Landscape Ecology Approaches to Wetland Species Conservation: a Case Study of Two Turtle Species in Southern Maine

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Abstract: *We investigated the habitat use and movements of two turtle species to assess the importance of conserving multiple wetlands and the upland matrix in which they occur. Spotted turtles (*Clemmys guttata*) and Blanding's turtles (*Emydoidea blandingii*) are considered threatened and endangered, respectively, in Maine where they are near the northeastern periphery of their geographic range. We used resightings of marked individuals (69 spotted, 16 Blanding's) and radiotelemetry (13 spotted, 9 Blanding's, radiotagged for one or two seasons) to investigate the movements and habitat use of both species. Individuals of both species used multiple wetlands throughout the year, including permanent and seasonal pools, forested swamps, and wet meadows. Pools occupied by spotted and Blanding's turtles were small (<0.4 ha), and they were less isolated from other wetlands than pools that did not contain turtles. Both species used uplands extensively for nesting, dormancy, and traveling between wetlands. Turtles traveled 70–570 m (spotted) and 100–1620 m (Blanding's) to nest, and nests were located 1–120 m (spotted) and 70–410 m (Blanding's) from the nearest wetland. Spotted and Blanding's turtles entered relatively dormant stages for 15–89 and 3–21 consecutive days, respectively, and upland dormancy sites were 12–80 m (spotted) and 30–110 m (Blanding's) from the nearest wetland. Total distance traveled overland throughout a season was 0–1680 m and 0–6760 m for radiotagged spotted and Blanding's turtles, respectively. Most spotted turtles followed a seasonal pattern of habitat use: pools for spring activity, upland forest for relative dormancy during part of the summer, and wet meadows or forested swamps for overwintering. A seasonal pattern in the habitat use of Blanding's turtles was not as evident. Our study suggests that protecting small wetlands, maintaining generous terrestrial buffers around individual wetlands, and conserving wetlands in groups are important components of a landscape approach to species conservation.*

Aproximaciones de la Ecología de Paisaje a la Conservación de Especies de Humedales: Estudio de Caso de Dos Especies de Tortugas en el Sur de Maine

Resumen: *Investigamos el uso de hábitat y los movimientos de dos especies de tortugas para evaluar la importancia de conservar múltiples humedales y la matriz terrestre en la que ocurren. Tortugas manchadas (*Clemmys guttata*) y tortugas de Blanding (*Emydoidea blandingii*) están consideradas como amenazadas y en peligro, respectivamente, en Maine donde se encuentran cerca de la periferia noreste de su rango geográfico. Utilizamos reavistamientos de individuos marcados (69 manchadas, 16 de Blanding) y radiotelemetría (13 manchadas, 9 de Blanding, radiomarcadas por 1-2 temporadas) para investigar los movimientos y uso de hábitat de ambas especies. Los individuos de ambas especies utilizaron múltiples humedales a lo largo del año incluyendo charcas permanentes y temporales, ciénagas boscosas y praderas inundadas. Las charcas ocupadas por tortugas manchadas y de Blanding fueron pequeñas (<4 ha), y estaban menos aisladas de los demás humedales que no contenían tortugas. Ambas especies usaron terrenos elevados extensivamente para anidar, para los períodos de aletargamiento,*

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para moverse entre humedales. Las tortugas viajaron entre 50 y 570 m (manchadas) y entre 100 y 1620 m (de Blanding) para anidar, y los nidos se localizaron entre 1 y 120 m (manchadas) y entre 70 y 410 m (de Blanding) del humedal más cercano. Las tortugas manchadas y de Blanding entraron en etapas relativo de letargo por 15-89 y 3-21 días consecutivos, respectivamente, y los sitios de letargo estaban entre 12 y 80 m (manchadas) y 30 y 110 m (de Blanding) del humedal más cercano. La distancia total recorrida en tierra en una temporada varió entre 0 y 1680 m y entre 0 y 6760 m para las tortugas manchadas y de Blanding radiomarcadas respectivamente. La mayoría de las tortugas manchadas tuvieron un patrón estacional de uso del hábitat: charcas para la actividad de primavera, bosque elevado cuando la etapa en letargo la etapa de léfargo relativo durante parte del verano y praderas inundadas o ciénagas boscosas durante el invierno. En los movimientos de la tortuga de Blanding no fue evidente un patrón estacional de uso de hábitat. Nuestro estudio sugiere que la protección de humedales pequeños, la presencia de amortiguadores terrestres alrededor de los humedales y la conservación de humedales en grupos son componentes importantes de una aproximación de paisaje a la conservación de especies.

Introduction

Organisms that inhabit wetlands are often described as having a metapopulation structure (Sjogren 1991; Gibbs 1993; Burke et al. 1995; Vos & Stumpel 1995), based on the assumptions that (1) they form populations within wetlands, either as demes or as groups of conspecifics occupying the same space at the same time, and (2) the populations interact with adjacent populations through emigration and immigration (Hanski & Simberloff 1997). Although the metapopulation concept is no doubt relevant to the conservation of some species, the generality of metapopulation structure in wetland-dependent species has been questioned by some researchers (Laan & Verboom 1990; Sinsch 1992). We describe two freshwater turtle species that challenge the metapopulation paradigm because a single population will use multiple wetlands. This distinction between a metapopulation structure and a single population that occupies an array of habitat patches (Harrison 1991) has important implications for wetland conservation strategies in the United States and elsewhere.

Currently, wetland permit review in the United States rarely addresses the cumulative effects of wetland destruction or protection and infrequently results in the conservation of uplands surrounding a wetland. As a result, wetland regulations fail to protect many wetland flora and fauna (Burke & Gibbons 1995; Findlay & Houlahan 1997; Semlitsch & Bodie 1998). To address these inadequacies, recent studies have emphasized the need for protection of smaller wetlands (Gibbs 1993; Semlitsch & Bodie 1998) and increased protection of wetland buffer zones (Burke & Gibbons 1995; Dodd & Cade 1998; Semlitsch 1998). Although these suggestions may have merit for a subset of biodiversity, they may be insufficient to protect wetland organisms that exhibit frequent interwetland movements and use multiple wetland types, and whose populations are spread out over several wetlands. For such wetland-dependent species, a landscape ecology approach to wetland conservation may be necessary.

Cumulative evidence suggests that the spotted turtle (*Clemmys guttata*) and Blanding's turtle (*Emydoidea blandingii*) have declined in many parts of their range (Cook et al. 1980; Minton et al. 1982; Lovich 1989; Hunter et al. 1999); thus, several states, including Maine, have classified these species as threatened or endangered. Wetland alteration or destruction has been suggested as an important factor in the decline of both species (Minton 1971; Christiansen 1981; Minton et al. 1982; Kofron & Schreiber 1985; Lovich 1989), but relatively little is known about how populations of spotted (Ward et al. 1976; Graham 1995) or Blanding's turtles (Ross & Anderson 1990; Power et al. 1994) use wetland complexes and surrounding uplands or how fragmentation processes affect these species. Spotted turtles are often described as aquatic or semiaquatic, yet they have commonly been recorded in terrestrial habitats (Babcock 1919; Cahn 1937; Ernst et al. 1994). With the exception of Lovich's (1990) description of two males, the extent of this behavior has not been quantified. Interwetland movement by Blanding's turtles has also received scant attention in the literature (Ross & Anderson 1990; Rowe & Moll 1991). As such, the knowledge of habitat use and movements for these species is insufficiently developed and may hamper conservation.

Our goal was to determine whether, to be effective, conservation efforts for spotted and Blanding's turtles in Maine required consideration of multiple wetlands and the upland matrix. Specifically, we measured (1) the number, size, and type of wetlands used by individual turtles, (2) whether wetland isolation was related to wetland occupancy, and (3) the extent of upland use. We also extrapolate from our results to make generalizations about wetland conservation from the perspective of species that use an array of wetlands and their upland matrix.

Methods

Study Area

We collected data from May to November during 1992 and 1993 at a 9-km^2 study area in York County, Maine. The study area was characterized by second-growth northern hardwood forest, uneven terrain (43–110 m elevation), and shallow depth to bedrock; it can be described as forested with pocket wetlands and rocky outcrops. Well-drained Lyman and Hermon soils occurred beneath the upland matrix, whereas the larger wetlands were typically underlain by Chocorua peat and muck (Flewelling & Lisante 1982). The mixed deciduous-coniferous forest was dominated by eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and northern red oak (*Quercus rubra*). The wetlands in the area included forested swamps, scrub-shrub swamps, wet meadows, small seasonal pools (<1 ha), remnant beaver flowages, farm ponds, and an acidic fen. Typical plant species in the wetlands included sphagnum (*Sphagnum* spp.), yellow water lily (*Nuphar advena*), sedges (*Carex* spp. and *Dulichium* spp.), winterberry (*Ilex verticillata*), buttonbush (*Cephalanthus occidentalis*), highbush blueberry (*Vaccinium corymbosum*), and red maple (*Acer rubrum*). The rural study area contained approximately 25 houses and 5 km of roads.

A base map of the study area was delineated from aerial infrared photographs (1:9600) and digitized into a geographic information system (GIS) with ARC/INFO software (ESRI, Redlands, California). We located and digitized the perimeter of 76 wetlands and then georeferenced the map using universal transverse mercator (UTM) coordinates of road intersections that were determined with a global positioning system (GPS). Wetland boundaries were flagged, measured with measuring tape and compass, and sketched to scale. Throughout the field season, we measured the distance the water had receded from the flags and sketched changes in wetland shape. Sketches were digitized into ARC/INFO to estimate changes in water surface area (ha) throughout the season. We obtained temperature and rainfall data from the Sanford Water District, approximately 25 km from the study area.

We captured a total of 69 mature spotted and 16 mature Blanding's turtles by hand or by baited aquatic hoop net and individually marked them by filing the marginal scutes of the shell (Ernst et al. 1974). We also painted identification numbers on the carapace of each turtle with Testor markers (Testor Corp., Rockford, Illinois) to aid identification from a distance. We visually surveyed 35 permanent and seasonal pools for turtles once every 2 weeks (or until they dried up) from late May to early August 1992. During 1993, we resurveyed 21 pools. We classified a pool as occupied if a spotted or Blanding's turtle was sighted during at least one survey. We determined total wetland area (ha) within a 250- and 500-m radius for each pool using ARC/INFO, and these were used as measurements of wetland isolation. Spotted turtles used different types of wetlands during summer and winter, so we measured distance (kilometers) from each pool to the nearest overwintering wetland. An overwintering wetland was defined as a permanent pool, forested swamp, or a riparian meadow. We compared occupied and unoccupied pools using Mann-Whitney tests. We then used logistic regression to examine the effects of wetland isolation on the probability of wetland occupancy.

In addition, we radiotracked several turtles throughout a complete season, approximately May-June through October-November. During 1992, eight female spotted turtles were radiotagged. Eight females were also radiotagged during 1993, three of which had been radio- tagged in 1992. Five female and two male Blanding's turtles were equipped with radiotransmitters during 1992, and four females and one male were radiotagged during 1993. Three of these females had been radiotagged in 1992. We located gravid females twice each day. Otherwise, we located radiotagged turtles once every 2–4 days from May-June through September and one to four times during October–November. Wetlands started to freeze by the time last contact was made in October–November, so we assumed that turtles overwintered in the wetland where they were last radiolocated. Ultimately, turtle radiolocations were entered into the GIS.

Turtles periodically established well-defined terrestrial "forms"—shallow depressions in the ground that were partially or wholly covered with leaf litter or vegetation—and would remain in their forms in a relatively inactive state for >5 days. In general, dormancy in reptiles is not inherently seasonal but may be due to environmental temperature, moisture, photoperiod, and food supply (Hutchison 1979). "Dormant" spotted turtles exhibit intermittent activity (Ward et al. 1976; Ernst 1982; Joyal 1996), perhaps to thermoregulate, avoid predators, or forage.

We classified habitat types used by turtles as permanent pools, seasonal pools, wet meadows, forested swamps (dominated by trees or shrubs), and upland. Permanent pools included semipermanently flooded pools that had surface water throughout the growing season in most but not all years. Seasonal pools were vernal or autumnal, and surface water was usually absent by the end of the growing season (Cowardin et al. 1979). Using only locations 2–4 days apart, we determined the proportion of turtle locations in each habitat type. We tested for differences in habitat use between 1992 and 1993 with a log-likelihood ratio analysis (Zar 1984). Statistical analyses were performed with SYSTAT (Wilkinson 1990).

Results

Wetland Use

Individual radiotagged spotted turtles (n = 16) spent ≥5 days in 1–4 ($\bar{x}$ = 2.3, SD = 0.6) wetlands each season, and Blanding's turtles (n = 12) occupied 1–6 ($\bar{x}$ = 2.8, SD = 1.5) wetlands. Both species used several wetland types, including permanent and seasonal pools, forested swamps, and wet meadows (spotted only) (Fig. 1). We found low

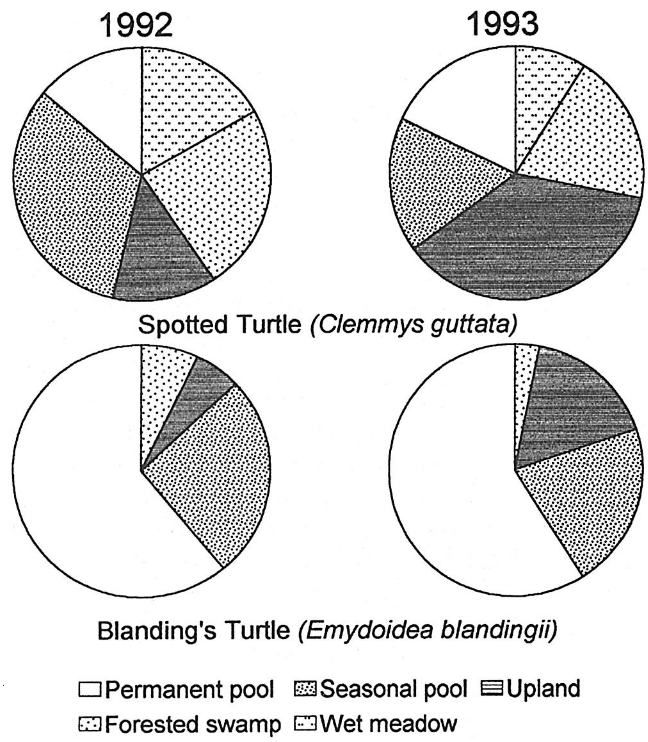

Figure 1. Proportion of locations in each habitat type for spotted and Blanding's turtles radiotracked from late May to September during 1992 and 1993 in southern Maine.

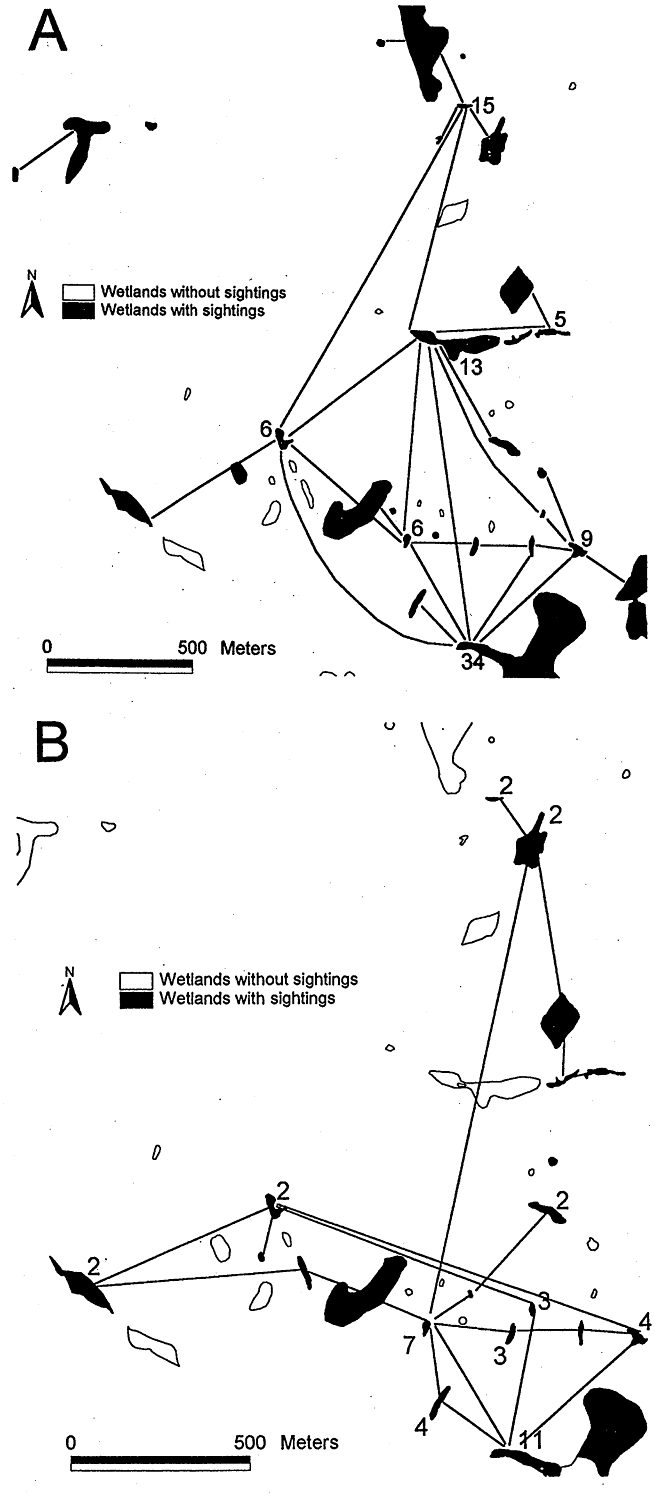

Figure 2. Movement between wetlands (black lines) by (a) spotted turtles (wetlands without numbers had fewer than four unique turtles) and (b) Blanding's turtles (wetlands without numbers had fewer than two unique turtles) in southern Maine during 1991–1993. Movement is based solely on capture data and lines do not necessarily represent actual routes taken by turtles. Wetland numbers correspond to the number of unique turtles captured in that wetland from 1991 to 1993.

numbers of turtles in most wetlands at any given time, and low numbers of unique turtles were captured in each wetland throughout the study period (Fig. 2).

Although the proportion of radiolocations in different habitat types varied among individual turtles, all of the Blanding's turtles used permanent pools, and most spent >50% of their time in this habitat type. Most spotted turtles, however, spent 0–33% of the time in permanent pools. The majority of Blanding's turtles (10 of 14 sites) overwintered in permanent pools, but only a few (3 of 17 sites) spotted turtles remained in permanent pools during winter. Most individuals of both species spent spring and summer in seasonal and permanent pools. In addition, a few individuals (1 of 17 spotted sites; 2 of 14 Blanding's sites) overwintered in seasonal pools that had refilled with water from autumn rain.

Permanent and seasonal pools occupied by spotted and Blanding's turtles were <0.4 ha in size ($\bar{x}$ = 0.146 ha, SD = 0.090, spotted; $\bar{x}$ = 0.176 ha, SD = 0.117, Blanding's) and less isolated than unoccupied pools (Fig. 3). For Blanding's turtles, the difference in surrounding wetland area between occupied and unoccupied pools was significant within a 500-m radius ($\bar{x}$ = 7.078 ha, SD = 3.719, occupied; $\bar{x}$ = 3.595 ha, SD = 2.155, unoccupied; Mann-Whitney test, p = 0.002) but not within a 250-m radius. The opposite was true for spotted turtles (250 m: $\bar{x}$ =

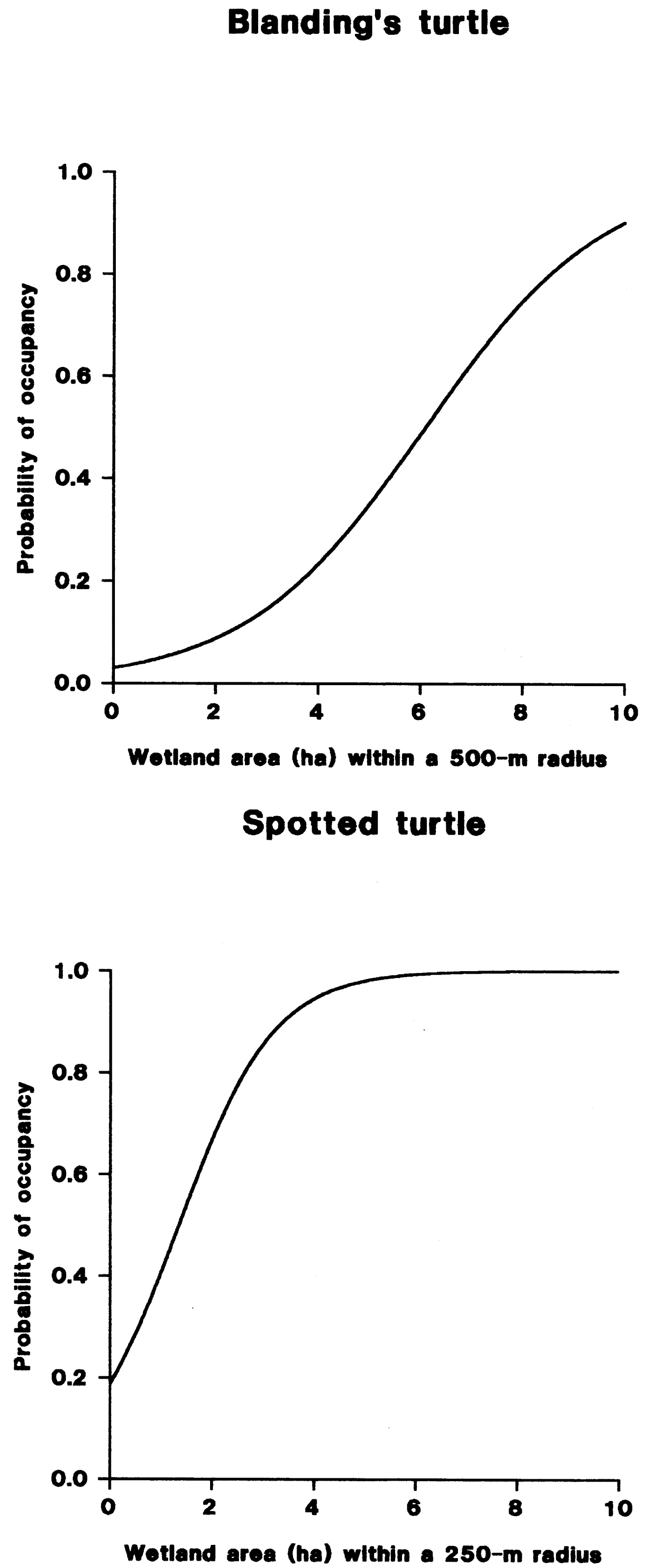

Figure 3. Predicted relationship between wetland isolation and the probability of occupancy by spotted turtles ($B_0 = -1.457$, $B_1 = 1.081$, $G = 7.682$, $p < 0.01$) *and Blanding's turtles* ($B_0 = -3.471$, $B_1 = 0.570$, $G = 11.752$, $p < 0.001$) *in southern Maine during 1992 and 1993.*

1.724 ha, SD = 1.181, occupied; $\bar{x}$ = 0.799 ha, SD = 0.706, unoccupied; Mann-Whitney test, p = 0.009). In addition, pools occupied by spotted turtles were closer to suitable overwintering habitat ($\bar{x}$ = 0.083 km, SD = 0.078) than unoccupied pools ($\bar{x}$ = 0.198 km, SD = 0.156) (Mann-Whitney test, p = 0.019).

Forested swamps were a larger habitat component for spotted turtles than for Blanding's turtles. One spotted turtle nested 2 consecutive years on root hummocks in red maple swamps. Both species used forested swamps for periods of late-summer dormancy. The majority of spotted turtles (10 of 17 sites) overwintered under hummocks in red maple or highbush blueberry swamps, whereas only a few Blanding's turtles (2 of 14 sites) overwintered in this habitat type. We did not observe any Blanding's turtles in wet meadows, yet individual spotted turtles spent up to 77% of their time in this habitat type. Wet meadows were used for periods of late-summer dormancy, and some spotted turtles (3 of 17 sites) overwintered in a riparian meadow.

Upland Use

Turtles used uplands extensively (Table 1; Fig. 1) for nesting, short-term basking (Blanding's only), long-term dormancy, and travel between wetlands. Radiotagged individuals spent up to 74% (spotted) and 38% (Blanding's) of the time in uplands. During June, individuals traveled up to 570 m (spotted) and 1620 m (Blanding's), mostly overland, to nest (Table 1). Most of the nests (12 of 14, spotted; 6 of 6, Blanding's) were located in uplands: 2 Blanding's in outcrops of bedrock, and the rest in human-altered sites such as yards, roadsides, and pastures. Upland nest sites were located up to 120 m (spotted) and 410 m (Blanding's) from the nearest wetland. From 24 May through 8 July we also found radiotagged and untagged Blanding's turtles basking upland (Rowe & Moll 1991), up to 40 m from the nearest wetland boundary. Both species spent extended periods of relative dormancy in upland forest during late summer. Although they were not completely inactive when exhibiting this behavior, much of their time was spent in a form completely covered with leaf litter. These forms were located up to 80 m (spotted) and 110 m (Blanding's) from the nearest wetland (Table 1).

Because most individuals of both species used multiple wetlands annually, they frequently traveled overland between wetlands (Table 1, Fig. 2). Spotted turtles clustered in certain "hotspot" pools during spring and summer, and then scattered to overwinter in many different wetlands (Fig. 2). Likewise, turtles that overwintered communally often dispersed widely in the spring.

The summer (July-August) of 1993 (total rainfall = 14.9 cm; maximum daily temperature $\bar{x}$ = 28.5° C, SD = 3.4;) was drier and warmer than the summer of 1992 (total rainfall = 30.6 cm; maximum daily temperature

Table 1. Summary of use of the wetland patches and upland matrix of a southern Maine forested landscape by spotted and Blanding's turtles.

	Spotted turtle			*Blanding's turtle*		
	mean ± *SD*	*range*	n	*mean* ± *SD*	*range*	n
Distance (m) to nearest wetland from						
upland nest site	51 ± 34	1-120	12	242 ± 138	70-410	6
upland basking site	—	—	—	10 ± 8	1-40	36
upland dormancy site	37 ± 17	12-80	33	78 ± 36	30-110	7
Straight-line distance (m)[a]						
wetland[b] to nest	247 ± 169	70-570	14	633 ± 587	100-1620	6
between wetlands[c]	311 ± 272	110-1150	16	680 ± 550	90-2050	29
Minimum distance traveled (m)[a]						
overland/season[d]	800 ± 480	0-1680	16	2930 ± 2050	0-6760	12
total/season[d]	1120 ± 480	510-2010	16	3918 ± 1926	1320-7000	12

[a]*Data from radiotagged turtles.*
[b]*Wetland that turtle used prior to nesting.*
[c]*Wetlands where turtles spent a minimum of 5 days.*
[d]*Season is defined as approximately May-June to October-November.*

$\bar{x}$ = 26.3° C, SD = 3.4) (Mann-Whitney test of temperatures, $U = 1333, p = 0.003$). As a result, pools dried up and became unavailable earlier in the season during 1993 than during 1992 (Fig. 4).

Habitat use by spotted and Blanding's turtles also differed significantly between years ($G = 65.557$, df = 4, $p < 0.0005$; $G = 20.496$, df = 3, $p < 0.0005$, respectively; Fig.1); both species spent more time upland during 1993 than 1992. This increase in upland use was a result of more turtles entering dormancy in upland sites (8 of 10 spotted turtles in 1993 vs. 4 of 8 in 1992; 4 of 5 Blanding's turtles in 1993 vs. 1 of 7 in 1992) and turtles remaining dormant for longer periods of time (28-89 days in 1993 vs. 15-31 days in 1992 for spotted turtles; 9-21 days in 1993 vs. 9 days in 1992 for Blanding's turtles).

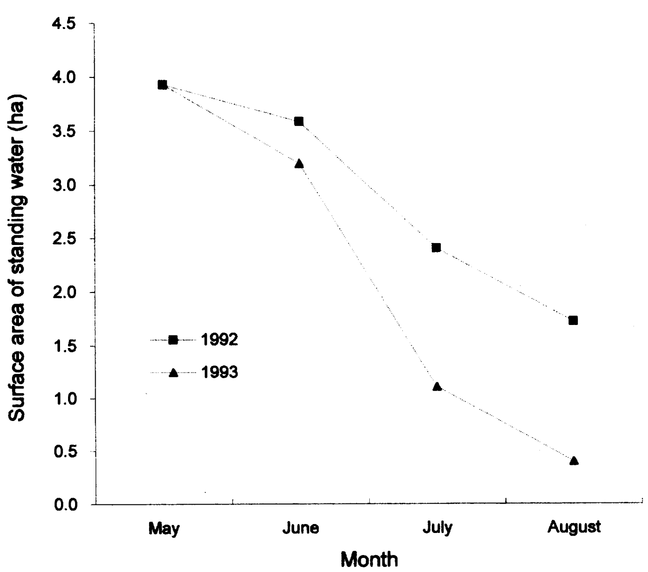

Figure 4. Area of standing water (ha) in surveyed wetlands in southern Maine from May to August of 1992 and 1993.

Seasonal Habitat Use

Most radiotagged spotted turtles seemed to follow a seasonal pattern of habitat use. During early spring, turtles dispersed from their overwintering sites to the small seasonal or permanent pools where most of their spring and summer activity occurred. From late June to early August, individual turtles moved to upland forest and remained relatively inactive for the remainder of the summer. Then, during August or September, they traveled to a forested swamp or wet meadow for overwintering. Some turtles traveled directly from pools to a forested swamp or wet meadow, where they remained until spring.

Blanding's turtles did not make a distinct change in habitat use throughout the season. Instead, individual Blanding's turtles alternated between activity in pools and periodic dormancy in uplands or forested wetlands for 3-21 days from July through September. Unlike spotted turtles, 10 of 14 Blanding's turtles overwintered in one of the pools used during spring or summer.

Discussion

Our study describes the habitat use of two semiaquatic turtle species in an environment that is naturally patchy, both spatially and temporally. This patchiness superficially suggests the existence of a metapopulation in which each wetland contains a local population that can be discussed in terms of extinction and colonization. In this study, however, each wetland (patch) did not support a separate population. Instead, the population structure was dynamic: individual turtles were mobile and used several wetlands of different types as well as the matrix of upland forests. As such, it is doubtful that these two species could self-perpetuate in this environment if development proceeded under current wetland protection statutes, which consider small wetlands and upland habitats to be developable.

Our results suggest three points pertinent to wetland conservation. First, small wetlands merit protection. Both turtle species used small (<0.4 ha) wetlands that are highly susceptible to degradation and destruction. Many of these small wetlands, especially vernal pools, escape detection or fail to meet the size criteria to be eligible for protection. York County has one of the fastest-growing human populations in Maine (Southern Maine Regional Planning Commission 1986), which has resulted in increased residential and commercial development. From the 1780s to the 1980s, Maine experienced a 20% decline in wetlands (Dahl 1990), with the greatest loss occurring in York County (Widoff 1988). Cumulative loss of small wetlands may not be trivial because these wetlands can make up a large percentage of the total wetlands in a landscape, and their loss may also greatly increase the isolation of remaining wetlands (Gibbs 1993; Semlitsch & Bodie 1998).

Second, wetlands need to be conserved in groups or complexes. Individuals of both turtle species used several wetlands, and each wetland had a low number of individual turtles at any one time. Consequently, conserving single wetlands case by case would likely fail to protect these turtles. Important features of wetland complexes include the overall size of the complex, the juxtaposition of wetlands of different types, and wetland isolation. Conservation areas must be large enough to allow for the long distances these turtles travel throughout a season. Furthermore, because Blanding's and spotted turtles occur at low densities in Maine (Joyal 1996; Maine Department of Inland Fisheries and Wildlife, unpublished data), large areas of suitable habitat may be needed to support viable populations. Further demographic research and population viability analyses should offer insights into how large a complex is needed to assure a reasonable probability of long-term persistence for individual species. Where large tracts cannot be protected, active management may be necessary to decrease adult mortality or to increase recruitment. In addition, because both species used different types of wetlands at different times of the year, wetland complexes need to contain a mixture of wetland types in a favorable juxtaposition to accommodate the turtles' seasonal habitat requirements. Furthermore, our results indicate that, within a population, increased wetland occupancy by spotted and Blanding's turtles was related to a decrease in wetland isolation. This suggests that inter-wetland distance may influence the seasonal movements of individual turtles within a population. This individual-scale isolation (Haila et al. 1993) may also have population-scale consequences (Hanski 1982).

Finally, the terrestrial matrix surrounding wetlands needs to be protected. Both species spent significant time in upland forests. For instance, individual turtles spent up to 74% of the active season in upland areas up to 410 m from the nearest wetland. Other studies have also documented "aquatic" turtle species that spend more time than was previously thought in terrestrial environments (Bennett et al. 1970; Burke et al. 1994; Buhlmann 1995). Upland buffers around individual wetlands (Burke & Gibbons 1995; Semlitsch 1998) have been suggested as a means for incorporating both the aquatic and terrestrial habitat required by many wetland inhabitants. This strategy may succeed where a single wetland supports a viable population, but it is based on a small temporal and geographic scale (Semlitsch 1998). Indeed, the buffer-zone approach to conserving wetland biota, although convenient for land-use planners, is likely to be insufficient for some species, especially those for which a "population" is distributed among several wetland and upland habitats and is often difficult to define. We suggest that, for these species, wetland complexes need to be surrounded by an intact upland matrix that allows individuals to move between wetlands and provides other needs such as nesting and dormancy sites. Protecting large, unfragmented wetland complexes and their upland matrix through acquisition, easements, or management agreements might conserve both these species and many others. Houses and roads in such areas should be kept at low densities, because these elements have been associated with reduced wetland biodiversity (Findlay & Houlahan 1997; Lehtinen et al. 1999).

In conclusion, species without discrete population-habitat associations, such as the turtles described here, may require a reserve approach to wetland conservation. This approach differs from that of current reserves, which focus narrowly on large, obvious wetlands, and instead would conserve large areas containing a cluster of wetlands of a variety of sizes and all interceding uplands. This approach would augment other forms of wetland conservation (Gibbs 1993; Burke & Gibbons 1995; Semlitsch 1998; Semlitsch & Bodie 1998) and would require more of a landscape perspective.

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