

## Seasonally Dynamic Habitat Use by Spotted (*Clemmys guttata*) and Blanding's Turtles (*Emydoidea blandingii*) in Maine

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**ABSTRACT.**—We used radio-telemetry to investigate the seasonal dynamics of wetland use by Spotted Turtles (*Clemmys guttata*) and Blanding's Turtles (*Emydoidea blandingii*) in southern Maine. Habitat use was examined in a temporally segregated manner, comparing wetland use among seasonally discrete activity periods. Distinct seasonal movement patterns were detected and logistic regression revealed significant differences in wetland characteristics across seasons for both species. Spotted Turtles exhibited a positive association with wetlands hosting abundant Wood Frog (*Lithobates sylvaticus*) egg masses in spring, and a negative association with forested wetlands from spring through late summer. Blanding's Turtles were closely associated with forested wetlands in spring, wetlands with abundant Wood Frog egg masses and good sun exposure in early summer, and deep-water wetlands in late summer and fall. The seasonal differences in habitat use found in this study highlight the complex and dynamic landscape required to sustain these rare turtles. Spotted and Blanding's Turtles' diverse habitat requirements require frequent terrestrial movements, exposing them to threats for which mitigation requires understanding spatial and temporal shifts in habitats use.

Understanding temporal variability in habitat relationships can aid in the identification of important seasonal trends in how animals meet their ecological and energetic needs (Sinclair, 1975). The habitat ecology of semiaquatic freshwater turtles is especially complex because individuals often make far-ranging terrestrial movements among a variety of wetlands for mating, foraging, basking, aestivating, and overwintering purposes (Bennett et al., 1970; Buhlmann and Gibbons, 2001; Bowne et al., 2006). The study of turtle movements among disjunct wetlands is also important to conservation and management because extensive overland travel may expose them to multiple threats, most notably road mortality (Gibbs and Shriver, 2002; Aresco, 2005; Beaudry et al., 2008; Litvaitis and Tash, 2008).

Spotted Turtles (*Clemmys guttata*) and Blanding's Turtles (*Emydoidea blandingii*) are two North American semiaquatic species that are known to use a number of aquatic ecosystems during an activity season (Ross and Anderson, 1990; Ernst et al., 1994; Piepgras and Lang, 2000). Throughout their range, habitat use changes seasonally for both Spotted Turtles (Haxton and Berrill, 1999; Litzgus and Brooks,

2000; Milam and Melvin, 2001) and Blanding's Turtles (Rowe and Moll, 1991; Rubin et al., 2001). In Maine, where Spotted and Blanding's Turtles occur near the northeastern edge of their range, both species typically visit a number of different wetlands over the course of the year by making frequent terrestrial movements (Joyal et al., 2001; Beaudry et al., 2008), presumably driven by the need for seasonally changing resource requirements. Both species emerge from overwintering in need of raising their body temperature through basking to increase metabolic rate (Jackson, 1971) and activity levels (Parmenter, 1980). Food resources then become critical to providing the energy used for growth and reproduction (Krawchuck and Brooks, 1998). After the nesting season, turtles may sustain activity or use aquatic and terrestrial refugia where activity is considerably reduced (Ernst et al., 1994; Perillo, 1997; Litzgus and Brooks, 2000; Joyal et al., 2001), followed in late summer and fall by movements to aquatic hibernacula, which in Maine are often permanent wetlands or seasonal pools (Joyal et al., 2001; Beaudry, 2007). Further research is needed across the geographical range of these and other semiaquatic turtles to fully understand temporal differences in species association with both wetland type and within-wetland characteristics.

Our goal for this study was to investigate and contrast the habitat ecology of Spotted and Blanding's Turtles near the northeastern edge of

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their ranges. Over a three-year period, we used radio-telemetry to monitor the movements of 40 Spotted and 50 Blanding's Turtles in southern Maine, first, to identify potential distinct temporal shifts in interwetland movement and habitat use and, second, to relate these patterns to seasonally dynamic habitat and life-history needs. The landscape of southern Maine supports a high density and diversity of wetlands that include small, isolated vernal pools to larger, permanent swamp and marsh complexes. We expected that both Spotted and Blanding's Turtles would hibernate in permanent, deep-water wetlands with subsequent movement to various wetland types during the spring and prior to the nesting season. Following the nesting season and through late summer, we expected both species to either sustain activity or to enter aestivation, eventually moving to hibernation sites in the fall.

#### MATERIALS AND METHODS

**Study Area.**—We conducted fieldwork at six study sites located in York County, Maine, (43°N, 70°W), an area with average road density ranging from 0.30–1.35 km/km<sup>2</sup>. Topography consists of low-elevation (<100 m), uneven terrain with shallow soils, rocky outcrops, and a high density of pocket wetlands. Land cover is mostly mixed broadleaf and coniferous secondary or tertiary growth forest interspersed with low to moderate density residential developments. Common wetland types are wet meadows, vernal pools, red maple (*Acer rubrum*) swamps, and scrub-shrub swamps dominated by highbush blueberry (*Vaccinium corymbosum*), buttonbush (*Cephalanthus occidentalis*), and winterberry (*Ilex verticillata*). Average minimum/maximum temperatures for 1 April and 31 October in Sanford, Maine (≤30 km from the study sites) are -2°C/7°C and 0°C/10°C, respectively, whereas the average maximum temperature peaks at 25°C in early August (National Climatic Data Center).

**Radio-Telemetry.**—We conducted radio-telemetry between April and November over a three-year period (2004–06). Turtles were captured by hand or with baited hoop-net traps starting at spring thaw in early April. Adults were fitted with a radio-transmitter positioned near the posterior carapace margin. Lotek MBFT, NTB (Newmarket, Ontario), and Holohil RI-2B (Carp, Ontario) transmitters were affixed with Biocryl rapid-curing dental acrylic (Great Lakes Orthodontics, Tonawonda, New York). Average transmitter mass, including acrylic, was 14.9 g (range: 11.4–19.2) for Spotted and 39.9 g (range: 32.5–55.6) for Blanding's Turtles, corresponding to 3–6% of body mass (Spotted Turtles: 268.5g ±

44.6 SD; Blanding's Turtles: 1361.6g ± 236.5 SD). Turtles were released at the site of capture within 24 h.

Each radio-tagged turtle was relocated every three to four days with a hand-held antenna and a digital receiver. Turtle locations were recorded with a hand-held GPS unit or on a one-foot resolution digital orthorectified quadrangle image (DOQ) acquired in May 2003 (Maine Office of GIS). Each radio-tagged individual was tracked for a single active season, generally five to seven months. Forty adult Spotted Turtles (24 females, 16 males) and 50 adult Blanding's Turtles (23 females, 27 males) were radio-tagged for one spring-to-fall field season each between 2004 and 2006.

**Habitat Measurements.**—Measuring habitat characteristics while turtles occupy a wetland can create a disturbance prompting turtles to move. To avoid disturbing turtles and thereby influencing movements, we measured habitat characteristics of wetlands the summer following use. Variables were selected based on observations from the 2004 field season, and prior research on Spotted and Blanding's Turtles in Maine (Joyal, 1996) and Massachusetts (Milam and Melvin, 2001). Forest type within a 10-m buffer around the wetland was recorded as deciduous (>80% deciduous), mixed, or coniferous (>80% coniferous). Sun exposure (the amount of time the sun is above the tree skyline on 1 May) was estimated by using a sun chart (University of Oregon: <http://solardat.uoregon.edu/SunChartProgram.html>) while standing at the sunniest location in the wetland. Wood Frogs (*Lithobates sylvaticus*) may be an important source of protein in the wetlands used by Spotted and Blanding's Turtles. Spotted Turtles have been observed feeding on Wood Frog egg masses (Milam and Melvin, 2001; Gibbs, 2007) and anuran tadpoles (*Anaxyrus*, *Lithobates*, or unspecified: Ernst, 1976; J. E. Lovich, pers. obs. cited in Ernst et al., 1994; Colburn, 2004; Gibbs, 2007. *Lithobates sylvaticus*: Milam and Melvin, 2001). Blanding's Turtles have been observed feeding on tadpoles (unspecified genus: Cahn, 1937; Ross, 1987; Colburn, 2004; Gibbs, 2007. *Lithobates sylvaticus*: PGD, pers. obs.). As a potentially important food resource, Wood Frog egg masses were counted in each wetland starting after the Wood Frog chorus peak and ending at the start of egg mass hatching (a 9- to 14-day period). Percent cover was visually estimated for the following vegetation types: tree (>5 m in height), shrub (woody stems, <5 m in height), aquatic emergent vegetation (e.g., *Carex* spp.), floating or submerged macrophytes (e.g., *Potamogeton* sp.), and sphagnum moss. Tree cover and shrub

cover included plants rooted on the periphery with a canopy extending over the wetland, or growing within it. Water depth was measured at the wetland's deepest point. To minimize temporal variations, water depth was recorded for every wetland over a single 11-day period, from 27 June to 7 July 2006. The area covered by roads, buildings, fields, right-of-ways, or recent (<10 year) forest cuts within 25 m of the wetland's edge was estimated in the field as percentage of land disturbed. We categorized each wetland following the National Wetland Inventory (NWI) classification (Cowardin et al., 1979). Wetlands with composite NWI classes were assigned the dominant class. Wetland area was estimated by digitizing the outline over the DOQ images. All variables except the count of Wood Frog egg masses and water depth were measured near the peak in vegetation growth during July 2005 and 2006.

For analyses of habitat use, the sample of radio-tagged turtles was restricted to 2004 and 2005, because only the wetlands used during those years were revisited for habitat measurements. Habitat characteristics were measured at 228 of the 230 wetlands used in 2004 and 2005 by 31 radio-tagged Spotted Turtles (78 wetlands) and 37 radio-tagged Blanding's Turtles (175 wetlands; Table 1), with some overlap (23 wetlands) in use between the two species. Two wetlands were excluded because access for habitat characterization was not granted by the landowners. Furthermore, because of time constraints, we only counted Wood Frog egg masses at 183 wetlands and measured water depth at 182 wetlands.

*Statistical Analyses.*—For each turtle species, all wetlands visited by any number of radio-tagged individuals for any length of time constituted use. Wetlands used by turtles were pooled across all individuals for each species but within discrete activity periods. Activity periods were defined by examining the seasonal pattern of interwetland movements using telemetry data from 2004–06 for all radio-tagged turtles. We define interwetland movement length, for an individual, as the distance between two successive telemetry locations occurring in different wetlands. We plotted average daily interwetland movement distances as a running mean with a window length of 10 days for Spotted Turtles and 15 days for Blanding's Turtles, with sexes pooled. Sampling duration was selected as the shortest time period required to visually detect trends among variable individual movement patterns as represented by  $\pm 1$  SE about the mean. Movement data were matched with field observations (e.g.,

nesting, aestivation, movements to wintering wetlands) and used to define activity periods.

Habitat selection analyses generally assume that animals have access to all potentially available resource units (Garshelis, 2000; Manly et al., 2002). However, Blanding's and Spotted Turtles are both species whose daily mobility is relatively limited but whose annual activity area includes sizeable landscapes. We avoided violating assumptions regarding which wetlands were available to turtles by examining habitat use across a series of time periods. For each wetland, a binary response variable was assigned for each activity period: used during a period versus not used but used during one or more other period (and, thus, available). The wetland type and measured characteristics comprised the independent variables. Variable distributions were transformed when data did not conform to the assumption of parametric statistical analyses. Dummy variables were created from the categorical variables: forest type was recoded into deciduous forest (DEC\_FOR), mixed forest (MIX\_FOR), or coniferous forest (CON\_FOR). One pair of forest type variables showed a correlation coefficient greater than 0.85 and so MIX\_FOR was removed to reduce multicollinearity. Water depth was recoded as DEPTH\_LOW (0–45 cm for Spotted Turtles, 0–60 cm for Blanding's Turtles), DEPTH\_MED (45–90 cm for Spotted Turtles, 60–120 cm for Blanding's Turtles), and DEPTH\_HI (>90 cm for Spotted Turtles, >120 cm for Blanding's Turtles). We classified wetland types as PFO (forested wetland), PUB (unconsolidated-bottom wetland), PSS (scrub-shrub wetland), PEM (emergent wetland), or LIUB (unconsolidated-bottom lake or reservoir).

To identify variables that could influence seasonal wetland choice, we conducted a combined forward and backward stepwise logistic regression for each period, with variables entered and removed from the model at a threshold of  $P = 0.20$  (Hosmer and Lemeshow, 2000). Statistical significance of the model and of individual variables was evaluated at  $P = 0.05$ . The importance of each variable as a predictor was assessed by dividing the coefficient estimate by the standard error yielding a  $t$ -ratio statistic, and the associated  $P$ -value was reported (Steinberg and Colla, 2004). The fit of each model was assessed using a likelihood-ratio chi-square test (Steinberg and Colla, 2004). The explanatory power of each model was estimated with the McFadden's Rho<sup>2</sup>-value, an analogue of the  $r^2$ -statistic used in linear regression (Steinberg and Colla, 2004). McFadden's Rho<sup>2</sup>-values are generally much lower than equivalent  $r^2$ , and estimates between 0.2 and 0.4 are considered as having a high

TABLE 1. Wetland characteristic variables used in habitat use analyses and descriptive statistics (all activity periods combined) for Spotted and Blanding's Turtles in Maine, 2005–06. For categorical variables, the number of wetlands in each category is reported.

Variable	Description	Spotted Turtles				Blanding's Turtles			
		Mean	SD	Min	Max	Mean	SD	Min	Max
WFEGG	Count of Wood Frog egg masses	86.2	138.91	0	595	90.9	106.00	0	517
SUN (hr)	Sun exposure	6.0	3.50	0.5	12.5	5.3	3.25	0	12.5
DISTURB (%)	Land disturbance	9.2	17.21	0	80	13.4	23.29	0	100
TREE (%)	Tree canopy cover	42.8	27.19	0	100	42.9	27.38	0	100
SHRUB (%)	Shrub cover	54.8	26.05	12	100	47.0	28.86	0	100
EMERG (%)	Aquatic emergent vegetation cover	54.0	36.59	0	100	32.1	33.19	0	100
SUBMERG (%)	Submergent, floating macrophyte cover	1.7	6.51	0	40	1.2	4.88	0	40
SPHAGN (%)	Sphagnum cover	61.2	38.34	0	100	46.6	38.76	0	100
AREA (ha)	Area	1.60	3.67	0.003	24.19	1.56	7.31	0.009	84.58
FOREST	Wetland or riparian forest type	Deciduous = 4, mixed = 73, coniferous = 1							
DEPTH (cm)	Water depth	Low = 28, medium = 23, high = 12							
NWI	Wetland type	PFO = 31, PUB = 14, PSS = 19, PEM = 14							

explanatory power (Steinberg and Colla, 2004). Differences between sexes were investigated by coding sex as a variable in each general model. When sex was selected as a significant variable, a supplementary analysis was repeated for each sex for that period. To compare overall wetland use between species, we pooled all used wetlands and compared the mean value for each variable using *t*-tests or Mann-Whitney *U*-tests.

It is unknown whether resource use by a radio-tagged turtle was independent of resource use by other radio-tagged turtles: ignoring territoriality or gregarious behavior may increase type I error rates (Erickson et al., 2001). We sought to minimize bias in variance estimates resulting from these statistical issues by maximizing annual sample sizes; ours is among the largest of any radio-telemetry study for either species.

RESULTS

We radio-tracked turtles beginning in early April or May through September to early November, for an average of  $162 \pm 30.5$  SD days for Spotted Turtles and  $155 \pm 34$  SD days for Blanding's Turtles. The earliest interwetland movement occurred on 11 April (2006) for Blanding's Turtles and on 29 April (2005) for Spotted Turtles. Spotted Turtles used an average of  $3.4 \pm 2.14$  SD unique wetlands per year (range: 1–9) compared to  $6.5 \pm 3.45$  SD wetlands per year (range: 1–20) for Blanding's Turtles, with no difference between sexes for either species (Spotted Turtles:  $t_{38} = 0.37, P = 0.714$ ; Blanding's Turtles:  $t_{48} = 0.83, P = 0.412$ ). The median distance between successive visits to wetlands by Spotted Turtles was 186 m (SD: 154 m, range: 36–1151 m;  $N = 161$  movements) and by Blanding's Turtles was 272 m (SD: 379 m, range: 5–3670 m;  $N = 397$ ). There were no intersexual differences in mean distance traveled between wetlands in either species (Spotted Turtles: Mann-Whitney  $U_{51, 107} = 2681.5, P = 0.863$ ; Blanding's Turtles: Mann-Whitney  $U_{175, 222} = 15787, P = 0.054$ ).

Four activity periods were defined for Spotted Turtles (Fig. 1A): spring (basking, foraging and mating period following emergence from wintering wetlands), early summer (foraging and nesting), late summer (reduced activity and aestivation), and fall (movements to deeper wetlands for overwintering). Similar phenological periods were defined for Blanding's Turtles with the exception of late summer and fall. A lack of a change in movement patterns, beginning in late July, led us to merge the late summer and fall seasons (Fig. 1B). Nesting occurred between 12 and 29 June for Spotted

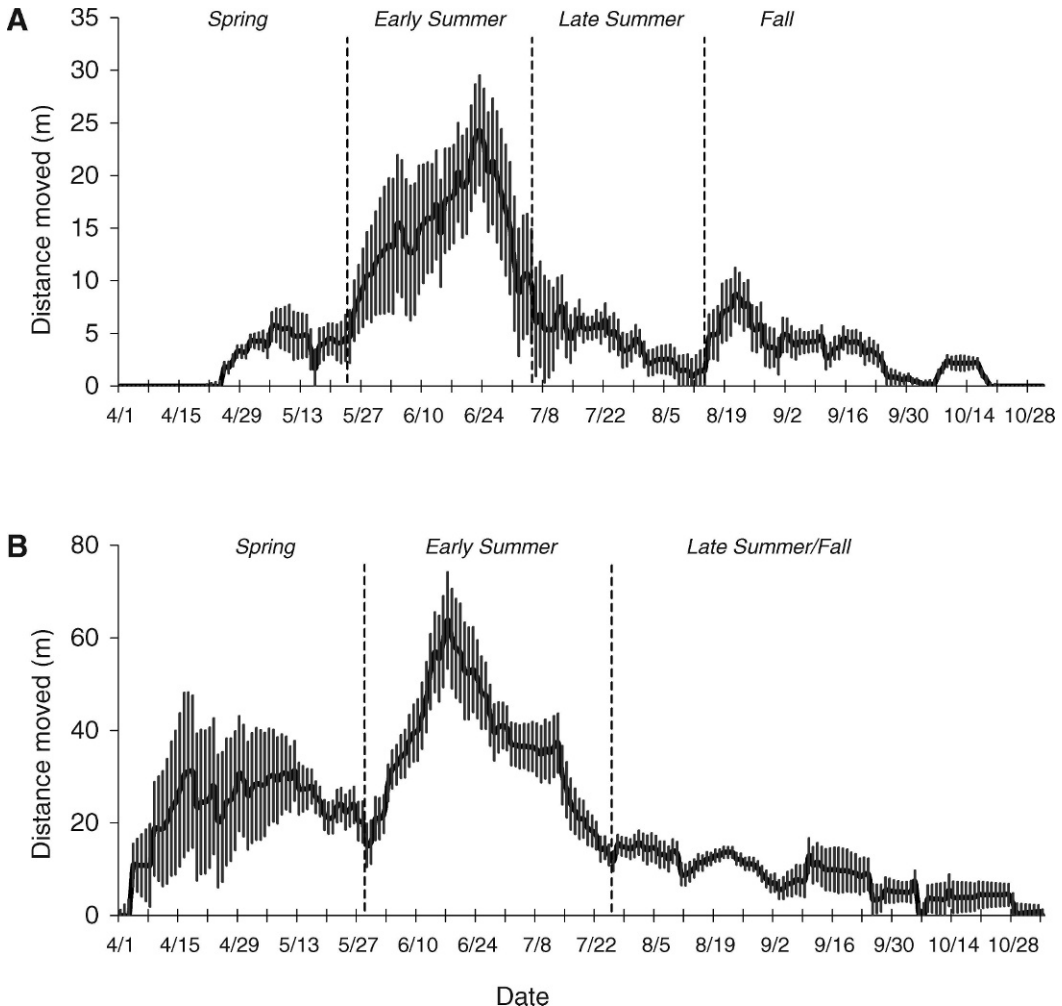


FIG. 1. Mean ( $\pm$  SE) daily interwetland movement distances of (A) Spotted Turtles (40 individuals, 10-day running mean) and (B) Blanding's Turtles (50 individuals, 15-day running mean) during annual active season, 2004–06. Activity period threshold dates are 24–25 May, 5–6 July, and 14–15 August for Spotted Turtles, and 29–30 May and 25–26 July or Blanding's Turtles. Interwetland movement distance corresponds to the distance between two successive telemetry locations occurring in different wetlands.

Turtles ( $N = 11$ ) and between 15 and 30 June for Blanding's Turtles ( $N = 23$ ).

The stepwise logistic regression produced models with adequate fit to the data for both Spotted Turtles (Table 2) and Blanding's Turtles (Table 3). In spring, Spotted Turtles used wetlands with abundant Wood Frog egg masses. Spotted Turtles showed a negative association with forested swamps (PFO) in spring, early summer, and late summer and in the fall used wetlands with high sun exposure (Table 2). The amount of sample variance explained was highest for the spring model and lowest for the fall model. Blanding's Turtles used wetlands within deciduous forest and with

a high cover of sphagnum in spring and with high sun exposure and Wood Frog egg mass count in early summer. During late summer and fall, Blanding's Turtles were associated with deep-water wetlands (Table 3). An association with unconsolidated-bottom wetlands (PUB) was apparent in late summer/fall. The amount of sample variance explained was highest for models in the early summer and late summer/fall periods.

We observed evidence of aestivation for 77.5% of radio-tagged Spotted Turtles (31 of 40) for periods varying from less than four days to over seven weeks. Terrestrial aestivation occurred in the leaf litter under the forest

TABLE 2. Results from a stepwise logistic regression of seasonal habitat use for Spotted Turtles in southern Maine, 2004–06. Significant ( $P < 0.05$ ) variables from selected models are shown, abbreviated as follows: WFEGG = count of Wood Frog egg masses, TREE = tree canopy cover, PFO = forested wetland, SUN = sun exposure.

Seasons	Likelihood-ratio $\chi^2$ ( $P$ )	McFadden's $Rho^2$	Variables	Coefficient	$P$
Spring	0.001	0.245	WFEGG	1.224	0.009
			TREE	0.072	0.013
			PFO	-1.871	0.047
Early summer	0.002	0.217	PFO	-2.646	0.003
Late summer	0.001	0.214	PFO	-2.507	0.003
Fall	0.014	0.162	SUN	0.061	0.019

canopy, in dried beds of ephemeral wetlands, or in floating sphagnum mats. No aestivation period was apparent for Blanding's Turtles.

No significant differences between the sexes in habitat use were detected for Spotted Turtles in any season. The positive association with deeper wetlands in the fall was significant for both sexes of Blanding's Turtles (Table 3) but with a larger slope coefficient for females (male  $\beta = 2.272$ ,  $P = 0.032$ ; female  $\beta = 8.485$ ,  $P = 0.001$ ). When habitat use of Spotted and Blanding's Turtles was compared with all seasons combined, Spotted Turtles used wetlands with higher mean emergent cover ( $t_{253} = -4.528$ ,  $P < 0.001$ ) and higher mean sphagnum cover ( $t_{253} = -3.172$ ,  $P = 0.001$ ) than Blanding's Turtles.

#### DISCUSSION

Turtle activity patterns showed clear seasonality with distinct patterns in interwetland movements during the year. For Spotted Turtles, inter-wetland movements peaked during the nesting season (late May to early July). Other reported nesting seasons for Spotted Turtles overlap closely with the egg-laying dates observed in Maine (Haxton and Berrill, 1999; Litzgus and Brooks, 2000), although a South Carolina population nested from early May through June (Litzgus and Mousseau,

2004). Our early summer period coincides closely to the nesting season, but our definition includes pre-egg-laying activities such as movements toward nesting sites and abandoned nesting attempts. Movements were infrequent after the nesting season, and very few were recorded in late summer. Spotted Turtles aestivated in shaded upland areas during the late summer period. Similarly, Spotted Turtles in Ontario populations showed low activity levels during postnesting periods from late June through late August (Haxton and Berrill, 1999; Litzgus and Brooks, 2000). Our Spotted Turtles reached their overwintering wetland by mid-October, as was observed in Ontario (Haxton and Berrill, 1999; Litzgus and Brooks, 2000) but later than in Massachusetts where all turtles were near their hibernacula by late September (Milam and Melvin, 2001).

Seasonally, Blanding's Turtles were active earlier than were Spotted Turtles and began frequent successive visits to vernal ponds from relatively deep overwintering ponds in April and May. The large year-to-year variation in spring movements, evident as large standard error values in Figure 1B, may be the result of differences in the timing of ice melt. As in Spotted Turtles, peak movement activity for Blanding's Turtles was in June and early July, overlapping with the nesting season. Other

TABLE 3. Results from a stepwise logistic regression of seasonal habitat use for Blanding's Turtles in southern Maine, 2004–06. Significant ( $P < 0.05$ ) variables from selected models are shown, abbreviated as follows: DEC\_FOR = deciduous riparian or wetland forest (dummy variable), SPHAGN = sphagnum cover, SUN = sun exposure, WFEGG = count of Wood Frog egg masses, DEPT\_HI = high water depth (dummy variable), PUB = unconsolidated bottom wetland.

Seasons	Likelihood-ratio $\chi^2$ ( $P$ )	McFadden's $Rho^2$	Variables	Coefficient	$P$
Spring	0.005	0.094	DEC_FOR	1.394	0.022
			SPHAGN	0.023	0.044
Early summer	< 0.001	0.206	SUN	0.017	0.002
			WFEGG	0.142	0.014
Late summer/fall	< 0.001	0.347	DEC_FOR	-1.249	0.033
			DEPT_HI	3.712	< 0.001
			PUB	1.609	0.039

reported nesting seasons largely overlapped with our observations but started earlier in Illinois (26 May; Rowe and Moll, 1991) and ended later in Minnesota (11 July; Piepgras and Lang, 2000). We found little evidence of aestivation in Blanding's Turtles, with a low but steady number of interwetland movements observed during the postnesting period, ceasing in late October. In a Massachusetts study, postnesting movements were distinguished as those moving away from ephemeral wetlands to hibernacula (Grgurovic and Sievert, 2005). We did not observe a change in movement patterns or behavior that justified treating the last two seasonal periods separately for Blanding's Turtles. Interwetland movements were relatively infrequent after August and turtles arrived at the overwintering wetlands anytime between late July and October. Movements to overwintering sites in Minnesota occurred comparatively later, in October and November (Piepgras and Lang, 2000).

From April through May, Spotted Turtles used wetlands characterized by abundant Wood Frog egg masses and high tree cover and avoided forested (PFO) wetlands. In both early and late summer, Spotted Turtles continued to avoid forested wetlands, and in the fall they used wetlands with high sun exposure. Our findings add to previous observations from Maine where Spotted Turtle wetland use was positively associated with wetland size, hydroperiod, sun exposure, proximity to hibernation site, and total wetland area within a radius of 250 m (Joyal, 1996). In spring, Spotted Turtles used wetlands with abundant Wood Frog egg masses, potentially a relative measure of available protein in those wetlands. During May and June, Wood Frogs and other amphibians appear to be one of the most abundant sources of animal protein in eastern U.S. ephemeral wetlands (e.g., in terms of biomass: Gibbons et al., 2006; proportion of wetlands occupied: Baldwin et al., 2006), where they are preyed upon by several vertebrate and invertebrate taxa (Mitchell et al., 2008; Kenney and Burne, 2001). Wood Frog egg masses are indicative of hydrologically isolated, fishless vernal pools (Colburn, 2004; Calhoun and deMaynadier, 2008), and their inclusion in the spring habitat use model is consistent with the spring use of vernal pools by Spotted Turtles in Massachusetts (Milam and Melvin, 2001). Spotted Turtles' negative association with forested wetlands in spring, early and late summer may be explained by the temporally segregated nature of our analysis. The strength of this negative relationship may be caused partly by a positive relationship with forested wetlands during the fall and partly by positive relationships in spring, early summer,

and late summer with other common wetland types: unconsolidated-bottom, scrub-shrub, and emergent wetlands. The use of wetlands with a high sun exposure in the fall is difficult to interpret. Although it may reflect the importance of choosing wintering wetlands with good sun exposure in early spring when turtles become active (Haxton and Berrill, 2001), it is seemingly contradictory with the potentially disproportionate use of forested (perhaps less sunny) wetlands during that period.

In addition to seasonal changes in the types of wetlands used, we found evidence of seasonal changes in habitat use reflected in within-wetland characteristics such as cover types or sun exposure. Our observations contrast with other studies of Spotted Turtle habitat, in which only seasonal changes in wetland type have been reported (Haxton and Berrill, 1999; Litzgus and Brooks, 2000; Milam and Melvin, 2001; Litzgus and Mousseau, 2004). From these studies, it appears that Spotted Turtles make wide use of available wetland types, with seasonal preferences that vary quite extensively between locations. Aestivation in Spotted Turtles appears to occur in a wide range of habitats in other areas as well, with a trend toward a greater use of terrestrial sites in the northern part of the turtle's range (Litzgus and Brooks, 2000).

In the early summer through fall periods, Blanding's Turtles used wetlands with high numbers of Wood Frog egg masses, a potentially important source of food. The beginning of the early summer period coincides with Wood Frog metamorphosis in southern Maine (Hunter et al., 1999), a phase during which Wood Frogs often remain at or near the water's edge, are slow and susceptible to predation. Alternatively, high levels of Wood Frog reproduction may be correlated with another variable of importance to the life history of Blanding's Turtles—semipermanent wetlands with a long hydroperiod that can serve as late season refugia and overwintering sites (Babbitt et al., 2003; Baldwin et al., 2006). Wetlands used by turtles during spring and early summer had high sun exposure and were most often located within deciduous forests. Both variables were likely related to the early season basking behavior exhibited by Blanding's Turtles, when basking was observed to occur mostly on the forest floor near wetlands prior to leaf emergence. After tree leaves came out, we did not observe basking outside of wetlands but rather from locations within the wetlands (FB pers. obs.). Thermoregulation through basking is a dominant behavior for Blanding's Turtles in spring and early summer (Sajwaj and Lang, 2000), and wetland use has previously been correlated with sun exposure in Maine (Joyal,

1996). The sample of wetlands used in the late summer and fall seasons include many that were used as hibernacula, which could explain the importance of water depth in that period's regression model. The use of deep wetlands in the fall in preparation for overwintering is likely advantageous in limiting the risk of predation and the possibility of the wetland drying out or freezing to the bottom.

We found that Blanding's Turtles were associated with sphagnum moss during spring but not with other vegetation variables at any time during the year. In contrast, Blanding's Turtles in New York showed an association with submerged aquatic vegetation in late July and August and a general selection for button-bush (Hartwig and Kiviat, 2007). Similar observations have been made in Illinois, where Blanding's Turtles moved to more highly vegetated and heterogeneous wetlands in July (Rowe and Moll, 1991). The only significant wetland type relationship among our Blanding's Turtle habitat models is the use of unconsolidated-bottom wetlands (PUB) in late summer and fall, a type that includes vernal pools and other small semipermanent wetlands. Elsewhere, wetland type also had an effect on Blanding's Turtle use in Minnesota, where shrub swamps were associated with longer residency times (Piegras and Lang, 2000).

The seasonal differences in habitat use found in this study highlight the complex and dynamic landscape required to sustain Spotted and Blanding's Turtles. Specifically, we found that both turtles use a variety of widely scattered wetland types in an attempt to fulfill seasonally shifting ecological needs. Future studies should focus on how potentially limiting resources such as food, thermal conditions, and the presence of conspecifics drive interwetland movements in Spotted and Blanding's Turtles. Frequent terrestrial movements expose Spotted and Blanding's Turtles to potentially unsustainable sources of adult mortality including road kill and illegal collection (Congdon et al., 1993; Garber and Burger, 1995; Heppell, 1998; Steen and Gibbs, 2004). Therefore, from a conservation perspective, understanding the interaction between habitat use and movement dynamics is critical to the development of sound conservation mitigation strategies in a human-dominated landscape.

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