Biological Conservation 150 (2012) 121–128

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Terrestrial habitat requirements of nesting freshwater turtles

D.A. Steen[a,b,*], J.P. Gibbs[c], K.A. Buhlmann[d], J.L. Carr[e], B.W. Compton[f], J.D. Congdon[d], J.S. Doody[g], J.C. Godwin[h], K.L. Holcomb[i], D.R. Jackson[j], F.J. Janzen[k], G. Johnson[l], M.T. Jones[m], J.T. Lamer[n], T.A. Langen[o], M.V. Plummer[p], J.W. Rowe[q], R.A. Saumure[r], J.K. Tucker[s], D.S. Wilson[t]

[a] *Joseph W. Jones Ecological Research Center, Newton, GA 39870, USA*
[b] *Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA*
[c] *Department of Forest and Environmental Biology, SUNY-ESF, Syracuse, NY 13210, USA*
[d] *Savannah River Ecology Laboratory, University of Georgia, Aiken, SC 29802, USA*
[e] *Department of Biology and Museum of Natural History, University of Louisiana at Monroe, Monroe, LA 71209, USA*
[f] *Department of Environmental Conservation, Holdsworth Natural Resources Center, University of Massachusetts, Amherst, MA, USA*
[g] *School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia*
[h] *Alabama Natural Heritage Program, Environmental Institute, Auburn University, AL 36849, USA*
[i] *Central Washington University, Ellensburg, WA 98926, USA*
[j] *Florida Natural Areas Inventory, Florida State University, Tallahassee, FL 32303, USA*
[k] *Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA*
[l] *Department of Biology, SUNY College at Potsdam, Potsdam, NY 13676, USA*
[m] *Department of Environmental Conservation, University of Massachusetts, Amherst, MA 01003, USA*
[n] *Department of Biological Sciences, Western Illinois University, Macomb, IL 61455, USA*
[o] *Department of Biology, Clarkson University, Potsdam, NY 13699-5805, USA*
[p] *Department of Biology, Harding University, Searcy, AR 72149, USA*
[q] *Biology Department, Alma College, Alma, MI 48801, USA*
[r] *Environmental Resources Division, Southern Nevada Water Authority, Las Vegas, NV 89106, USA*
[s] *Great Rivers Field Station, Illinois Natural History Survey, Brighton, IL, USA*
[t] *Southwestern Research Station, Portal, AZ 85632, USA*

ARTICLE INFO

Article history:
Received 1 December 2011
Received in revised form 28 February 2012
Accepted 11 March 2012

Keywords:
Buffer
Land use planning
Landscape
Nest
Migration
Reptile

ABSTRACT

Because particular life history traits affect species vulnerability to development pressures, cross-species summaries of life history traits are useful for generating management guidelines. Conservation of aquatic turtles, many members of which are regionally or globally imperiled, requires knowing the extent of upland habitat used for nesting. Therefore, we compiled distances that nests and gravid females had been observed from wetlands. Based on records of > 8000 nests and gravid female records compiled for 31 species in the United States and Canada, the distances that encompass 95% of nests vary dramatically among genera and populations, from just 8 m for *Malaclemys* to nearly 1400 m for *Trachemys*. Widths of core areas to encompass varying fractions of nesting populations (based on mean maxima across all genera) were estimated as: 50% coverage = 93 m, 75% = 154 m, 90% = 198 m, 95% = 232 m, 100% = 942 m. Approximately 6–98 m is required to encompass each consecutive 10% segment of a nesting population up to 90% coverage; thereafter, ca. 424 m is required to encompass the remaining 10%. Many genera require modest terrestrial areas (<200 m zones) for 95% nest coverage (*Actinemys*, *Apalone*, *Chelydra*, *Chrysemys*, *Clemmys*, *Glyptemys*, *Graptemys*, *Macrochelys*, *Malaclemys*, *Pseudemys*, *Sternotherus*), whereas other genera require larger zones (*Deirochelys*, *Emydoidea*, *Kinosternon*, *Trachemys*). Our results represent planning targets for conserving sufficient areas of uplands around wetlands to ensure protection of turtle nesting sites, migrating adult female turtles, and dispersing turtle hatchlings.

1. Introduction

A key factor in conserving biodiversity is the appropriate design of protected areas (Noss, 1983; Simberloff and Abele, 1982); however, determining the size and configuration of these areas requires integrating many threads of essential information (Rondinini and Chiozza, 2010; Wu and Hobbs, 2002). Organisms with biphasic natural histories complicate protected area delineation because they require both aquatic and terrestrial habitats. Specifically, core habitats of semi-aquatic species, including many amphibians (Semlitsch, 1998; Pope et al., 2000; Porej et al., 2004), snakes (Roe et al., 2003), turtles (Burke and Gibbons, 1995), mammals

---

[*] Corresponding author at: Joseph W. Jones Ecological Research Center, Newton, GA 39870, USA. Tel.: +1 229 734 4706; fax: +1 229 734 4707.
E-mail address: davidasteen@gmail.com (D.A. Steen).

0006-3207/$ - see front matter
http://dx.doi.org/10.1016/j.biocon.2012.03.012

(Kruchek, 2004), birds (Naugle et al., 1999), and insects (Bried and Ervin, 2006), encompass terrestrial uplands that are critical for conservation measures aimed at maintaining biodiversity (Semlitsch and Jensen, 2001).

Terrestrial zones around wetlands are important for protecting wetland fauna during all life stages (Bodie, 2001; Semlitsch, 1998; Semlitsch and Bodie, 2003). Such areas are often termed "core areas" (rather than buffer zones, Crawford and Semlitsch, 2007; Semlitsch and Jensen, 2001). By designating these areas as core, the critical importance of adjacent terrestrial areas to a wetland fauna is more accurately represented (Gibbons, 2003). Many taxa are of conservation concern because certain aspects of their life history bring them into conflict with land development. For example, many wetland-associated organisms, such as aquatic turtles, require upland habitats for reproduction because female turtles undergo terrestrial nesting migrations. Consequently, aquatic turtles represent a taxonomic group where a certain life stage (i.e., reproductively active females on terrestrial nesting migrations) is at disproportionate risk of mortality (Steen et al., 2006) and would benefit from terrestrial habitat protections.

Freshwater turtle populations and assemblages overall are influenced by anthropogenic change on the landscape level (e.g., Rizkalla and Swihart, 2006; Sterrett et al., 2011). In addition, adults of some species are at elevated risk of death due to predation, desiccation and overheating, harvest by humans, and road-kill during overland movements undertaken to move to more favorable foraging sites, escape unfavorable environmental conditions, migrate to or from hibernacula, or to locate mates (Gibbons, 1986; Buhlmann and Gibbons, 2001). However, of mortality incurred on land, that of females during nesting migrations may be the most significant threat to freshwater turtle population persistence (Gibbs and Shriver, 2002; Steen et al., 2006).

Turtle demography is characterized by relatively high nest and hatchling mortality, delayed sexual maturity, and high adult survivorship (Congdon et al., 1993, 1994), rendering populations at risk of decline when there is a loss of sexually mature individuals (Brooks et al., 1991; Gibbs and Shriver, 2002; Heppell, 1998). Thus, a synopsis of distances traveled overland by nesting females could generate useful targets for conservation planning. Although general reviews should not replace site-specific studies, they may provide guidance for regulators generating biologically appropriate wetland protection ordinances (McElfish et al., 2008).

Our objective was to synthesize the relevant published literature and to collate unpublished data on overland nesting migration distances to create a comprehensive dataset on the distances that nesting turtles move from water while demonstrating how land use policy can be informed by habitat use data from critical population segments. Here we summarize > 8000 nesting events reported from the United States and Canada to estimate (1) the spatial extent of nest sites surrounding wetlands, and (2) identify gaps in our knowledge regarding the distances of overland nesting migration by turtles. Our study provides defensible planning targets for land managers to conserve sufficient areas of uplands around wetlands to protect turtle nesting sites. Regulating development within these areas will simultaneously protect nesting females, nest sites, and hatchlings dispersing to nearby wetlands.

2. Methods

We compiled data from various sources on the distances of turtle nests from water, geographically restricting the study to the United States and Canada. First, we surveyed the published literature by searching ecological databases (Wildlife Worldwide, Science Direct) using relevant keywords (i.e., "turtle" and "nest") to locate reports of measured distances to nearest water for a turtle nest or gravid female. If appropriate data were not included within a particular article, we contacted the corresponding author for relevant additional information or clarification. We also posted a request for data on several herpetological e-mail lists (administered by Partners in Amphibian and Reptile Conservation, HerpDigest and the Center for North American Herpetology) and forwarded this request directly to known active turtle researchers and field biologists.

We determined the cumulative probability that turtles nested at a given distance from wetlands based on percentiles of nesting distances sorted from least to greatest at the generic level. For turtles in general, we calculated typical distances from wetlands corresponding to percentiles of nesting population included by calculating the median distance away from a wetland across genera for a given percentile.

Turtles of some genera seldom leave the water other than when females undergo nesting migrations; for our purpose, we categorized these genera as fully aquatic. For turtles of other genera, both sexes regularly undertake terrestrial movements independently of nesting; these genera were categorized as semi-aquatic. On this basis, we estimated average movement distances for a given percentile across genera for nesting female semi-aquatic turtles (*Actinemys*, *Clemmys*, *Deirochelys*, *Emydoidea*, *Glyptemys*, and *Kinosternon*) versus fully aquatic (all others). Different species within a genus may have different natural histories (e.g., *Pseudemys* includes both lentic and lotic species, and some species have a greater tendency to travel overland); thus, we are making generalizations by pooling data within genera. Because body size may affect the spatial extent of migrations, and therefore, resulting risk (Gibbs and Shriver, 2002), we also estimated average movement distances for a given percentile across genera based on size of sexually mature females; specifically, we compared large-bodied turtles (*Apalone*, *Chelydra*, *Macrochelys*, and *Pseudemys*) versus small-bodied (all others). Last, we examined costs of protecting sequential segments of a given nesting population (increasing from 0% to 100% in 10% segments) by calculating the zone width associated with protecting each additional nesting population segment.

3. Results

We obtained data for 7550 individual nests and 466 females on nesting migrations (this number includes 43 *Trachemys scripta* known to be returning from a nest) of 31 species from across the United States and Canada (Tables 1 and 2). Individual-level data were not always available; thus, we report mean distance to nearest wetland for an additional 2643 nests of 16 species (including four species for which we were unable to obtain individual level data; Table 3, Appendix A). Nesting distances varied considerably among genera with distance to include 50% of observations being <10 m for *Malaclemys*, *Sternotherus*, and *Macrochelys*; 17–34 m for *Clemmys*, *Apalone*, *Graptemys*, *Chelydra*, *Glyptemys*, *Actinemys*, and *Chrysemys*; 60 m for *Pseudemys*; 100–120 m for *Emydoidea*, *Kinosternon*, and *Deirochelys*; and 816 m for *Trachemys*. Distance to incorporate 95% of observations was <100 m for *Malaclemys*, *Sternotherus*, and *Macrochelys*; 100–200 m for *Actinemys*, *Chelydra*, *Apalone*, *Clemmys*, *Pseudemys*, *Chrysemys*, *Graptemys*, and *Glyptemys*; 200–300 m for *Kinosternon* and *Deirochelys*; 408 m for *Emydoidea*; and 1396 m for *Trachemys* (Table 4). Four of the five species requiring the greatest distances to encompass 95% of nests were characterized as semi-aquatic (Table 4). Zone widths to encompass varying fractions of nesting populations across all species (based on mean values across genera) were estimated as: 50% included = 93 m, 75% = 154 m, 90% = 198 m, 95% = 232 m, and 100% = 942 m. Costs in terms of additional increment in zone width needed to include sequential segments of nesting popula-

Table 1
Mean distance to nearest water and associated statistics for United States and Canada turtle nests based on individual records. Means are reported for locations (e.g., state or province) when ⩾ ten nests from a particular species were found. If less than ten nests were found but they were all from a single state or province, we indicate their location. Relevant citations are provided in Appendix A.

Species	Location	Mean	Standard deviation	Standard error	Median	Minimum	Maximum	*N*
Actinemys marmorata								
	California	38.9	38.4	9.1	31.5	6.0	170.0	18
	Overall	44.9	38.7	7.9	32.0	6.0	170.0	24
Apalone ferox								
	Florida	261.3	106.8	43.6	278.0	56.0	345.0	6
Apalone mutica								
	Arkansas	17.9	8.7	0.6	20.0	10.0	40.0	205
	Kansas	72.2	29.5	2.9	70.0	3.0	140.0	105
	Louisiana	13.4	11.2	1.8	8.8	2.2	46.1	38
	Texas	32.9	17.6	5.3	38.1	5.1	55.0	11
	Overall	33.7	30.7	1.6	20.0	2.2	140.0	359
Apalone spinifera								
	Louisiana	5.5	4.1	1.3	3.6	2.3	14.5	10
	Overall	37.9	101.2	18.8	3.4	0.3	424.3	29
Apalone sp.								
	South Dakota	61.3	49.5	7.7	45.4	10.1	175.1	41
Chelydra serpentina								
	Illinois	49.2	30.9	4.1	48.6	0.9	124.7	56
	Michigan	34.6	31.6	1.5	31.0	1.0	230.0	465
	Nebraska	24.2	20.6	3.1	25.0	1.0	81.0	43
	New York	20.2	26.8	2.2	9.9	0.0	142.0	154
	Ontario	51.8	109.9	6.6	23.5	0.3	982.0	280
	Overall	39.0	65.4	2.0	25.0	0.0	982.0	1024
Chrysemys picta								
	Idaho	5.5	1.6	0.4	6.0	3.0	7.7	13
	Illinois	28.1	22.5	0.5	23.1	<0.01	87.5	2563
	Michigan	83.4	64.9	1.9	65.0	<0.01	433.0	1165
	Minnesota	36.2	9.2	2.3	39.0	21.0	49.0	16
	Nebraska	37.9	19.2	2.3	30.0	18.0	100.0	69
	New York	13.7	26.2	4.6	8.9	<0.01	154.0	32
	Ohio	102.9	55.6	13.1	72.5	47.0	185.0	18
	Ontario	77.8	242.6	32.7	11.0	1.0	1233.0	55
	Oregon	56.1	24.8	2.4	54.6	0.6	135.0	104
	Overall	45.8	54.9	0.9	34.0	<0.01	1233.0	4056
Clemmys guttata								
	Massachusetts	36.0	37.1	7.6	17.0	0.5	130.0	24
	Ontario	33.5	39.8	6.8	21.4	2.0	139.0	34
	Overall	37.5	48.4	6.1	18.5	0.5	283.0	64
Deirochelys reticularia								
	South Carolina	145.7	97.8	18.5	175.6	1.5	247.2	28
	Overall	141.7	98.4	18.3	119.7	1.5	247.2	29
Emydoidea blandingii								
	Massachusetts	85.2	72.7	9.6	70.0	5.0	333.0	58
	Maine	128.0	94.2	25.2	99.5	19.0	365.0	14
	Michigan	126.8	96.5	6.1	100.0	4.0	448.0	254
	Minnesota[a]	481.3	426.8	93.2	353.0	100.0	2012.0	21
	New York	193.0	74.0	12.3	191.0	22.0	427.0	36
	Ontario	71.2	108.4	17.8	16.0	1.0	461.0	37
	Overall[a]	139.6	154.3	7.5	103.0	1.0	2012.0	420
Glyptemys insculpta								
	Massachusetts	51.2	59.6	5.9	28.2	0.2	273.0	103
	Maine	55.4	56.1	11.7	20.0	10.0	150.0	23
	Overall	54.5	68.6	6.0	25.0	0.2	462.0	129
Graptemys barbouri								
	Overall	16.6	24.4	10.0	1.2	0.5	50.0	6
Graptemys geographica								
	Ontario	35.7	55.8	12.8	10.0	2.0	252.0	19
Graptemys nigrinoda								
	Alabama	64.0	66.1	11.2	31.0	1.0	212.0	35
Graptemys ouachitensis								
	Arkansas	20.8	6.4	1.8	20.0	10.0	30.0	13
	Overall	16.1	8.3	1.7	20.0	4.4	30.0	23
Graptemys pseudogeographica								
	South Dakota	54.3	34.0	8.8	46.2	17.1	115.8	15
	Overall	46.7	31.8	5.7	41.4	6.0	115.8	31

(*continued on next page*)

Table 1 (*continued*)

Species	Location	Mean	Standard deviation	Standard error	Median	Minimum	Maximum	*N*
Graptemys pulchra								
	Alabama	16.3	2.5	1.8	16.3	14.5	18.0	2
Graptemys sabinensis								
	Overall	21.4	10.0	5.0	23.3	9.2	29.8	4
Kinosternon baurii								
	Florida	134.9	48.7	5.6	128.0	62.0	274.0	75
Kinosternon flavescens								
	Nebraska	109.0	47.8	7.7	107.0	23.0	262.0	39
Kinosternon subrubrum								
	Overall	26.5	30.7	12.5	17.2	0.3	78.3	6
Macrochelys temminckii								
	Louisiana	9.6	11.1	1.2	3.5	1.2	58.5	89
	Overall	15.8	21.2	2.1	4.0	1.2	87.0	102
Malaclemys terrapin								
	Georgia	3.5	2.8	0.3	1.5	1.5	13.5	100
	New Jersey	7.6	<0.01	<0.01	7.6	7.6	7.6	12
	Overall	3.9	2.9	0.3	1.5	1.5	13.5	112
Pseudemys alabamensis								
	Alabama	63.7	32.8	4.1	58.5	5.0	153.0	64
Pseudemys concinna								
	Florida	63.7	38.4	1.6	60.0	20.0	225.0	563
	Overall	65.1	46.7	2.0	60.0	20.0	681.0	565
Pseudemys floridana								
	Overall	102.3	104.7	37.0	73.4	3.5	268.8	8
Pseudemys rubriventris								
	Overall	83.1	9.8	6.9	83.1	76.2	90.0	2
Sternotherus depressus[b]								
	Alabama	42.2	63.1	36.4	7.5	5.0	115.0	3
Sternotherus carinatus								
	Louisiana	3.4			3.4	3.4	3.4	1
Sternotherus odoratus								
	Massachusetts	5.5	7.4	0.7	3.0	1.5	50.0	125
	Overall	5.5	8.0	0.7	3.0	0.0	50.0	140
Trachemys gaigeae								
	New Mexico	25.0			25.0	25.0	25.0	1
Trachemys scripta								
	Illinois	901.2	276.2	27.1	782.8	370.8	1766.7	104
	South Carolina	15.5	26.7	6.7	1.3	0.0	97.4	16
	Overall	725.6	425.9	37.2	739.1	0.0	1766.7	131

[a] Includes 21 radio-tagged individuals; distances represented are distance to wetland of origin, not necessarily nearest wetland.

[b] Records for this species were obtained late in the study and were not incorporated into analyses.

tions of turtles (based on medians across genera) were about 6–98 m for each additional 10% segment from 0% to 90% whereas approximately 424 m would be required to include the remaining 10% (Fig. 1).

4. Discussion

Generating effective terrestrial land-use policies to protect wetland habitats requires data on the extent of terrestrial habitat used by wetland-associated animals (McElfish et al., 2008). Our results provide a geographical framework for conserving turtle populations by identifying the spatial extent of area required to protect the most vulnerable population segments: nesting females, eggs, and hatchlings. Our data indicate that freshwater turtles in aggregate use considerably more terrestrial habitat for nesting than is typically included in the wetland protection zones generally delineated as 30–120 m from wetland boundaries in the United States and Canada (Houlahan and Findlay, 2004; Lee et al., 2004; see also Castelle et al., 1994). For example, a 93 m zone surrounding wetlands encompasses just 50% of nests (Table 4). Full protection of all nests would require a protected zone approximately 10 times as wide (ca. 942 m; Table 4). Our large database corroborates the 287 m mean maximum core terrestrial zone suggested by Semlitsch and Bodie (2003) to protect all wetland-associated amphibian and reptile species; a zone of this size would encompass more than 95% of the observations included in our analysis. However, our estimates are generally larger than previously published values. For example, Burke and Gibbons (1995) suggested that a 73 m zone was necessary to protect 90% of nesting and hibernation sites used by three turtle species in a single Carolina Bay in South Carolina. However, our continent-wide study suggests a 198 m zone is necessary to protect the same proportion of nests among all species (Table 4). Our results further corroborate the 150 m zone suggested by Bodie (2001) to protect riparian areas used by riverine turtles. Of riverine-associated genera, we estimate that a protected area of 150 m would protect approximately 95% or more of nesting *Apalone*, *Macrochelys*, *Pseudemys* and *Graptemys* (Table 4; note, our sample drew chiefly from riverine species of *Apalone* and *Pseudemys*, although some species in those genera are primarily lentic).

We may have generated underestimates of the distances turtles typically travel overland to nest because we included nest

Table 2
Mean distance to nearest water and associated statistics for gravid United States and Canada turtles based on individual records. Relevant citations are provided in Appendix A.

Species	Location	Mean	Standard deviation	Standard error	Median	Minimum	Maximum	*N*
Actinemys marmorata								
	Overall	33.7	25.6	9.1	20.4	14.3	83.0	8
Apalone ferox								
	Florida	80.0	102.4	72.4	80.0	7.6	152.4	2
Chelydra serpentina								
	Overall	56.8	69.6	16.0	30.0	1.0	278.0	19
Chrysemys picta								
	Ontario	9.8	6.1	1.43	8.5	2.0	24.0	18
	Overall	239.7	467.0	70.40	37.0	2.0	2479.5	44
Clemmys guttata								
	Massachusetts	38.3	41.3	10.04	3.0	0.5	177.0	27
	Overall	37.4	50.7	9.42	3.0	0.5	177.0	29
Emydoidea blandingii								
	Massachusetts	80.3	41.3	9.73	85.0	2.0	150.0	18
	Overall	334.6	709.0	129.45	85.0	2.0	3421.0	30
Glyptemys insculpta								
	Massachusetts	74.3	79.1	18.63	40.4	0.4	291.0	18
	Overall	61.9	76.0	16.21	28.7	0.4	291.0	22
Graptemys barbouri								
	Georgia	36.0				36.0	36.0	1
Kinosternon subrubrum								
	New Jersey	91.4				91.4	91.4	1
Malaclemys terrapin								
	New Jersey	7.6				7.6	7.6	1
Pseudemys concinna								
	Georgia	350.0				350.0	350.0	1
Sternotherus odoratus								
	Illinois	850.9	892.1	446.03	535.1	175.8	2157.5	4
Trachemys scripta								
	Illinois	977.0	349.8	20.10	1007.3	82.0	2205.6	303
	Overall	974.0	353.3	20.26	1004.6	45.0	2205.6	304

data that were associated with turtle nest studies; these studies often focus on areas close to wetland edges, likely under-representing distant nests. In addition, we quantified only the distance to nearest wetland yet many species that reside within upland–wetland complexes use multiple bodies of water; a nesting turtle may not have originated from nearest body of water (e.g., *Clemmys guttata*, Joyal et al., 2001; *Emydoidea blandingii*, Congdon et al., 1983, 2011; *Chelydra serpentina*, Obbard and Brooks, 1980; *Chrysemys picta*, Rowe et al., 2005). As a consequence, these turtles may travel well beyond the distances we report. Conversely, for some species, our sample may be biased towards sites where turtles travel further than is the norm elsewhere. Generating management plans based on these animals may result in protecting areas larger than necessary; this may be of concern when resources are limited and underscores the need for site-specific data.

Modeling is required to estimate the relationship between various protection boundaries we delineate here and population-level effects of adult mortality or nest-site loss resulting from development (e.g., Gibbs and Shriver, 2002; Row et al., 2007). Specifically, it is unknown what percentage of nest sites must be protected to ensure long-term viability of turtle populations. However, protecting terrestrial areas around wetlands will unquestionably preserve nesting areas that are necessary for hatchling recruitment into populations. Simultaneously, by limiting development within these zones, female turtles undergoing nesting migrations will experience reduced risk of individual mortality. Population persistence is unlikely with additive mortality of sexually mature females concurrent with loss of nesting areas (e.g., Heppell, 1998). Finally, by protecting and managing existing nesting areas near wetlands, females will not be forced to travel farther to nest, limiting their exposure to terrestrial threats.

Our generalizations about nesting distances can obscure important, fine-scale considerations about site- or species-specific nesting habitat requirements. Even if no development occurs within the core areas we defined, subsidized predators originating from urban or suburban areas can penetrate a protected area, although predation patterns are not always easily discerned (Marchand and Litvaitis, 2004; Strickland and Janzen, 2010). In addition, turtles may have a preferred nesting site around a particular wetland (e.g., Lindeman, 1992; Schwarzkopf and Brooks, 1987) or be restricted to a particular nesting area that is within or beyond the core area designations we have identified. Moreover, although some turtles return to a given nesting area in multiple years, others may not (Congdon et al., 1987, 2011). Finally, height above water, as well as density of vegetation, may be important determinants of the distances riverine turtles travel to nest. For example, turtles may travel farther when slopes are gentle to reduce nest mortality from flooding (Doody, 1995; Doody et al., 2004; Plummer, 1976). Likewise, females in some populations travel as far as needed to secure a site with sufficient solar exposure to facilitate egg development (Jackson and Walker, 1997).

Our study provides a description of generalized patterns based on available data. These data may be useful in generating management plans when site-specific information is unavailable. However, critical zone designations will only be practical if indeed turtles perceive nesting habitat within them. When applying the distances reported here to protected zones, it is essential to ensure the presence of nesting habitat and consider potential edge effects (Kolbe and Janzen, 2002a,b).

Table 3
Mean distance to nearest water and associated statistics for United States and Canada turtle nests. Distances for individual nests were not available. Relevant citations are provided in Appendix A. In some cases, it was necessary to calculate the standard deviation (SD) or standard error (SE) from values within the original text.

Species	Location	Mean (m)	*N*	SD	SE	Min	Max	Source
Actinemys marmorata	Oregon	133	54	52	7	27	145	Holte (1998)
Actinemys marmorata	Oregon	48	12	7	2	38	58	Holte (1998)
Actinemys marmorata	Oregon	171	16	31	8	125	212	Holte (1998)
Actinemys marmorata	Oregon	6	27	2	<1	3	8	Holte (1998)
Actinemys marmorata	Oregon	5	27	4	<1	<1	22	Holte (1998)
Apalone spinifera	Vermont	3	5	<1	<1	2	4	Graham and Graham (1997)
Chelydra serpentina	Quebec	8	113	7	<1			Robinson and Bider (1988)
Chelydra serpentina	Quebec	9	21	7	2			Robinson and Bider (1988)
Chelydra serpentina	New York	27	40			<1	89	Petokas and Alexander (1980)
Chelydra serpentina	Minnesota	37	87					Pappas et al. (2009)
Chelydra serpentina	Virginia	100	85	118	13	<1	350	Gotte (1988)
Chrysemys picta	Quebec	89	16			1	328	Christens and Bider (1987)
Chrysemys picta	Quebec	82	17			16	618	Christens and Bider (1987)
Chrysemys picta	Quebec	100	18			19	621	Christens and Bider (1987)
Chrysemys picta	Tennessee	14	8			14	15	Cagle (1937)
Chrysemys picta	New Mexico	2	34	2	<1	<1	11	Morjan (2003)
Chrysemys picta	North Carolina	36	37	29	5	1	115	Foley et al. (2012)
Chrysemys picta	Illinois	32	364	24	1	<1	86	Morjan (2003)
Chrysemys picta	Illinois	34	147	25	2			Bowen and Janzen (2008)
Chrysemys picta	Illinois	29	158	24	2			Bowen and Janzen (2008)
Chrysemys picta	Illinois	25	218	25	2			Bowen and Janzen (2008)
Chrysemys picta	Ontario	20	37			2	50	Whillans and Crossman (1977)
Chrysemys picta	Virginia	43	98	64	7	<1	310	Gotte (1988)
Chrysemys picta	Pennsylvania	9	14			2	21	Ernst (1970)
Chrysemys picta	Minnesota	66	58					Pappas et al. (2009)
Clemmys guttata	Maine	51	12	34	10	1	120	Joyal et al. (2001)
Emydoidea blandingii	Wisconsin	168	16	91	23			Ross and Anderson (1990)
Emydoidea blandingii	Maine	242	6	138	56	70	410	Joyal et al. (2001)
Emydoidea blandingii	Minnesota	622	138					Pappas et al. (2009)
Emydoidea blandingii	Illinois	815	3	146	84	650	900	Rowe and Moll (1991)
Emydoidea blandingii	Nova Scotia	5	46	2	<1			Standing et al. (1999)
Emydoidea blandingii	Nova Scotia	3	49	3	<1			Standing et al. (1999)
Glyptemys insculpta	Minnesota	426	13			100	1609	Piepgras and Lang (2000)
Glyptemys insculpta	Quebec	19	60			5	43	A. Walde (pers. comm.)
Glyptemys insculpta	New Hampshire	60	9	18	6			Tuttle and Carroll (1997)
Glyptemys insculpta	Ontario	10	5	4	2			Hughes et al. (2009)
Graptemys flavimaculata	Mississippi	8	70	4	1	1	17	Horne et al. (2003)
Graptemys oculifera	Mississippi	18	133	14	1	<1	61	Jones (2006)
Kinosternon subrubrum	South Carolina	49	68	19	2	17	90	Burke et al. (1994)
Kinosternon subrubrum	Virginia	211	24	147	30	<1	320	Gotte (1988)
Macrochelys temminckii	Florida	12	12	10	3	3	22	Ewert (1976)
Pseudemys alabamensis	Alabama	63	20	28	6	30	123	Nelson et al. (2009)
Pseudemys nelsoni	Florida	5	5					Goodwin and Marion (1977)
Pseudemys texana	Texas	88	108	29	3	15	159	Rose (2011)
Sternotherus odoratus	Pennsylvania	7	32			3	11	Ernst (1986)
Sternotherus odoratus	Tennessee	14	4			14	15	Cagle (1937)
Trachemys scripta	Texas	87	52	35	5	10	170	Rose (2011)
Trachemys scripta	Tennessee	14	47			13	15	Cagle (1937)

There are many unanswered questions pertaining to how habitat preferences may influence turtle nesting migrations. It is unknown whether longer migrations are associated with a lack of nesting habitat near the wetland of origin, although this is undoubtedly the case in at least some instances (Jackson and Walker, 1997). Similarly, it remains to be seen whether construction of artificial nesting areas near wetlands or away from development may be an effective conservation strategy (Buhlmann and Osborn, 2011). The extent to which turtle populations are able to respond to development-induced changes by life-history trait evolution is likewise not yet known (Bowen and Janzen, 2008; Rowe, 1997; Wolak et al., 2010). Although some turtle populations may adapt to the loss of nesting areas (and subsequent reduction in recruitment) or of sexually mature females (Fordham et al., 2007), it is not known if contemporary evolution of life history traits can track the ongoing rate of human conversion of turtle habitats and associated effects on turtle populations (e.g., Gibbs and Steen, 2005).

This review lends support to efforts to protect freshwater turtles within their core terrestrial zones and indicates that, overall, modest increases in protected area size may disproportionately enhance the fraction of nest sites protected. For some genera, however, considerable area is required to protect the majority of nests, and that represents a serious potential conflict between current land-use patterns and turtle conservation. Development of terrestrial areas could impact turtles in several ways. For example, vehicle-induced road mortality is of conservation concern to turtles (e.g., Aresco, 2005a; Gibbs and Steen, 2005; Steen and Gibbs, 2004). Where roads intersect turtle migration routes and result in high mortality, barrier walls in association with culverts facilitate safe turtle movements (Aresco, 2005b; Dodd et al., 2004). Although retroactive changes in roads have lowered turtle mortality rates, they are expensive and there may be species-specific preferences regarding appropriate culvert type and placement (e.g., Langen et al., 2009; Woltz et al., 2008). More cost-effective measures include incorporating landscape-scale ecological

Table 4
Summary of distances (m) of aquatic turtle nests or gravid females to wetlands; results are presented by genera, ecological habit and body size, and overall. Movement distance for a given percentile is the average across genera within a category for that percentile.

Category	Percentile[c]					N[d]
	50%	75%	90%	95%	Maximum	
All	93	154	198	232	3421	8013
Ecological habit[a]						
Fully aquatic	123	195	236	275	1159	7137
Semi-aquatic	69	124	178	211	810	876
Body size[b]						
Large-bodied	27	50	84	113	544	2222
Small-bodied	117	192	239	275	1088	5791
Genus						
Malaclemys	2	8	8	8	14	113
Sternotherus	3	4	20	25	2158	145
Macrochelys	4	22	42	72	87	102
Actinemys	31	52	83	104	170	32
Chelydra	25	49	80	116	982	1043
Apalone	20	47	93	123	424	437
Clemmys	17	55	108	127	283	93
Pseudemys	60	82	119	140	681	640
Chrysemys	34	60	98	154	2479	4100
Graptemys	24	46	91	173	252	121
Glyptemys	25	71	150	178	462	151
Kinosternon	118	153	183	206	274	121
Deirochelys	120	239	241	245	247	29
Emydoidea	102	172	302	408	3421	450
Trachemys	816	1251	1345	1396	2206	436

[a] Based on a species' proclivity to undertake terrestrial movements not necessarily associated with nesting (see Section 2 for details).

[b] Based on the typical size of sexually mature females (see Section 2 for details).

[c] Percentiles identify the distances required to include that fraction of the sample, ranked from shortest to longest distance from nearest wetland; genera are sorted by distance to incorporate 95% of observations.

[d] Sample size.

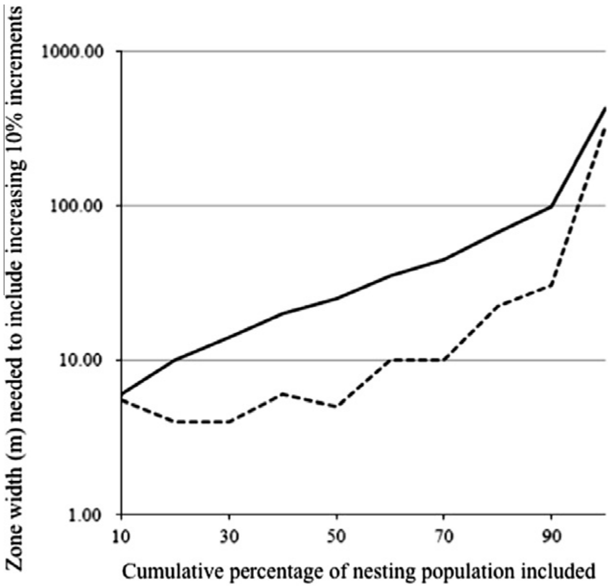

Fig. 1. Zone widths required to include turtle nesting populations (i.e., nests, hatchlings, and gravid females). Solid line represents distance away from a water body needed to encompass the associated cumulative proportion of nesting populations. Dotted line represents incremental distance needed to include each additional 10% of nesting populations. Both lines are derived from median distance estimates (calculated across genera) for each additional population segment (see Section 2).

requirements of resident flora and fauna into initial development plans.

Acknowledgments

Data for this review were graciously provided by A. Platt, A. Walde, B. Wong, C. Millar, C. Bogard, C. Edge, C. O'Neill, D. Becker, L. Smith, J. Connelly, J. Refsnider, J. Humphries, J. Andrews, J. Applegarth, J. Iverson, J. Jensen, K. Irwin, K. Crump, K. Loucks, L. Willey, L. Dixon, L Guderyahn, L. Haines, L. Johnson, M. Grgurovic, M. Aresco, M. Rasmussen, P. Lindeman, R. Burnford and the Friends of Petrie Island and Ottawa Stewardship Council, G. Sorrell, R. Thiel, S. Beilke, T. Cervi, and the Toronto Zoo Turtle Tally. C. and D. Sharpe kindly granted land access. We acknowledge all biologists and naturalists who take careful field notes and make them available for reviews of this type, as these data may often represent novel and essential natural history information unreported in the published literature. E.P. Cox at the Joseph W. Jones Ecological Research Center and Auburn University librarians assisted with obtaining references. F.J.J. would like to thank the U.S. National Science Foundation for continued funding of his turtle nesting research. This material is based upon work supported by the Department of Energy under Award Number DE-FC09-07SR22506 to the University of Georgia Research Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.03.012.

References

Aresco, M.J., 2005a. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biol. Conserv. 123, 37–44.

Aresco, M.J., 2005b. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. J. Wildlife Manage. 69, 549–560.

Bodie, J.R., 2001. Stream and riparian management for freshwater turtles. J. Environ. Manage. 62, 443–455.

Bowen, K.D., Janzen, F.J., 2008. Human recreation and the nesting ecology of a freshwater turtle (*Chrysemys picta*). Chelonian Conserv. Biol. 7, 95–100.

Bried, J.T., Ervin, G.N., 2006. Abundance patterns of dragonflies along a wetland buffer. Wetlands 26, 878–883.

Brooks, R.J., Brown, G.P., Galbraith, D.A., 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Can. J. Zool. 69, 1314–1320.

Buhlmann, K.A., Gibbons, J.W., 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. Chelonian Conserv. Biol. 4, 115–127.

Buhlmann, K.A., Osborn, C.P., 2011. Use of an artificial nesting mound by wood turtles (*Glyptemys insculpta*): a tool for turtle conservation. NE. Nat. 18, 315–334.

Burke, V.J., Gibbons, J.W., 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina Bay. Conserv. Biol. 9, 1365–1369.

Castelle, A.J., Johnson, A.W., Connolly, C., 1994. Wetland and stream buffer size requirements – a review. J. Environ. Qual. 23, 878–882.

Congdon, J.D., Tinkle, D.W., Breitenbach, G.L., Van Loben Sels, R.C., 1983. Nesting ecology and hatching success in the turtle *Emydoidea blandingi*. Herpetologica 39, 417–429.

Congdon, J.D., Breitenbach, G.L., Van Loben Sels, R.C., Tinkle, D.W., 1987. Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. Herpetologica 43, 39–54.

Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conserv. Biol. 7, 826–833.

Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived species. Am. Zool. 34, 397–408.

Congdon, J.D., Kinney, O.M., Nagle, R.D., 2011. Spatial ecology and core area protection of Blanding's turtle (*Emydoidea blandingii*). Can. J. Zool. 89, 1098–1106.

Crawford, J.A., Semlitsch, R.D., 2007. Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. Conserv. Biol. 21, 152–158.

Dodd Jr., C.K., Barichivich, W.J., Smith, L.L., 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biol. Conserv. 118, 619–631.

Doody, J.S., 1995. Comparative Nesting Study of Two Species of Softshell Turtle (*Apalone mutica* and *A. spinifera*) in Southcentral Louisiana. Unpubl. Masters Thesis, Hammond.

Doody, J.S., Georges, A., Young, J.E., 2004. Determinants of reproductive success and offspring sex in a turtle with environmental sex determination. Biol. J. Linn. Soc. Lond. 80, 1–16.

Fordham, D.A., Georges, A., Brook, B.W., 2007. Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia. J. Anim. Ecol. 76, 1231–1243.

Gibbons, J.W., 1986. Movement patterns among turtle populations: applicability to management of the desert tortoise. Herpetologica 42, 104–113.

Gibbons, J.W., 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands 23, 630–635.

Gibbs, J.P., Shriver, W.G., 2002. Estimating the effects of road mortality on turtle populations. Conserv. Biol. 16, 1647–1652.

Gibbs, J.P., Steen, D.A., 2005. Historic trends in sex ratios of turtle populations in the United States. Conserv. Biol. 19, 552–556.

Heppell, S.S., 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998, 367–375.

Houlahan, J.E., Findlay, C.S., 2004. Estimating the ‘critical’ distance at which adjacent land-use degrades wetland water and sediment quality. Landscape Ecol. 19, 677–690.

Jackson, D.R., Walker, R.W., 1997. Reproduction in the Suwannee cooter, *Pseudemys concinna suwanniensis*. Bull. Fl. Mus. Nat. Hist. 41, 69–167.

Joyal, L.A., McCollough, M., Hunter Jr., M.L., 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conserv. Biol. 15, 1755–1762.

Kolbe, J.J., Janzen, F.J., 2002a. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. Ecology 83, 269–281.

Kolbe, J.J., Janzen, F.J., 2002b. Spatial and temporal dynamics of turtle nest predation: edge effects. Oikos 99, 538–544.

Kruchek, B.L., 2004. Use of tidal marsh and upland habitats by the marsh rice rat (*Oryzomys palustris*). J. Mammal. 85, 569–575.

Langen, T.A., Ogden, K.M., Schwarting, L.L., 2009. Predicting hot spots of herpetofauna road mortality along highway networks. J. Wildlife Manage. 73, 104–114.

Lee, P., Smyth, C., Boutin, S., 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. J. Environ. Manage. 70, 165–180.

Lindeman, P.V., 1992. Nest-site fixity among painted turtles (*Chrysemys picta*) in northern Idaho. Northwest. Nat. 73, 27–30.

Marchand, M.N., Litvaitis, J.A., 2004. Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests. Biol. Conserv. 117, 243–251.

McElfish Jr., J.M., Kihslinger, R.L., Nichols, S., 2008. Setting buffer sizes for wetlands. Natl. Wetlands Newsl. 30, 6–17.

Naugle, D.E., Higgins, K.F., Nusser, S.M., Johnson, W.C., 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecol. 14, 267–276.

Noss, R.F., 1983. A regional landscape approach to maintain diversity. Bioscience 33, 700–706.

Obbard, M.E., Brooks, R.J., 1980. Nesting migrations of the snapping turtle (*Chelydra serpentina*). Herpetologica 36, 158–162.

Plummer, M.V., 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. Herpetologica 32, 353–359.

Pope, S.E., Fahrig, L., Merriam, H.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81, 2498–2508.

Porej, D., Micacchion, M., Hetherington, T.E., 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. Biol. Conserv. 120, 399–409.

Rizkalla, C.E., Swihart, R.K., 2006. Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation. Landscape Ecol. 21, 1361–1375.

Roe, J.H., Kingsbury, B.A., Herbert, N.R., 2003. Wetland and upland use patterns in semi-aquatic snakes: implications for wetland conservation. Wetlands 23, 1003–1014.

Rondinini, C., Chiozza, F., 2010. Quantitative methods for defining percentage area targets for habitat types in conservation planning. Biol. Conserv. 143, 1646–1653.

Row, J.R., Blouin-Demers, G., Weatherhead, P.J., 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biol. Conserv. 137, 117–124.

Rowe, J.W., 1997. Reproductive variation and the egg size-clutch size trade-off within and among populations of painted turtles (*Chrysemys picta bellii*). Oecologia 99, 35–44.

Rowe, J.W., Coval, K.A., Dugan, M.R., 2005. Nest placement, nest-site fidelity, and nesting movements in midland painted turtles (*Chrysemys picta marginata*) on Beaver Island, Michigan. Am. Midl. Nat. 154, 383–397.

Schwarzkopf, L., Brooks, R.J., 1987. Nest site selection and offspring sex ratio in painted turtles, *Chrysemys picta*. Copeia 1987, 53–62.

Semlitsch, R.D., 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conserv. Biol. 12, 1113–1119.

Semlitsch, R.D., Jensen, J.B., 2001. Core habitat, not buffer zone. Natl. Wetlands Newsl. 23, 5–11.

Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conserv. Biol. 17, 1219–1228.

Simberloff, D., Abele, L.G., 1982. Refuge design and island biogeographic theory: effects of fragmentation. Am. Nat. 120, 41–50.

Steen, D.A., Gibbs, J.P., 2004. Effects of roads on the structure of freshwater turtle populations. Conserv. Biol. 18, 1143–1148.

Steen, D.A. et al., 2006. Relative vulnerability of female turtles to road mortality. Anim. Conserv. 9, 269–273.

Sterrett, S.C., Smith, L.L., Golladay, S.W., Schweitzer, S.H., Maerz, J.C., 2011. The conservation implications of riparian land use on river turtles. Anim. Conserv. 14, 38–46.

Strickland, J.T., Janzen, F.J., 2010. Impacts of anthropogenic structures on predation of painted turtle (*Chrysemys picta*) nests. Chelonian Conserv. Biol. 9, 131–135.

Wolak, M.E., Gilchrist, G.W., Ruzicka, V.A., Nally, D.M., Chambers, R.M., 2010. A contemporary, sex-limited change in body size of an estuarine turtle in response to commercial fishing. Conserv. Biol. 24, 1268–1277.

Woltz, H.W., Gibbs, J.P., Ducey, P.K., 2008. Road crossing structures for amphibians and reptiles: informing design through behavioral analysis. Biol. Conserv. 141, 2745–2750.

Wu, J., Hobbs, R., 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecol. 17, 355–365.