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Terrestrial habitat requirements of nesting freshwater turtles

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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 ≥ 8 000 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 1 400 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.
Key Words: *buffer, land use planning, landscape, nest, migration, reptile*

1. Introduction

Key factors in conserving biodiversity are the sizes and configurations of protected areas (Noss, 1983; Simberloff and Abele, 1982); however, identifying the size 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 development 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 (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. Specifically, 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.

Turtle demography is characterized by relatively high nest and embryonic mortality, delayed sexual maturity, and high adult survivorship (Congdon et al., 1993, 1994), rendering populations particularly sensitive to 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 to protect critical population segments. 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 ≥ 8 000 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. We also estimated distances from wetlands for more homogeneous groups of turtle based on the arithmetic mean of distances moved within groups.

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). Because different species within a genera may exhibit disparate behavior (e.g., *Pseudemys* includes both lentic and lotic species, and some species have a greater tendency to travel overland) 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 7 550 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 2 606 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 1 396 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 populations of turtles (based on medians across genera) were about 6-98 m for each additional 10% segment from 0-90% 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 associated organisms (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. More specifically, our data indicate that aquatic turtles in aggregate use considerably more terrestrial habitat for nesting than 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 extensive 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 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, in press; *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, in press). 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).

There are many unanswered are 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).

To conclude, freshwater turtles may represent a group particularly sensitive to anthropogenic development of terrestrial habitats. 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, mortality of females during nesting migrations and nesting habitat loss may be the most significant threats to freshwater turtle population persistence (Gibbs and Shriver, 2002; Steen et al., 2006). By focusing on life stages that are most at risk and are critical for population persistence and most at risk, we derived information required to generate targets for conservation planning to accommodate the movements of freshwater turtles dictated by their natural history requirements.

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 requirements of resident flora and fauna into initial development plans.

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Appendix A Supplementary material

Supplementary material associated with this article, can be found in the online version, at

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Figure 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 Methods).

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 Error	Median	Minimum	Maximum	N
Actinemys marmorata							
	California	38.93	9.06	31.50	6.00	170.00	18
	Overall	44.91	7.91	32.00	6.00	170.00	24
Apalone ferox							
	Florida	261.33	43.60	278.00	56.00	345.00	6
Apalone mutica							
	Arkansas	17.85	0.61	20.00	10.00	40.00	205
	Kansas	72.18	2.88	70.00	3.00	140.00	105
	Louisiana	13.41	1.82	8.83	2.20	46.10	38
	Texas	32.88	5.32	38.10	5.10	55.00	11
	Overall	33.73	1.62	20.00	2.20	140.00	359

Apalone spinifera							
	Louisiana	5.51	1.30	3.58	2.30	14.49	10
	Overall	37.94	18.79	3.40	0.30	424.27	29
Apalone sp.							
	South Dakota	61.27	7.72	45.36	10.06	175.05	41
Chelydra serpentina							
	Illinois	49.20	4.13	48.60	0.90	124.70	56
	Michigan	34.57	1.46	31.00	1.00	230.00	465
	Nebraska	24.19	3.14	25.00	1.00	81.00	43
	New York	20.15	2.16	9.88	0.00	142.00	154
	Ontario	51.80	6.57	23.50	0.30	982.00	280
	Overall	39.03	2.04	25.00	0.00	982.00	1024
Chrysemys picta							
	Idaho	5.48	0.44	6.00	3.00	7.70	13
	Illinois	28.14	0.45	23.14	0.00	87.48	2563

	Michigan	83.41	1.90	65.00	0.00	433.00	1165
	Minnesota	36.23	2.29	39.00	21.00	49.00	16
	Nebraska	37.91	2.31	30.00	18.00	100.00	69
	New York	13.70	4.63	8.94	0.00	154.00	32
	Ohio	102.94	13.11	72.50	47.00	185.00	18
	Ontario	77.83	32.71	11.00	1.00	1233.00	55
	Oregon	56.06	2.43	54.63	0.60	135.00	104
	Overall	45.84	0.86	33.99	0.00	1233.00	4056
Clemmys guttata							
	Massachusetts	35.99	7.57	17.00	0.50	130.00	24
	Ontario	33.49	6.84	21.35	2.00	139.00	34
	Overall	37.48	6.05	18.50	0.50	283.00	64
Deirochelys reticularia							
	South Carolina	145.69	18.47	175.60	1.50	247.20	28

	Overall	141.70	18.27	119.70	1.50	247.20	29
Emydoidea blandingii							
	Massachusetts	85.16	9.55	70.00	5.00	333.00	58
	Maine	128.00	25.18	99.50	19.00	365.00	14
	Michigan	126.78	6.06	100.00	4.00	448.00	254
	Minnesota[a]	481.33	93.15	353.00	100.00	2012.00	21
	New York	193.03	12.34	191.00	22.00	427.00	36
	Ontario	71.22	17.82	16.00	1.00	461.00	37
	Overall[a]	139.58	7.53	103.00	1.00	2012.00	420
Glyptemys insculpta							
	Massachusetts	51.23	5.87	28.22	0.19	273.00	103
	Maine	55.43	11.69	20.00	10.00	150.00	23
	Overall	54.53	6.04	25.00	0.19	462.00	129
Graptemys barbouri							
	Overall	16.56	9.96	1.23	0.45	50.00	6

Graptemys geographica							
	Ontario	35.74	12.79	10.00	2.00	252.00	19
Graptemys nigrinoda							
	Alabama	64.00	11.18	31.00	1.00	212.00	35
Graptemys ouachitensis							
	Arkansas	20.77	1.78	20.00	10.00	30.00	13
	Overall	16.10	1.73	20.00	4.40	30.00	23
Graptemys pseudogeographica							
	South Dakota	54.25	8.77	46.17	17.10	115.80	15
	Overall	46.86	5.71	41.40	6.00	115.80	31
Graptemys pulchra							
	Alabama	16.25	1.75	16.25	14.50	18.00	2
Graptemys sabinensis							
	Overall	21.38	5.02	23.25	9.20	29.80	4
Kinosternon baurii							

	Florida	134.85	5.62	128.00	62.00	274.00	75
Kinosternon flavescens							
	Nebraska	109.03	7.66	107.00	23.00	262.00	39
Kinosternon subrubrum							
	Overall	26.53	12.54	17.20	0.25	78.30	6
Macrochelys temminckii							
	Louisiana	9.55	1.18	3.50	1.18	58.50	89
	Overall	15.84	2.10	3.95	1.18	87.00	102
Malaclemys terrapin							
	Georgia	3.48	0.28	1.50	1.45	13.53	100
	New Jersey	7.60	0.00	7.60	7.60	7.60	12
	Overall	3.92	0.28	1.50	1.45	13.53	112
Pseudemys alabamensis							
	Alabama	63.67	4.09	58.50	5.00	153.00	64
Pseudemys concinna							

	Florida	63.74	1.62	60.00	20.00	225.00	563
	Overall	65.10	1.97	60.00	20.00	681.00	565
Pseudemys floridana							
	Overall	102.33	37.02	73.40	3.50	268.80	8
Pseudemys rubriventris							
	Overall	83.10	6.90	83.10	76.20	90.00	2
Sternotherus depressus[b]							
	Alabama	42.17	36.42	7.5	5.00	115.00	3
Sternotherus carinatus							
	Louisiana	3.35		3.35	3.35	3.35	1
Sternotherus odoratus							
	Massachusetts	5.54	0.66	3.00	1.50	50.00	125
	Overall	5.46	0.67	3.00	0.00	50.00	140
Trachemys gaigeae							
	New Mexico	25.00		25.00	25.00	25.00	1

Trachemys scripta							
	Illinois	901.24	27.08	782.76	370.77	1766.71	104
	South Carolina	15.52	6.67	1.30	0.00	97.40	16
	Overall	725.64	37.21	739.12	0.00	1766.71	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.

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 Error	Median	Minimum	Maximum	N
Actinemys marmorata							
	Overall	33.70	9.05	25.58	14.30	83.00	8
Apalone ferox							
	Florida	80.00	72.40	102.39	7.60	152.40	2
Chelydra serpentina							
	Overall	56.78	15.98	69.65	1.00	278.00	19
Chrysemys picta							
	Ontario	9.83	1.43	6.05	2.00	24.00	18
	Overall	239.71	70.40	466.98	2.00	2479.45	44
Clemmys guttata							
	Massachusetts	38.30	10.04	52.19	0.50	177.00	27
	Overall	37.37	9.42	50.72	0.50	177.00	29

Emydoidea blandingii							
	Massachusetts	80.28	9.73	41.28	2.00	150.00	18
	Overall	334.62	129.45	709.04	2.00	3421.00	30
Glyptemys insculpta							
	Massachusetts	74.25	18.63	79.06	0.35	291.03	18
	Overall	61.90	16.21	76.03	0.35	291.03	22
Graptemys barbouri							
	Georgia	36.00			36.00	36.00	1
Kinosternon subrubrum							
	New Jersey	91.40			91.40	91.40	1
Malaclemys terrapin							
	New Jersey	7.60			7.60	7.60	1
Pseudemys concinna							
	Georgia	350.00			350.00	350.00	1
Sternotherus odoratus							

	Illinois	850.88	446.03	892.07	175.82	2157.51	4
Trachemys scripta							
	Illinois	977.04	20.10	349.82	82.04	2205.59	303
	Overall	973.98	20.26	353.31	45.00	2205.59	304

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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.

Genus	Species	Location	Mean (m)	N	SE*	Min	Max	Source
Actinemys	*marmorata*	Oregon	132.9	54	7.1	27.3	145.07	Holte (1998)
Actinemys	*marmorata*	Oregon	48.2	12	1.9	37.5	58.4	Holte (1998)
Actinemys	*marmorata*	Oregon	171.1	16	7.7	125	212	Holte (1998)
Actinemys	*marmorata*	Oregon	5.6	27	0.3	3	8.3	Holte (1998)
Actinemys	*marmorata*	Oregon	5.3	27	0.8	0.8	22	Holte (1998)
Apalone	*spinifera*	Vermont	3.1	5	0.1	2	3.7	Graham and Graham (1997)
Chelydra	*serpentina*	Quebec	8.2	113	0.7			Robinson and Bider (1988)
Chelydra	*serpentina*	Quebec	9	21	1.5			Robinson and Bider (1988)
Chelydra	*serpentina*	New York	27.4	40		0.7	89	Petokas and Alexander (1980)
Chelydra	*serpentina*	Minnesota	37	87				Pappas et al. (2009)
Chelydra	*serpentina*	Virginia	99.7	85	12.8	0.3	350	Gotte (1988)
Chrysemys	*picta*	Quebec	89.4	16		1.1	328	Christens and Bider (1987)

Chrysemys	*picta*	Quebec	82.1	17		16.2	617.5	Christens and Bider (1987)
Chrysemys	*picta*	Quebec	99.7	18		18.6	620.5	Christens and Bider (1987)
Chrysemys	*picta*	Tennessee	14.3	8		13.7	15.24	Cagle (1937)
Chrysemys	*picta*	New Mexico	2.3	34	0.4	0.7	11.4	Morjan (2003)
Chrysemys	*picta*	Illinois	32.1	364	1.3	0	86.3	Morjan (2003)
Chrysemys	*picta*	Illinois	34.3	147	2.0			Bowen and Janzen (2008)
Chrysemys	*picta*	Illinois	28.6	158	1.9			Bowen and Janzen (2008)
Chrysemys	*picta*	Illinois	24.7	218	1.7			Bowen and Janzen (2008)
Chrysemys	*picta*	Ontario	20	37		2	50	Whillans and Crossman (1977)
Chrysemys	*picta*	Virginia	43.4	98	6.5	0.3	310	Gotte (1988)
Chrysemys	*picta*	Pennsylvania	8.5	14		2	21.3	Ernst (1970)
Chrysemys	*picta*	Minnesota	66	58				Pappas et al. (2009)
Clemmys	*guttata*	Maine	51	12	9.8	1	120	Joyal et al. (2001)
Emydoidea	*blandingii*	Wisconsin	168	16	22.7			Ross and Anderson (1990)
Emydoidea	*blandingii*	Maine	242	6	56.3	70	410	Joyal et al. (2001)

Emydoidea	*blandingii*	Minnesota	622	138				Pappas et al. (2009)
Emydoidea	*blandingii*	Illinois	815	3	84.0	650	900	Rowe and Moll (1991)
Emydoidea	*blandingii*	Nova Scotia	4.5	46	0.3			Standing et al. (1999)
Emydoidea	*blandingii*	Nova Scotia	2.8	49	0.3			Standing et al. (1999)
Glyptemys	*insculpta*	Minnesota	426	13		100	1609	Piepgras and Lang (2000)
Glyptemys	*insculpta*	Quebec	19.3	60		5	43	A. Walde (pers. comm.)
Glyptemys	*insculpta*	New Hampshire	60.3	9	6.1			Tuttle and Carroll (1997)
Glyptemys	*insculpta*	Ontario	10.4	5	1.7			Hughes et al. (2009)
Graptemys	*flavimaculata*	Mississippi	8	70	0.5	1.3	17.1	Horne et al. (2003)
Graptemys	*oculifera*	Mississippi	18.3	133	1.2	0.33	61.2	Jones (2006)
Kinosternon	*subrubrum*	South Carolina	49.3	68	2.2	17.3	90	Burke et al. (1994)
Kinosternon	*subrubrum*	Virginia	211	24	30.0	0.01	320	Gotte (1988)
Macrochelys	*temminckii*	Florida	12.2	12	2.8	2.5	22	Ewert (1976)
Pseudemys	*alabamensis*	Alabama	63	20	6.3	30	123	Nelson et al. (2009)
Pseudemys	*nelsoni*	Florida	5.3	5				Goodwin and Marion (1977)

Pseudemys	*texana*	Texas	88	108	2.8	15	159	Rose (2011)
Sternotherus	*odoratus*	Pennsylvania	6.6	32		3	11	Ernst (1986)
Sternotherus	*odoratus*	Tennessee	14.3	4		13.7	14.9	Cagle (1937)
Trachemys	*scripta*	Texas	87	52	4.8	10	170	Rose (2011)
Trachemys	*scripta*	Tennessee	14.3	47		13.41	15.24	Cagle (1937)

* When only standard deviation was reported in original citation, standard errors were calculated from available data

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.

	Percentile[c]					
Category	50%	75%	90%	95%	Maximum	*N*[d]
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

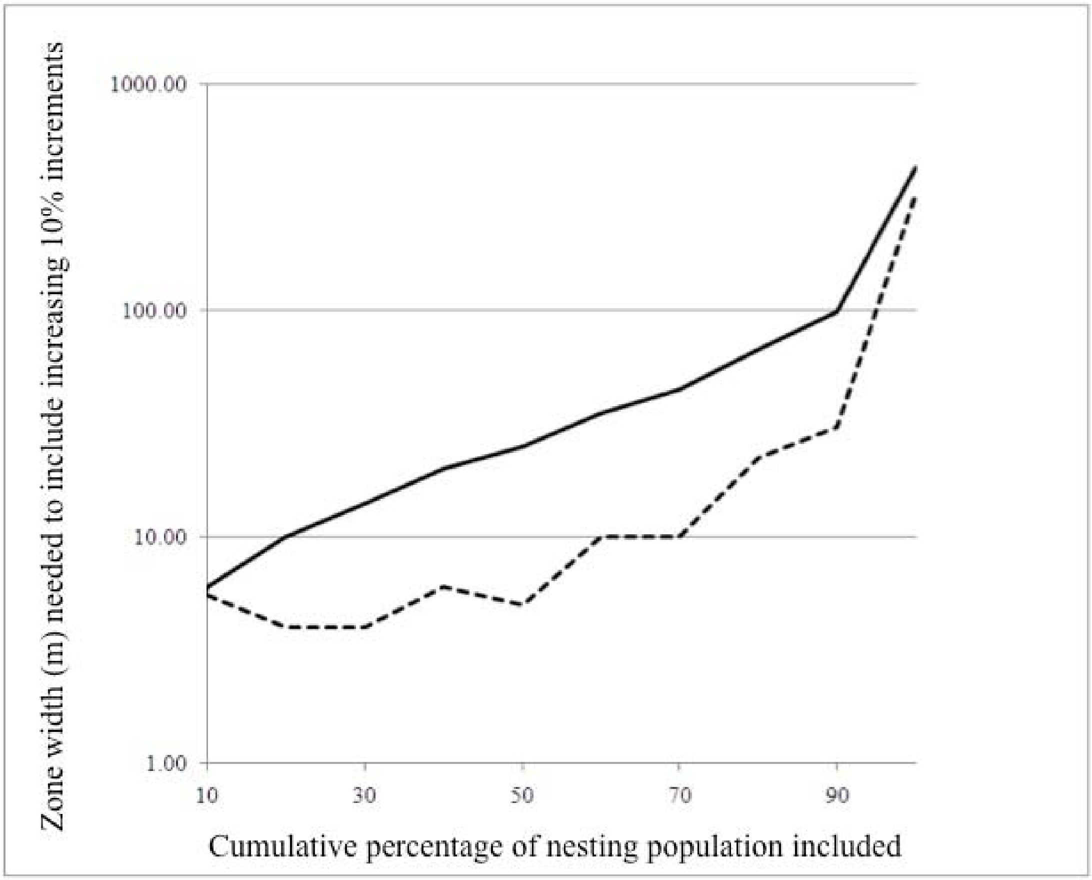
Graptemys	24	46	91	173	252	121
Glyptemys	25	71	150	178	462	151
Kinosternon	118	153	183	206	274	121
Deirochelys	120	239	241	245	247	29
Emydoidea	102	172	302	408	3421	450
Trachemys	816	1251	1345	1396	2206	436

[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


Zone width (m) needed to include increasing 10% increments
1000.00
100.00
10.00
1.00
10
30
50
70
90
Cumulative percentage of nesting population included