other land use practices. We apply univariate kernel estimation in a new manner to determine the distribution of amphibians during the non-breeding season. We summarized data from 13 radio telemetry studies that reported net maximum distance traveled from the breeding site for each individual (n = 404 individuals), and calculated a univariate kernel density estimate for all data combined. Kernel density estimation provides a function for the probability of an amphibian being present at a given distance from the breeding site and bootstrap methods allow for error estimates of isopleth values. Amphibians generally occurred at a short distance from the wetland (50% isopleth was at 93 m) and declined at greater distances (95% isopleth was at 664 m); however, use of habitat immediately adjacent (e.g., < 30 m) to the breeding site was lower than the peak for all species. The shape of the distribution was consistent for frogs and salamanders; however, the 95% kernel isopleth for the salamander estimate (245 m) was less than half the distance of the frog estimate (703 m), indicating that frogs distributed themselves at much greater distances from the breeding site than salamanders. Kernel estimates for the two western species, Rana luteiventris and Bufo boreas, did not peak near the breeding site as in the other species, suggesting that non-breeding habitat for these species is not located near breeding sites. We were unable to detect a statistical difference between sexes, but females tend to use habitat at greater distances from the wetland than males. Our results revealed that amphibians are not uniformly distributed in terrestrial habitats surrounding wetlands.

Key Words: buffer zone, core habitat, habitat use, kernel density estimation, local population, utilization distribution

### INTRODUCTION

Wetlands are the integration of aquatic and terrestrial systems that vary across a hydrologic continuum (Euliss et al. 2004). Wetland biota are adapted to these hydrologic conditions and contribute to the ecological functioning of wetlands (Semlitsch 2006). For example, adult amphibians require both wetland breeding sites and habitat that extends 290 m into terrestrial ecosystems surrounding wetlands (Semlitsch 1998, Semlitsch and Bodie 2003), and thus large amounts of energy are transferred between wetland and terrestrial ecosystems as amphibians migrate between breeding and non-breeding habitats (Gibbons et al. 2006, Regester et al. 2006). Terrestrial habitat is thus a vital component of wetlands for local amphibian populations.

We currently have estimates of the extent of terrestrial habitat used (Semlitsch 1998, Semlitsch

and Bodies 2003); however, we lack error estimates around these values, we do not know where amphibians occur within this area, and we cannot estimate the probability of amphibians occurring at distances where individuals have not been observed. For example, amphibians may be uniformly spaced throughout the non-breeding habitat to reduce density-dependent effects or clumped near specific resources. Reliance on aquatic breeding habitat may cause individuals to clump close to breeding sites with the number of individuals declining at greater distances from the wetlands. At the other extreme, the majority of individuals may migrate away from breeding sites to reach a particular resource, such as an overwintering site or refugia with high food availability, and thus the distribution may be skewed towards the outer extent of the terrestrial habitat used by a local population. Determining the spatial location of individuals within terrestrial habitat and understanding why amphibians use these specific locations is central to predicting how habitat loss or modification may affect the persistence of these populations (Trenham and Shaffer 2005).

To estimate the distribution of amphibians, we apply univariate kernel density estimation, in a new manner that allows us to estimate the distribution of amphibians within terrestrial habitat surrounding wetlands. Kernel methods are nonparametric and do not require assumptions about underlying processes causing movement or space use. Bivariate kernel estimates have been used to describe the space use of individuals since the late 1980s (Worton 1987, 1989). Bivariate kernel density estimates are three-dimensional, composed of X and Y spatial coordinates and a third coordinate that corresponds to the estimated probability density function or utilization distribution. Bivariate kernel estimation is currently the preferred home range estimator in most situations (Seaman et al. 1999, Kernohan et al. 2001), but can produce biased estimates of space use when data are linear in nature (Blundell et al. 2001) and thus produces poor descriptions of amphibian habitat use from migration data.

Univariate kernel density estimates we present here are population-level estimates composed of one spatial coordinate and the probability density function that describes the distribution of individuals along a line. In this scenario, the origin of the line is placed at an amphibian breeding site and the line is oriented perpendicular to that wetland edge. Estimating amphibian use of habitats at distances in the tail of this distribution (i.e., at distances far from the wetland) is important for determining the amount of habitat required to sustain a local amphibian population. Although histograms have previously been used to describe the distribution of amphibians along this line during the non-breeding season (e.g., Regosin et al. 2005, Smith and Green 2005), histograms provide minimal information about distances at which individuals were not observed and these distances often occur in the tail of the distribution. Univariate kernel density estimation provides a more useful description of the distribution of amphibians because it allows for interpolation at distances where individuals were not observed and bootstrapping methods can produce error estimates for these calculations.

Our primary objective is to determine how amphibians distribute themselves in terrestrial habitat during the non-breeding season. We generate a composite distribution that includes multiple species using data sets available in the literature. In addition, we separate the data and generate taxon-, sex-, and species-specific estimates to test for differences between these groups.

#### METHODS

We collected data from 13 published radio telemetry or radioactive isotope tagging studies that were available to us when the analysis began in January 2006 (Table 1). Each study directly monitored at least 10 individuals as they emigrated from breeding sites and reported the maximum straightline distance from the wetland edge traveled by each individual during the study period (hereafter referred to as net distance). Annual migratory movements between breeding and non-breeding habitat are typically up to several hundred meters and thus at least an order of magnitude larger than movements within the breeding and non-breeding season. Migratory movements are also directed, linear, and occur over short-time spans (i.e., 24 hrs to a few weeks). We therefore used net distance as the unit of analysis and thus assumed that this distance represented the center of the non-breeding season home range of each individual (as in Semlitsch 1998, Semlitsch and Bodie 2003).

We calculated univariate kernel density estimates based on Gaussian density using the PROC KDE command within SAS (SAS version 9.1). We used the Sheather-Jones Plug In (SJPI) smoothing parameter (Jones et al. 1996, Vokoun 2003) applied equally across the grid (i.e., fixed kernel) to provide the most accurate estimates at the edges of the distribution, i.e., 50% and 95% isopleths (Seaman et al. 1999). The 99% isopleth value in all cases occurred at distances less than 1,000 m and thus we truncated figures at 1,000 m. We used SAS default settings of 401 grid points and a bandwidth multiplier of 1 when estimating the density functions (as in Vokoun 2003).

We combined data from all studies to reflect an aggregate distribution for all amphibians (n = 404)individuals) and calculated a composite kernel density estimate. The number of radio-tagged individuals varied among studies, and thus data sets with more individuals could influence the composite kernel estimate more than data sets with fewer individuals, causing one species to influence the composite estimate more than another species. We used a bootstrap approach to correct for sample size differences between studies and to produce error estimates around the isopleth values (e.g., 25%, 50%, 75%, 90%, and 95%), reported in distance from the wetland edge. We randomly selected (with replacement) 10 observations from each data set, resulting in an artificial data set with 130 total observations, and calculated a univariate kernel density estimate for the artificial data set. We repeated this procedure 1,000 times to generate

Species	n	m	f	Study Length	Mean	Min	Max	50% Isopleth	95% Isopleth
Ambystoma californiense	59			1 night	41	10	130	40	83
Ambystoma maculatum	27	21	6	17-451 days	69	0	213	85	160
Ambystoma maculatum	16	7	9	4–73 days	40	2	153	18	158
Ambystoma talpoideum	17	8	9	1 year	164	5	272	180	300
Ambystoma tigrinum	23	13	10	1–378 days	71	1	287	33	245
Triturus cristatus, T. marmoratus	29	13	16	5-31 days	32	2	146	25	145
Pseudacris triseriata	72			2-134 days	9	0	213	75	150
Bufo boreas	15	9	6	9–16 weeks	627	171	2324	515	970
Bufo boreas	18	10	8	7-17 weeks	625	43	2278	375	980
Bufo japonicus	25			7–24 days	87	25	275	93	175
Rana luteiventris	48	2	46	2–57 days	405	23	1025	498	708
Rana sylvatica	42	37	5	50 days	110	1	394	133	293
Rana sevosa	13	7	6	24-88 days	158	29	279	223	280
	Species Ambystoma californiense Ambystoma maculatum Ambystoma maculatum Ambystoma talpoideum Ambystoma tigrinum Triturus cristatus, T. marmoratus Pseudacris triseriata Bufo boreas Bufo boreas Bufo boreas Bufo japonicus Rana luteiventris Rana sylvatica Rana sevosa	SpeciesnAmbystoma californiense59Ambystoma maculatum27Ambystoma maculatum16Ambystoma talpoideum17Ambystoma tigrinum23Triturus cristatus, T.29marmoratus23Pseudacris triseriata72Bufo boreas15Bufo boreas18Bufo japonicus25Rana luteiventris48Rana sylvatica42Rana sevosa13	SpeciesnmAmbystoma californiense59Ambystoma maculatum2721Ambystoma maculatum167Ambystoma talpoideum178Ambystoma tigrinum2313Triturus cristatus, T.2913marmoratusPseudacris triseriata72Bufo boreas159Bufo boreas1810Bufo japonicus25Rana luteiventris482Rana sylvatica4237Rana sevosa137	SpeciesnmfAmbystoma californiense59Ambystoma maculatum27216Ambystoma maculatum1679Ambystoma talpoideum1789Ambystoma tigrinum231310Triturus cristatus, T.291316marmoratus7289Bufo boreas1596Bufo boreas18108Bufo japonicus2525Rana luteiventris48246Rana sylvatica42375Rana sevosa1376	SpeciesnmfLengthAmbystoma californiense591 nightAmbystoma maculatum2721617-451 daysAmbystoma maculatum16794-73 daysAmbystoma maculatum16794-73 daysAmbystoma talpoideum17891 yearAmbystoma tigrinum2313101-378 daysTriturus cristatus, T.2913165-31 daysmarmoratus722-134 days8ufo boreas15Pseudacris triseriata722-134 daysBufo boreas181087-17 weeksBufo boreas257-24 daysRana luteiventris482462-57 daysRana sylvatica4237550 daysRana sevosa137624-88 days	SpeciesnmfStudy LengthAmbystoma californiense591night41Ambystoma maculatum2721617–451days69Ambystoma maculatum16794–73days40Ambystoma talpoideum17891year164Ambystoma tigrinum2313101–378days71Triturus cristatus, T.2913165–31days32marmoratus722–134days9Bufo boreas15969–16weeks627Bufo boreas181087–17weeks625Bufo boreas257–24days87Rana luteiventris482462–57days110Rana sylvatica4237550days110Rana sevosa137624–88days158	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$

Table 1. Sources of data used to produce univariate kernel density estimates. We report the number of individuals (n) in each study separated by male (m) and female (f) when data were available; mean, minimum, and maximum net distance (m) traveled from the breeding site; and 50% and 95% isopleth values in distance (m) from the breeding site.

a bootstrapped distribution of the composite kernel density estimate. This approach simultaneously weighted each study equally and provided an empirical-bootstrap estimate of kernel-estimation uncertainty, including bandwidth-selection uncertainty. We then calculated the mean and variance for each isopleth value from the bootstrapped distribution, reported as distance from the breeding site edge.

We separated the data sets by those reporting distances for frogs (n = 233) and salamanders (n =171) and calculated univariate kernel density estimates for each taxon separately using the same bootstrapping approach described previously. We calculated univariate kernel density estimates for males (n = 117) and females (n = 113) when sex data were available, but we did not bootstrap these estimates due to small sample size when data was separated by study and sex (e.g., n = 2 males in Pilliod et al. 2002). We compared average net distance from each study for frogs and salamanders, and males and females using a Mann-Whitney test with a normal approximation for large sample sizes. Finally, we calculated univariate kernel density estimates for each data set separately, but low sample sizes may result in biased estimates. Accuracy of bivariate kernel density estimates is biased when sample sizes drop below 50 observations (Seaman et al. 1999, Kernohan et al. 2001). This bivariate guideline provides a conservative guideline for univariate analysis until further simulation work suggests otherwise.

## RESULTS

We found that 95% of amphibians occur within 664 m from the wetland edge and 50% of amphibians occur within 93 m (Figure 1). The composite distribution of amphibians within non-breeding season habitat was skewed towards the pond. The peak of the distribution occurred 30 m from the wetland, and the density estimate declined with increasing distance from the wetland (Figure 1). Error around the composite kernel density estimates, as determined by bootstrapping, increased as the isopleth value increased (Table 2). For example,



Figure 1. Composite univariate kernel density estimate calculated from 1,000 bootstrap samples drawn equally from all data sets. Distance is the net distance away from a wetland edge (edge = 0 m). Arrows represent the mean distances of the 50% (93 m) and 95% isopleths (664 m).

	Isopleth	Density	Distance	Variance	Max Distance
All Data Combined	95	0.00029	664	13972	14636
	90	0.00042	493	5079	5572
	75	0.00161	205	698	903
	50	0.00303	93	257	350
	25	0.00474	46	19	65
Frogs	95	0.00032	703	6458	7161
	90	0.00048	572	3158	3730
	75	0.00103	312	1072	1384
	50	0.00205	183	115	298
	25	0.00252	131	87	218
Salamanders	95	0.00094	245	979	1225
	90	0.00122	180	560	741
	75	0.00291	142	659	801
	50	0.00679	41	19	61
	25	0.00977	26	6	32

Table 2. Mean distance (m) from wetland edge and variance (m) from 1,000 bootstrap samples by all data sets together, frogs, and salamanders and reported by 25%, 50%, 75%, 90%, and 95% isopleth values. Max Distance is the mean distance plus the variance.

the 25% isopleth value was estimated at 46 m and the error estimate suggested that distance could be as large as 65 m; whereas, the 90% isopleth value was estimated at 493 m and the distance could be as large as 5,572 m.

The extent of the 50% and 95% isopleths varied among species (Table 1). The shape of the distribution was similar for 11 of the 13 data sets, with the distribution peak occurring from 20 m to 200 m and declining as distance from the wetland edge increased (Figure 2A–D). The shape of the kernel density estimate for *Rana luteiventris* and *Bufo boreas* did not follow the same general pattern (i.e., was not skewed towards the breeding site; Figure 2E–F).

The general shape of the distributions was similar for both frogs and salamanders. However, the extent of the distribution as determined by the 95%



Figure 2. Univariate kernel density estimates for selected data sets. The arrow with small dashes represents the distance of the 50% isopleth and the arrow with large dashes represents the distance of the 95% isopleth. Sample sizes and the distance value of each isopleth are reported in Table 1.



Figure 3. Univariate kernel density estimates calculated from 1,000 bootstrap samples for A) frogs and B) salamanders. Arrows represent the mean distance of 50% and 95% isopleths. For frogs, the 50% isopleth is at 183 m and the 95% isopleth is at 703 m. For salamanders, the 50% isopleth is at 41 m and the 95% isopleth is at 245 m.

isopleth value was significantly greater for frogs than salamanders (U<sub>208, 171</sub> = 8115, P < 0.001), indicating that frogs distributed themselves at greater distances from breeding sites than salamanders. The 50% isopleth was 183 m for frogs and 41 m for salamanders, and the 95% isopleth was 703 m for frogs and 245 m for salamanders (Figure 3). The shape and extent of distributions were similar for males and females and net distance did not differ (U<sub>10, 10</sub> = 48, P = 0.88); however, our results suggest females may occur at greater distances than males, and this trend has been reported in several species using a variety of techniques (Table 3). The 50% isopleth was 150 m for females and 82.5 m for males, and the 95% isopleth was 635 m for females and 497.5 m for males (Figure 4).

## DISCUSSION

The distribution of amphibians in terrestrial habitats surrounding wetlands is essential informa-

tion for determining how much habitat is required to maintain viable populations and how much habitat maybe allocated to other land use practices, such as agriculture or housing developments (Trenham and Shaffer 2005). Anthropogenic destruction and degradation of habitat continues to be the largest conservation threat to biodiversity and is the cause of many amphibian population declines (Stuart et al. 2004). We found that individuals do not distribute themselves uniformly throughout non-breeding habitat and that the terrestrial habitat used by 95% of the adult breeding population extends 664 m beyond the high water mark of wetland breeding sites. The peak in the distribution was skewed towards the wetland with 50% of adults spending the nonbreeding season within 93 m. Notably, the probability of an individual being present at distances near the wetland edge (e.g., < 30 m) was consistently lower than at intermediate distances. Drift-fence data have also led to the conclusion that adults do not remain immediately adjacent to wetlands during the non-breeding season (Regosin et al. 2005, Patrick et al. 2006).

In general, both frogs and salamanders distributed themselves during the non-breeding season so that most individuals traveled a moderate distance from breeding sites and the number of individuals decreased with increasing distance from the breeding site. This distribution suggests that amphibians use resources that are readily available near breeding sites. Further, these resources are likely dispersed evenly, so that as resources near the breeding site are used by conspecifics (i.e., carrying capacity is reached at that particular distance) individuals migrate slightly greater distances from the breeding site to reduce density-dependent effects (Fretwell and Lucas 1969, Regosin et al. 2003a). This resource use pattern fits well with our knowledge of resource use by some species, such as gray tree frogs that migrate to large oak trees (Johnson 2005) or spotted salamanders that migrate to small mammal burrows (Madison 1997). Although fairly similar in shape, the distributions of frogs and salamanders during the non-breeding season differed greatly in extent, with frogs using habitat at distances more than twice as far from breeding sites as salamanders. This taxa difference indicates that conservation efforts that provide an adequate amount of habitat for salamanders may be inadequate for frogs.

Females of some amphibian species have recently been reported to migrate greater distances than males (see literature summary in Table 3), and thus our lack of clear differences between males and females was unexpected. Amphibian density declined at greater distances from a breeding site, and

foraging sites.						
Species	u	Female (m)	Male (m)	Methods <sup>1</sup>	Test	Reference
Anura:						
Bufo boreas	17	$1105 \pm 272$	$581 \pm 98$	þ	t = 2.31, P = 0.041	Bartelt et al. 2004
Bufo boreas	14	$721 \pm 167$	$218 \pm 142$	þ	t = 2.29, P = 0.04	Muths 2003
Hyla versicolor	86	89	57	а	t = 1.99, P = 0.004	Johnson 2005
Rana luteiventris					$F_{1, 112} = 47.2, P < 0.001$	Pilliod et al. 2002
1995	38	$470 \pm 62$	$161 \pm 21$	а	×	
1996	39	$450\pm 65$	$196 \pm 38$	а		
1997	41	$430 \pm 44$	$123 \pm 34$	а		
Rana sylvatica	198	12.5% < 65  m	87.5% < 65  m		$\chi^2 = 13.7,  P < 0.001$	Regosin et al. 2003a
Caudata:						
Ambystoma maculatum	1121	51% > 100  m	43% > 100  m	С	$\chi^2 = 7.41, P = 0.006$	Windmiller 1996
Ambystoma maculatum	> 46	12.3% < 65  m	87.7% < 65  m	c	$\chi^2 = 14.3,  \mathrm{P} < 0.001$	Regosin et al. 2003b
A. jeffersonianum & maculatum	16	$211 \pm 55.9$	$86.8 \pm 15.2$	q	U = 32.00, P = 0.079	Faccio 2003
Triturus carnifex	51	168	53	þ	P = 0.006	Schabetsberger et al. 2004
a = mark-recapture, b = radio-telemetr	ry, c = marl	k-recapture and drift	t fences at varying di	stances.		



Figure 4. Univariate kernel density estimates for males (gray line) and for females (black line). Arrows (gray for males and black for females) represent the distance of the 50% and 95% isopleths. For males, the 50% isopleth is at 82.5 m and the 95% isopleth is at 497.5 m. For females, the 50% isopleth is at 150 m and the 95% isopleth is at 635 m.

thus competition for food resources may also decrease. Females may benefit from long migrations more than males because energy demands are high for egg production, mating benefits of arriving first at the breeding site are low, and migrations risks are lower than males if breeding migrations are not made annually. We may not have detected a difference between sexes because some studies primarily contained one sex or because females may continue to travel away from breeding sites after transmitters are removed while males may not. Alternatively, differences in migration distance between sexes may be species-specific; thus, by combining species, the sex-specific effect may have been lost in our analysis. Measuring differences in the use of non-breeding habitats between males and females is important for determining how core habitat affects local population persistence. If females distribute themselves at greater distances from breeding sites than males, our kernel density estimates may not reflect the added conservation importance of habitat located away from breeding sites. Habitat loss in the tail of the distributions that reduces adult female survival more than male survival may have a stronger influence on amphibian population dynamics (Biek et al. 2002, Halpern et al. 2005).

Kernel estimates for the two western species, *Rana luteiventris* and *Bufo boreas*, did not peak near the breeding site as in the other species. The shape of these distributions suggests that these two species travel to a specific resource that is not evenly distributed on the landscape and is not located near the breeding site. Specific resources have been identified for some species, such as Columbia spotted frogs that travel between palustrine breeding sites and lacustrine summer and wintering sites (Pilliod et al. 2002). Migration distances may thus reflect the distance between breeding and nonbreeding resources on the landscape, which likely occur at greater distances in the western U.S. than in eastern states. Similarly, some species of anurans (family: Ranidae) in the eastern U.S. and Canada also require specific non-breeding habitats, such as wood frog use of forested wetlands in Maine (Baldwin 2005) or green frogs using springs in New York (Lamoreaux and Madison 1999). Kernel density estimates for wood frogs and gopher frogs were slightly shifted away from the breeding site, but the tail of the distributions did not exceed 500 m, suggesting that required habitats occur within close proximity in the eastern U.S.

We estimated the distribution of amphibians with radio-telemetry data because net distance traveled is a continuous response variable and provides direct observation of movements for a reasonable sample of individuals between breeding sites and nonbreeding habitats. We acknowledge that radiotelemetry data may underestimate the true extent of the local populations because tracking does not occur for long time periods (e.g., an entire year) due to the limits of transmitter battery life (but see Semlitsch 1981). Reports of amphibians moving greater distances than those used in our analysis have been observed using techniques other than telemetry (e.g., Marsh et al. 1999, Lemckert 2004, Smith and Green 2005). We did not use these data because sample sizes were too low for kernel estimation, distinguishing between migrating and dispersing animals was difficult, and authors often assigned the breeding site of an individual based on known breeding sites in the area, not by direct observation of movements between breeding and non-breeding habitat. We therefore assumed that most large movements between breeding sites and non-breeding habitats are detected with short-term telemetry studies because amphibians are rarely observed moving large distances outside of breeding migrations (Semlitsch 1981).

Wetlands are encompassed when our linear distribution of amphibians in terrestrial habitat is applied in a circular manner surrounding wetland breeding sites. This application of our results assumes that terrestrial habitat surrounding wetlands is uniform. Estimates for both the direction and distance of non-breeding habitat used by amphibians are clearly important for effective management decisions (Dodd and Cade 1998) because adult migration to and from breeding sites can be non-random. For example, habitat on one side of the wetland may be of higher quality, and thus attract or sustain more individuals on that side of the wetland relative to the other (e.g., Schabetsberger et al. 2004, Rittenhouse and Semlitsch 2006). However, we think that the direction from breeding sites to high quality non-breeding habitat is likely unique to each wetland. Site-specific habitat information and a detailed understanding of speciesspecific habitat requirements are therefore required to produce estimates that include direction. Our application of univariate kernel density estimation provides a general estimate of amphibian density at various distances that can be applied to all wetlands in all directions when information regarding directional migration is unavailable.

Core amphibian habitat encompasses all aquatic and terrestrial habitats required for the completion of their complex life cycles (Semlitsch and Jensen 2001, Semlitsch and Bodie 2003). A few important components for defining core amphibian habitat are not included in our estimates and need further exploration. First, the location of juvenile amphibians is largely unknown and not included in our study. Juveniles may distribute at greater distances from wetland edges than adults (Trenham and Shaffer 2005) because competition with adults may be greatest near wetlands, juveniles do not expend energy on annual breeding migrations to wetlands, and some juveniles likely disperse to other local populations (Smith and Green 2005). Second, the area immediately adjacent to the wetland, although not heavily used in the non-breeding season, may be essential for recently metamorphosed juveniles or for adults during the breeding season. For example, amphibians with prolonged breeding seasons make short feeding forays into terrestrial habitats immediately adjacent to wetlands (Wells et al. 1995, Johnson 2005), and vegetation at the wetland edge is often used as calling sites for advertising males (Fellers 1979). Third, our analysis does not address species that shift breeding sites within or among years (Petranka and Holbrook 2006) or situations where net distance traveled by amphibians during migration is altered due to movement barriers in the landscape or disturbances (e.g., timber harvest or development) that fragment the terrestrial habitat (Montieth and Paton 2006). Furthermore, our kernel estimates do not explain how or why amphibians are using the terrestrial habitat. Amphibians in terrestrial habitat must successfully avoid predators especially around wetland edges (Wassersug and Sperry 1977), find summer refuges and overwintering sites that allow for thermoregulation and hydration (Rothermel and Semlitsch 2006), and obtain enough prey to allocate energy to reproduction the following year. Both the

amount of habitat used by local amphibian populations and the distribution of individuals within that habitat likely vary based on the spatial location of competitors, predators, prey, refuge sites, and potentially anthropogenic alterations to the landscape; therefore, predictions regarding how habitat use will change over time will require a better understanding of these mechanisms.

## Management Implications

We used amphibians to highlight the biological connection between wetlands and surrounding terrestrial ecosystems, and this biological connection likely occurs for other wetland species, such as turtles or dragonflies. Our amphibian example accentuates several points for management. First, the area immediately adjacent and within the buffer zone typical for managing wetland water quality (30 m, Castelle et al. 1994, Houlahan and Findlay 2004) is not regularly used by adult amphibians outside of breeding seasons and thus does not protect amphibians. Second, most adult amphibians use habitats at short to intermediate distances from breeding sites (30-200 m) during the non-breeding season. However, species that migrate to resources that are clumped throughout the landscape may be exceptions to this general pattern; thus, managers must consider species-specific habitat requirements and ensure successful movements between these resources. Finally, the distribution of individuals at different distances from wetland breeding sites is not uniform, and therefore reducing the zone of protection around a wetland by 50% does not translate into 50% of adult population being affected by the habitat loss. Habitat loss at moderate distances from wetlands will likely affect a large proportion of the adult population. Our estimates of the spatial distribution of individuals accomplished the first step towards predicting how habitat loss or modification will affect population viability. The next step is to estimate the amount and degree of habitat modification that can occur within this habitat without affecting the long-term persistence of amphibian populations (Trenham and Shaffer 2005). Habitat loss and modification threatens the persistence of wetland biodiversity (Stuart et al. 2004, Comer and Goodwin 2006) and will likely continue as long as the human population and economy grows (Trauger et al. 2003).

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