Review

Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles

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Abstract: *Terrestrial habitats surrounding wetlands are critical to the management of natural resources. Although the protection of water resources from human activities such as agriculture, silviculture, and urban development is obvious, it is also apparent that terrestrial areas surrounding wetlands are core habitats for many semiaquatic species that depend on mesic ecotones to complete their life cycle. For purposes of conservation and management, it is important to define core habitats used by local breeding populations surrounding wetlands. Our objective was to provide an estimate of the biologically relevant size of core habitats surrounding wetlands for amphibians and reptiles. We summarize data from the literature on the use of terrestrial habitats by amphibians and reptiles associated with wetlands (19 frog and 13 salamander species representing 1363 individuals; 5 snake and 28 turtle species representing more than 2245 individuals). Core terrestrial habitat ranged from 159 to 290 m for amphibians and from 127 to 289 m for reptiles from the edge of the aquatic site. Data from these studies also indicated the importance of terrestrial habitats for feeding, overwintering, and nesting, and, thus, the biological interdependence between aquatic and terrestrial habitats that is essential for the persistence of populations. The minimum and maximum values for core habitats, depending on the level of protection needed, can be used to set biologically meaningful buffers for wetland and riparian habitats. These results indicate that large areas of terrestrial habitat surrounding wetlands are critical for maintaining biodiversity.*

Criterios Biológicos para Zonas de Amortiguamiento Alrededor de Hábitats de Humedales y Riparios para Anfibios y Reptiles

Resumen: *Los hábitats terrestres que rodean humedales son críticos para el manejo de recursos naturales. Aunque la protección de recursos acuáticos contra actividades humanas como agricultura, silvicultura y desarrollo urbano es obvia, también es aparente que las áreas terrestres que rodean a humedales son hábitat núcleo para muchas especies semiacuáticas que dependen de los ecotonos mésicos para completar sus ciclos de vida. Para propósitos de conservación y manejo, es importante definir los hábitats núcleo utilizados por las poblaciones reproductivas locales alrededor de humedales. Nuestro objetivo fue proporcionar una estimación del tamaño biológicamente relevante de los hábitats núcleo alrededor de humedales para anfibios y reptiles. Resumimos datos de la literatura sobre el uso de hábitats terrestres por anfibios y reptiles asociados con humedales (19 especies de ranas y 13 de salamandras, representando a 1363 individuos; 5 especies de serpientes y 28 de tortugas representando a más de 2245 individuos). Los hábitats núcleo terrestres variaron de 159 a 290 m para anfibios y de 127 a 289 para reptiles desde el borde del sitio acuático. Datos de estos estudios también indicaron la importancia de los hábitats terrestres para alimentación, hibernación y anidación, y, por lo tanto, que la interdependencia biológica entre hábitats acuáticos y terrestres es esencial para la persistencia de poblaciones. Dependiendo del nivel de protección requerida, se pueden utilizar los valores mínimos y máximos de hábitats núcleo para definir amortiguamientos biológicamente significativos para hábitats de humedales y riparios. Estos resultados indican que extensas áreas de hábitats terrestres que rodean humedales son críticas para el mantenimiento de la biodiversidad.*

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Introduction

Terrestrial habitats surrounding wetlands are critical for the management of water and wildlife resources. It is well established that these terrestrial habitats are the sites of physical and chemical filtration processes that protect water resources (e.g., drinking water, fisheries) from siltation, chemical pollution, and increases in water temperature caused by human activities such as agriculture, silviculture, and urban development (e.g., Lowrance et al. 1984; Forsythe & Roelle 1990). It is generally acknowledged that terrestrial buffers or riparian strips 30–60 m wide will effectively protect water resources (e.g., Lee & Samuel 1976; Phillips 1989; Hartman & Scrivener 1990; Davies & Nelson 1994; Brosofske et al. 1997).

However, terrestrial habitats surrounding wetlands are important to more than just the protection of water resources. They are also essential to the conservation and management of semiaquatic species. In the last few years, a number of studies have documented the use of terrestrial habitats adjacent to wetlands by a broad range of taxa, including mammals, birds, reptiles, and amphibians (e.g., Rudolph & Dickson 1990; McComb et al. 1993; Darveau et al. 1995; Spackman & Hughes 1995; Hodges & Krementz 1996; Semlitsch 1998; Bodie 2001; Darveau et al. 2001). These studies have shown the close dependence of semiaquatic species, such as amphibians and reptiles, on terrestrial habitats for critical life-history functions. For example, amphibians, such as frogs and salamanders, breed and lay eggs in wetlands during short breeding seasons lasting only a few days or weeks and during the remainder of the year emigrate to terrestrial habitats to forage and overwinter (e.g., Madison 1997; Richter et al. 2001). Reptiles, such as turtles and snakes, often live and forage in aquatic habitats most of the year but emigrate to upland habitats to nest or overwinter (e.g., Gibbons et al. 1977; Semlitsch et al. 1988; Burke & Gibbons 1995; Bodie 2001).

The biological importance of these habitats in maintaining biodiversity is obvious, yet criteria by which to define habitats and regulations to protect them are ambiguous or lacking (Semlitsch & Bodie 1998; Semlitsch & Jensen 2001). More importantly, a serious gap is created in biodiversity protection when regulations or ordinances, especially those of local or state governments, have been set based on criteria to protect water resources alone, without considering habitats critical to wildlife species. Further, the aquatic and terrestrial habitats needed to carry out life-history functions are essential and are defined here as "core habitats." No summaries of habitat use by amphibians and reptiles exist to estimate the biologically relevant size of core habitats surrounding wetlands that are needed to protect biodiversity.

For conservation and management, it is important to define and distinguish core habitats used by local breeding populations surrounding wetlands. For example, adult frogs, salamanders, and turtles are generally philopatric to individual wetlands and migrate annually between aquatic and terrestrial habitats to forage, reproduce, and overwinter (e.g., Burke & Gibbons 1995; Semlitsch 1998). The amount of terrestrial habitats used during migrations to and from wetlands and for foraging defines the terrestrial core habitat of a population. This aggregation of breeding adults constitutes a local population centered on a single wetland or wetland complex. Local populations are connected by dispersal and are part of a larger metapopulation, which extends across the landscape (Pulliam 1988; Marsh & Trenham 2001).

Annual migrations centered on a single wetland or wetland complex are biologically different than dispersal to new breeding sites. It is thought that dispersal among populations is achieved primarily by juveniles for amphibians (e.g., Gill 1978; Breden 1987; Berven & Grudzien 1990) or by males for turtles (e.g., Morreale et al. 1984). Dispersal by juvenile amphibians tends to be unidirectional and longer in distance than the annual migratory movements of breeding adults (e.g., Breden 1987; Seburn et al. 1997). Thus, habitats adjacent to wetlands can serve as stopping points and corridors for dispersal to other nearby wetlands. Ultimately, conservation and management plans must consider both local and landscape dynamics (Semlitsch 2000), but core habitats for local populations need to be defined before issues of connectivity at the metapopulation level are considered.

Literature Review

We summarize data from the literature on the use of terrestrial habitats by amphibians and reptiles associated with wetlands. We define wetlands as both lentic (pond) and lotic (stream) habitats that are either permanent or temporary (Cowardin et al. 1979). Also, we use the term riparian in the broadest sense of encompassing the shore, bank, or edge of any wetland. We used data from studies that define habitat use mainly by the adult population and report a mean, mode, or range of distance of migrations from the outer edge of wetlands (Appendices 1 & 2). We used these values to calculate a grand mean for major taxa (Table 1). Rather than calculating a 95% confidence limit, which depends on knowing the distribution of migration distances, and because some studies did not report means, we calculated a mean minimum and maximum distance for amphibians and reptiles from the distance values reported for species in each study (Table 1). These minimum and maximum values likely encompass a large portion of populations and adequately represent the majority of species. We did not use observations of individuals of unknown origin, especially juveniles, found at some distance from a wet-

Table 1. Mean minimum and maximum core terrestrial habitat for amphibians and reptiles.*

Group	*Mean minimum (m)*	*Mean maximum (m)*
Frogs	205	368
Salamanders	117	218
Amphibians	159	290
Snakes	168	304
Turtles	123	287
Reptiles	127	289
Herpetofauna	142	289

**Values represent mean linear radii extending outward from the edge of aquatic habitats compiled from summary data in Appendices 1 and 2.*

land. Such anecdotal observations are relevant to maximum dispersal distances and the probability of recolonization and connectivity for species (Pulliam 1988) but are misleading for the calculation of core terrestrial habitat for the maintenance of local populations. The data we report reflect the size of terrestrial habitats that are biologically necessary for the conservation of amphibian and reptile diversity at individual wetlands. Further, we discuss the use of core habitat sizes in conjunction with a buffer zone and how land-use practices in the surrounding landscape matrix may modify the amount of habitat needed for adequate protection.

Amphibian Core Habitat

Amphibians constitute an important and diverse fauna associated with both isolated wetlands (e.g., Texas, 15 species [Wiest 1982]; Florida, 16 species [Dodd 1992]; South Carolina, 27 species [Semlitsch et al. 1996]; Tennessee, 19 species [Scott & Bufalino 1997]) and stream or river floodplains (e.g., Virginia, 21 species [Buhlmann et al. 1993]; California, 4 species [Panik & Barrett 1994]; Illinois, 14 species [Burbrink et al. 1998]). The studies we reviewed indicate that amphibians use a wide range of terrestrial habitats adjacent to wetlands and streams. Most of these habitats are related to foraging, refuge, or overwintering sites and typically consist of leaf litter, coarse woody debris, boulders, small mammal burrows, cracks in rocks, spring-seeps, and rocky pools. Data on emigration distances from wetlands were found for 19 species of frogs and 13 species of salamanders representing 1363 individuals (Appendix 1).

Patterns of variation in distances traveled appear related to life-history differences between major taxonomic groups. In general, the plethodontid stream salamanders (e.g., *Desmognathus fuscus, Eurycea bislineata, Eurycea longicauda*), although migratory at some stage of their life cycle, remain close to the edges of ponds and streams and seldom move more than 20–30 m from aquatic habitats. Alternatively, some species of frogs, toads, and newts are highly vagile and move 1000–1600 m (e.g., *Bufo bufo, Rana catesbeiana, Notophthalmus viridescens*). The majority of the remaining species use intermediate distances, where they emigrate to find suitable terrestrial habitats. The overall core terrestrial habitat for amphibians ranged from 159 to 290 m from the edge of the aquatic site (Table 1).

Reptile Core Habitat

We summarized data for five snake and 28 turtle species from 25 U.S. states and five countries (Appendix 2). We gathered migration distances from studies of known sample size (total $n = 2245$ individuals) and from those of unknown sample size. Relatively few studies have been conducted on terrestrial migrations of hydrophilic snakes. Snakes migrated into adjacent uplands for the purpose of aestivating, basking, hibernating, or nesting. Although most studies of terrestrial migrations by turtles have focused on nesting, turtles also migrated for the purposes of aestivating, feeding, and hibernating.

Similar to that of amphibians, variation in reptile migration distances appears related to taxon-specific differences in life-history patterns. Some colubrid snakes (e.g., *Nerodia* sp., *Opheodrys aestivus*), trionychid turtles (e.g., *Apalone* sp.), some emydid turtles (e.g., *Graptemys geographica*, *Sternotherus* sp.), and one chelydrid turtle (i.e., *Macroclemys temminckii*) rarely migrate >30 m from aquatic habitats. In contrast, one colubrid snake (i.e., *Coluber constrictor*), viperid snakes (e.g., *Crotalus horridus*, *Sistrurus catenatus*), many kinosternid turtles (e.g., *Kinosternum leucostomum*, *K. subrubrum*), and several emydid turtles (e.g., *Chrysemys picta*, *Clemmys* sp., *Emydoidea blandingi*, *Trachemys scripta*) routinely migrate >100 m. The length of time spent in the terrestrial habitat ranges from <1 hour (e.g., nesting *Chelydra serpentina*; Punzo 1975) to 88% of recorded activity (e.g., *Nerodia sipedon*; Tiebout & Cary 1987). Some migrations into terrestrial habitats occurred following significant rainfall or stream flooding when uplands were temporarily inundated with water (e.g., *Graptemys pseudogeographica* foraging in flooded forest; Bodie & Semlitsch 2000). The overall core terrestrial habitat for reptiles ranged from 127 to 289 m from the edge of the aquatic site (Table 1).

Protection and Management of Terrestrial Habitat

It is not surprising that the terrestrial ecology of semiaquatic species is often underappreciated or overlooked by managers and conservation planners. Some semiaquatic reptiles make only brief visits to terrestrial habitats when nesting, and hibernacula are rarely observed. Additionally, many pond-breeding amphibians are fossorial and are also rarely observed in terrestrial habitats. Surveys and studies of these animals are consequently concentrated within stream and wetland sites, where they are found seasonally, rather than in terrestrial habitats, where detection is extremely difficult but where much of their life history occurs. Aquatic habitats may not be used by semiaquatic species for extended periods of their lives, including between breeding seasons and during droughts. For example, a population of striped newts (*Notophthalmus perstriatus*) in northern Florida was relegated to predominantly terrestrial activity during a 5-year drought (Dodd 1993). Eastern mud turtles (*Kinosternon subrubrum*) in South Carolina often leave aquatic sites after mating in late spring and do not return until the following spring (Bennett et al. 1970). In both cases, the upland forest habitat had obvious importance as a reservoir for adults of these species until breeding and reproduction again occurred.

Although wetlands vary in many characteristics related to type, region, topography, climate, and land-use surrounding them, the data we compiled suggest that a single all-encompassing value for the size of core habitats can be used effectively. Maximum values generated from a taxon with the greatest need for terrestrial habitat—that is, the largest core area or home range (Table 1)—would likely encompass all other taxa and could be used more broadly. On public lands or reserve systems, where first priority is given to conserving biodiversity, this maximum value can facilitate management objectives. On private lands or areas, however, where sustainable land use is the priority, a stratified system of protection zones can minimize impacts on wildlife and support desired land uses. For example, for streams in managed forests in North America, it is recommended by deMaynadier and Hunter (1995) that criteria be adjusted for stream attributes such as width, intensity of logging, and slope adjacent to the stream. Further, the authors recommend a two-tiered approach in which the terrestrial habitat closest to the water is fully protected and a second, outer area provides limited protection (e.g., the forestry practice of light partial cutting and removal of no more than 25% of the basal area).

We propose that stratification should include three terrestrial zones adjacent to core aquatic and wetland habitats (Fig. 1): (1) a first terrestrial zone immediately adjacent to the aquatic habitat, which is restricted from use and designed to buffer the core aquatic habitat and protect water resources; (2) starting again from the wetland edge and overlapping with the first zone, a second terrestrial zone that encompasses the core terrestrial habitat defined by semiaquatic focal-group use (e.g., amphibians 159–290 m; Table 1); and (3) a third zone, outside the second zone, that serves to buffer the core terrestrial habitat from edge effects from surrounding land use (e.g., 50 m; Murcia 1995).

All things being equal, these zones of protection should extend outward from the edge of wetlands far enough to encompass all species populations. However, the habitats used by various species or at different life-history stages are probably not evenly distributed. To protect those habitats essential for species functions, we need to know more about species requirements at each

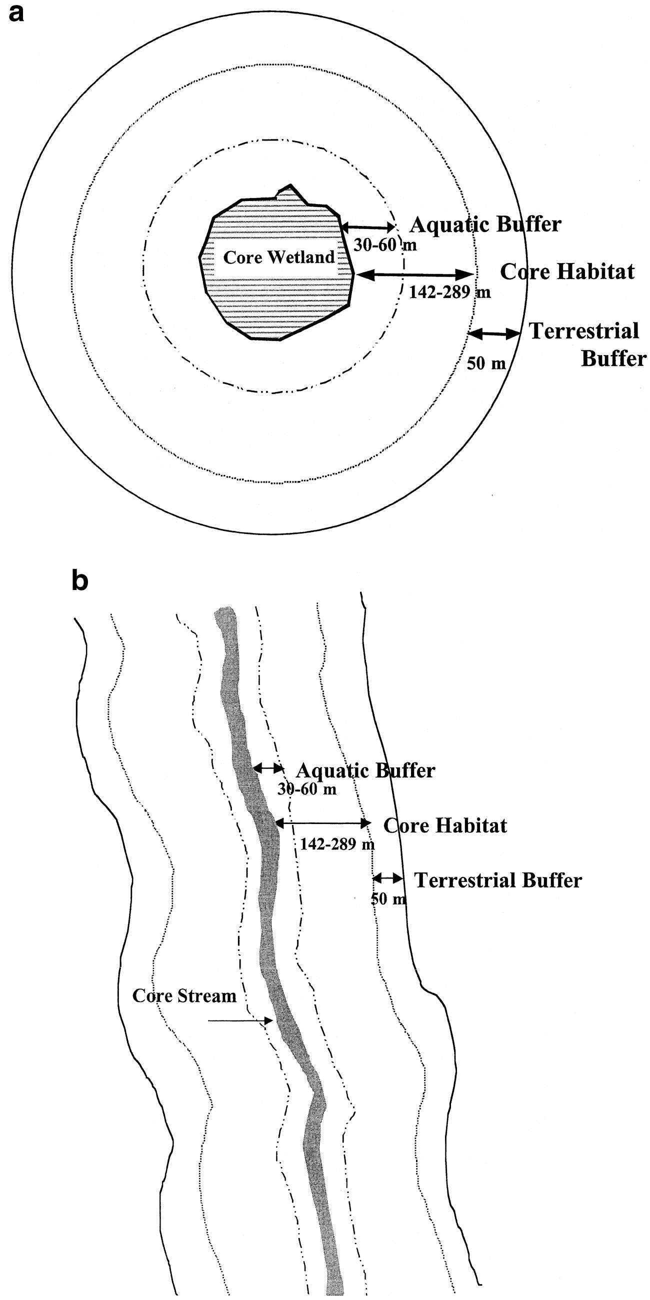

Figure 1. Proposed zones of protection of (a) wetlands and (b) streams. Both core habitat and aquatic buffer requirements are met within the second zone, which may range from 142 to 289 m for amphibians and reptiles (see Table 1 for taxon-specific values). An additional 50-m buffer is recommended to protect core habitat from edge effects (Murcia 1995).

life-history stage and season of the year. We know that special habitats are required by some species, such as the presence of highly aerated pools along small streams or caves for thermal refuges (e.g., overwintering sites for green frogs [*Rana clamitans*; Lamoureux & Madison 1999; Birchfield & Semlitsch unpublished data], yellow-legged frogs [*Rana muscosa*; Matthews & Pope 1999], and pickerel frogs [*Rana palustris*; R.D.S., personal observation]) and mammal burrows for thermal and predatory refuges (e.g., gopher frog [*Rana sevosa*; Richter et al. 2001]), and must be included within protective zones. Habitat generalists probably use whatever habitat is available, and land use such as silviculture may be compatible with maintaining their populations. Little is known, however, about habitat requirements for even common species such as the American toad (*Bufo americanus*), often used as an example of a generalist but which may not be a generalist during all life stages. Newly metamorphosed *B. americanus* exhibit strong selection for forest habitat in the summer in Missouri (Rothermel & Semlitsch 2002). Adjusting the size of terrestrial zones, such as the core habitat, could be done on the basis of protecting different portions of the population (e.g., for turtles 50–90% [Burke & Gibbons 1995]; for ambystomatid salamanders 50–95% [Semlitsch 1998]). It is not known, however, how protecting different amounts of terrestrial habitat affects the population persistence of any species or how habitat quality (e.g., density of mammal burrows; Loredo et al. 1996) might influence that decision.

Decisions about how restrictive each zone might be to land-use practices would depend on management goals and species of concern. Although little data are available on how various amphibians and reptiles might respond to major land-use practices (e.g., logging, farming, residential development), it is reasonable to assume that some activities (e.g., hiking, bicycling), especially those not destroying essential habitats (e.g., for amphibians, vegetation canopy for shade, coarse woody debris and a litter layer used for refuge and food sources), could be conducted in this outer zone of protection and be compatible with the goal of protecting biodiversity. In applying these criteria and bolstering the biological values of core terrestrial habitats, policymakers could develop stratified habitat zones that guide associated protection or management intensity, resulting in more effective conservation of biodiversity along with sustainable land use.

Conclusions

We provide biologically based estimates for the protection of terrestrial habitats surrounding wetlands. Our data clearly indicate that buffers of 15–30 m, used to protect wetland species in many states, are inadequate for amphibians and reptiles. Further, we emphasize that our estimates are derived from the core terrestrial habitats used by amphibians and reptiles and therefore are not buffers per se but necessary habitat. Additional area of terrestrial habitat is needed to fully protect core habitats and minimize edge effects (Fig. 1). For maximum protection, this may be more land than managers can provide, although we do not believe that our estimates are excessive biologically. And we are not naïve enough to believe that all terrestrial land-use activities around wetlands must be excluded. It is our intent, however, to ensure that managers and conservation biologists recognize that both aquatic and terrestrial habitats are essential for maintaining biodiversity and that they must be managed as an integral unit to protect biodiversity. Further, we want managers to know that little is known about the effects of land-use practices on amphibians and reptiles and that without further research it cannot be known whether any such practices used within the core habitat are potentially harmful to their long-term persistence. We hope this discussion generates more research on the effects of land-use practices on plants and animals and that biologists begin testing the effectiveness of various criteria for protecting the core habitats of species. A sustainable balance between continuing economic development and protecting natural resources depends on knowing and responding to species' biological requirements and knowing how tradeoffs affect the maintenance of biodiversity.

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Appendix 1. **Summary of terrestrial migration distances from aquatic breeding sites for amphibians.**

Species and location	Distance in m (sample size)	*Data source*
Frogs		
Acris crepitans, Illinois	range 8–22 (189)	O'Neil 2001[a]
Bufo americanus, Ontario	range 23–480 (176)	Oldham 1966[a]
Bufo boreas, Colorado	mode = 900	Campbell 1970[b]
Wyoming	maximum = 101	Carpenter 1954[a]
Bufo bufo, Germany	mode 70–760, maximum = 1600	Sinsch 1988[a]
Bufo hemiophrys, Minnesota	range 23–35 (6)	Breckenridge & Tester 1961[b]
Bufo japonicus formosus, Japan	mean = 98.5, range 27–260 (19)	Kusano et al. 1995[c]
Bufo marinus, New Guinea	mean = 150	Zug & Zug 1979[a]
Bufo valliceps, Texas	range 31–72	Blair 1953[a]
Hyla andersoni, New Jersey	mean = 70, maximum = 106 (8)	Freda & Gonzalez 1986[b]
Hyla regilla, Oregon	mode = 92, maximum = 240	Jameson 1956[a]
Pseudacris ornata, Florida	maximum = 55	Ashton & Ashton 1977[b]
Pseudacris triseriata, Indiana	mean = 75, maximum = 213 (9)	Kramer 1973[b]
Rana capito, Florida	range 280–480	Greenberg 2001[a]
Rana catesbeiana, New York	mean = 406, mode = 1046 (22)	Ingram & Raney 1943[a]
Rana clamitans, Ontario	mean = 137, maximum 457	Oldham 1967[a]
New York	mean = 121, maximum = 360	Lamoureux & Madison 1999[c]
Missouri	mean = 485, range 321–570 (6)	Birchfield & Semlitsch 2002[c]
Rana muscosa, California	range 66–142 (81)	Matthews & Pope 1999[a]
Rana pretiosa, Montana	range 41–443	Hollenbeck 1976[a]
Wyoming	maximum = 46	Carpenter 1954[a]
Wyoming	range 369–462	Turner 1960[a]
Rana sevosa , Mississippi	mean = 173, range 49–299 (12)	Richter et al. 2001[c]
Syrrhophus marnocki, Texas	mean = 213, range 114–303	Jameson 1955[a]
Salamanders		
Ambystoma californiense, California	mean = 36, range 8–129 (59)	Loredo et al. 1996[a]
California	mean = 114, maximum = 248 (11)	Trenham 2001[c]
Ambystoma jeffersonianum, Michigan	mean = 39, range 22–108 (6)	Wacasey 1961[a]
Michigan	mean = 92, range 15–231 (45)	Wacasey 1961[d]
Indiana	mean = 252, range 20–625 (86)	Williams 1973[b]
Kentucky	mean = 250 (10)	Douglas & Monroe 1981[b]
Ambystoma maculatum, Michigan	mean = 67, range 26–108 (2)	Wacasey 1961[a]
Michigan	mean = 103, range 15–200 (14)	Wacasey 1961[d]
Indiana	mean = 64, range 0–125 (7)	Williams 1973[b]
Kentucky	mean = 150, range 6–220 (8)	Douglas & Monroe 1981[b]
Michigan	mean = 192, range 157–249 (6)	Kleeberger & Werner 1983[b]
New York	mean = 118, range 15–210 (8)	Madison 1997[c]
Ambystoma opacum, Indiana	mean = 194, range 0–450 (12)	Williams 1973[b]
Kentucky	mean = 30 (6)	Douglas & Monroe 1981[b]
Ambystoma talpoideum, South Carolina	mean = 178, range 13–287 (17)	Semlitsch 1981[b]
Ambystoma texanum, Indiana	mean = 52, range 0–125 (10)	Williams 1973[b]
Ambystoma tigrinum, South Carolina	162 (1)	Semlitsch 1983[b]
South Carolina	mean = 215, range 112–450 (4)	Semlitsch et al., unpublished data[c]
New York	mean = 60, range 0–286 (27)	Madison & Farrand 1998[c]
Desmognathus fuscus, Kentucky	maximum = 17 (14)	Barbour et al. 1969[b]
Ohio	maximum = 20 (16)	Ashton 1975[b]
Eurycea bislineata, Ohio	maximum = 31 (20)	Ashton & Ashton 1978[b]
Eurycea longicauda, New Jersey	mode = 6, maximum = 31	Anderson & Martino 1966[a]
Hynobius nebulosus tokyoensis, Japan	maximum = 100 (48)	Kusano & Miyashita 1984[a]
Notophthalmus viridescens, Massachusetts	mode = 800 (383)	Healy 1975[a]
Taricha torosa granulosa, Oregon	mode = 185	Pimentel 1960[a]

[a] *Uniquely marked individuals.*
[b] *Radioactive tags.*
[c] *Radiotransmitters.*
[d] *Unmarked individuals.*

Appendix 2. **Summary of terrestrial migration distances from aquatic sites for reptiles.**

Species and location	*Distance in m (sample size)*	*Data source*
Snakes		
Crotalus horridus, New Jersey	maximum = 700 (15)	Reinert & Zappalorti 1988[a]
Nerodia harteri, Texas	mean = 2.1, range 0–15 (8)	Whiting et al. 1997[a]
Nerodia sipedon, Wisconsin	maximum = 6 (10)	Tiebout & Cary 1987[a]
Opheodrys aestivus, Arkansas	mode = 3, range 0–5 (31)	Plummer 1981[b]
Sistrurus catenatus, Pennsylvania	mode = 200 (25)	Reinert & Kodrich 1982[a]
Turtles		
Apalone ferox, Florida	22.9 (1)	Goff & Goff 1935[c]
Apalone mutica, Iowa	range 3–18	Muller 1921[c]
Iowa	range 2–8	Goldsmith 1945[c]
Kansas	mean = 38.2, range 4–90 (104)	Fitch & Plummer 1975[c]
Apalone spinifera, Arkansas	mean = 2.5, range 2–3 (4)	Plummer et al. 1997[b]
Indiana	mode = 2	Newman 1906[c]
Minnesota	0.3 (1)	Hedrick & Holmes 1956[c]
Nebraska	4.5 (1)	Gehlbach & Collette 1959[c]
Chelydra serpentina, Florida	mean = 93.7, range 38–141 (7)	Punzo 1975[c]
Michigan	mean = 37.2, range 1–183 (210)	Congdon et al. 1987[b]
Nebraska	mode = 25, maximum =100	Iverson et al. 1997[b,c]
New York	mean = 27.4, range 1–89	Petokas & Alexander 1980[b]
Chrysemys picta, Idaho	mode = 200, maximum = 600	Lindeman 1992[b]
Michigan	mean = 60.4, range 1–164 (185)	Congdon & Gatten 1989[b]
Quebec, Canada	mean = 90.4, range 1–621 (51)	Christens & Bider 1986[a,b]
Clemmys guttata, Connecticut	range = 3–265 (9)	Perillo 1997[a]
Michigan	maximum = 150	Harding & Bloomer 1979[b]
Pennsylvania	range 60–250 (207)	Ernst 1976[b]
Clemmys insculpta, Canada	mean = 27, range 0–500 (10)	Foscarini & Brooks 1993[b]
Pennsylvania	mode = 300, maximum = 600 (50)	Kaufmann 1992[a,b]
New Hampshire	mean = 60.3 (9)	Tuttle & Carroll 1997[a]
New York	maximum = 200 (189)	Carroll & Ehrenfeld 1978[b]
Clemmys marmorata, California	mean = 168, range 39–423 (19)	Reese 1996[a]
Deirochelys reticularia, Texas	30 (1)	David 1975[c]
Virginia	mean = 95, range 32–192 (4)	Buhlmann 1995[a]
Emydoidea blandingi, Illinois	mean = 815, range 650–900 (3)	Rowe & Moll 1991[a]
Michigan	mean = 135, range 2–1115 (105)	Congdon et al. 1983[b]
Wisconsin	mean = 168 (16)	Ross & Anderson 1990[a,b]
Graptemys barbouri, Florida	200 (1)	Ewert & Jackson 1994[c]
Graptemys ernsti, Alabama	range 3–15	Shealy 1976[b]
Graptemys flavimaculata, Mississippi	mode = 100 (20)	Jones 1996[a]
Graptemys geographica, Quebec, Canada	mean = 2.3, range 2–3 (3)	Gordon & MacCulloch 1980[b]
Graptemys oculifera, Mississippi	range 7–17	Jones 1991[c]
Graptemys pseudogeographica, Missouri	mean = 353, range 0–1133 (15)	Bodie & Semlitsch 2000[a]
Kinosternon baurii, Florida	mean = 15.6, range 1–49 (23)	Wygoda 1979[b]
Kinosternon flavescens, Iowa	range 100–450	Christiansen et al. 1985[a]
Nebraska	range 21–191 (33)	Iverson 1990[a]
Kinosternon leucostomum, Mexico	mean = 275, range 0–600 (14)	Morales-Verdeja & Vogt 1997[a]
Kinosternon subrubrum, South Carolina	mean = 103.4, range 1–600 (20)	Bennett et al. 1970[d]
South Carolina	mean = 200, range 100–300 (2)	Bennett 1972[d]
South Carolina	mean = 49.3, range 17–90 (25)	Burke et al. 1994[a]
South Carolina	mean = 61.6, range 18–135 (115)	Burke 1995[a]
Macroclemys temminicki, Florida	mean = 12.2, range 3–22 (12)	Ewert 1976[c]
Florida	maximum = 200 (106)	Ewert & Jackson 1994[c]
Malaclemys terrapin, New Jersey	mode = 150 (40)	Burger & Montevecchi 1975[c]
Podocnemis unifilis, Venezuela	mean = 38.3, range 21–80 (422)	Escalona & Fa 1998[c]
Pseudemys floridana, South Carolina	mean = 106.7, range 62–286 (19)	Burke 1995[a]
Pseudemys rubriventris, Massachusetts	range 10-250	Ernst et al. 1994[b]
Sternotherus depressus, Alabama	6.5 (1)	Dodd 1988[c]
Sternotherus odoratus, Pennsylvania	mean = 6.6, range 3–11 (27)	Ernst 1986[c]
Trachemys scripta, Florida	mode = 180	Carr 1952[c]
Louisiana	maximum = 1600	Cagle 1950[c]
Missouri	mean = 348, range 0–1394 (11)	Bodie & Semlitsch 2000[a]
Panama	mean = 50, range 2–320 (139)	Moll & Legler 1971[b]
South Carolina	mean = 86.5, range 23–299 (11)	Burke 1995[a]

[a] *Radiotransmitters.*
[b] *Uniquely marked individuals.*
[c] *Unmarked individuals.*
[d] *Radioactive tags.*