

Population Structure and Reproductive Ecology of Blanding's Turtle (*Emydoidea blandingii*) in Maine, near the Northeastern Edge of its Range

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ABSTRACT.— We investigated the population structure and reproductive ecology of a small population of Blanding's turtles in Maine near the northeastern periphery of their range. From 1991–93 we captured 34 turtles on two 9 km² study sites and radiotagged 6 females 1–2 years. The sex ratio was not significantly different from 1:1, and we did not detect any differences in body size between males and females. The age structure of the population was uneven, with an apparent scarcity of juveniles. Although the turtles occupied several discrete wetlands, the population seemed to be panmictic. Nesting dates of 6 nests ranged from 13–20 June and clutch size ranged from 5–11 (mean = 8.50) eggs. Hatchlings emerged after 68–118 days (25 Aug – 10 Oct). Twenty-five of 51 (49%) eggs hatched successfully. Egg failure was due to infertility or arrested development (24%), or invertebrate predation (27%). Four nests were in human-altered sites, and two were in soil-filled cracks in bedrock. Nests were located 70–410 m (mean = 242) from the nearest water. This small Maine population has a low density, uneven age structure, and relatively small mean clutch size compared to other *E. blandingii* populations, and as such its future is uncertain. Nevertheless, Blanding's turtles in Maine represent a relictual component of the state's biodiversity and are worthy of protection even though they represent a peripheral population of a species that is more common elsewhere.

KEY WORDS.— Reptilia; Testudines; Emydidae; *Emydoidea blandingii*; turtle; ecology; population structure; reproduction; Maine; USA

Blanding's turtle (*Emydoidea blandingii*) is a semi-aquatic species whose status varies from locally abundant to rare across its range. The distribution of Blanding's turtle is centered around the Great Lakes region and extends from southern Quebec to Nebraska. Disjunct populations also exist in New York, New England, and Nova Scotia (McCoy, 1973). This species tends to have localized population distributions with archeological evidence suggesting that some peripheral populations have undergone recent extinction (Preston and McCoy, 1971; McCoy 1973; Jackson and Kaye, 1974; Van Devender and King, 1975). Blanding's turtle is listed as Threatened in the state of Maine where the past status of this species is poorly known (Graham et al., 1987). Although Blanding's turtles may never have been abundant in New England (Babcock, 1919), archeological records document the presence of this species in Maine and Massachusetts since pre-colonial times (French, 1986; Rhodin, 1992, 1995; Spiess and Sobolik, 1997).

Several papers have documented growth and population ecology of Blanding's turtles (Gibbons, 1968; Graham and Doyle, 1977; Congdon et al., 1983; Ross, 1989; Congdon and van Loben Sels, 1991; Rowe, 1992). Also, various aspects of the reproductive biology have been described, including courtship behavior (Graham and Doyle, 1979; Baker and Gillingham, 1983), nests and nesting behavior (Snyder, 1921; Brown, 1927; Linck et al., 1989), and clutch size (DePari et al., 1987; MacCulloch and Weller, 1988; Congdon and van Loben Sels, 1991; Rowe, 1992). Nesting

ecology, however, has only been studied in Michigan (Congdon et al., 1983), Wisconsin (Ross and Anderson, 1990), and Nova Scotia (Standing et al., 1999), and only two of these studies (Congdon et al., 1983; Standing et al., 1999) documented hatching success.

The purpose of this study was to investigate the population structure and reproductive ecology of a population of Blanding's turtles in southern Maine near the northeastern periphery of the species' geographic range.

METHODS

Study Area.— Our study area was located in York County, Maine, USA, and consisted of two 9 km² sites. Both sites are characterized by second-growth northern hardwood forest, uneven terrain (43–110 m elevation), and shallow soil depth to bedrock, which results in pocket wetlands and rocky outcrops. The primary study site (Site 1) is 9 km² of mixed deciduous-coniferous forest dominated by eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and northern red oak (*Quercus rubra*), and interspersed with wetlands in the watersheds of two small streams. The other 9 km² site (Site 2) consists of a similar upland/wetland matrix. Wetland types include red maple (*Acer rubrum*) swamps, scrub-shrub swamps dominated by highbush blueberry (*Vaccinium corymbosum*) or button-bush (*Cephalanthus occidentalis*), wet meadows, small seasonal pools (<1 ha), permanent ponds, remnant beaver

flowages, a graminoid swale, and an acidic fen. Typical plant species in the wetlands include sphagnum (*Sphagnum* spp.), yellow water lily (*Nuphar advena*), sedges (*Carex* spp. and *Dulichium* spp.), highbush blueberry, buttonbush, and winterberry (*Ilex verticillata*). Site 1 had 25 houses and 5.0 km of roads during the study period, while the more developed Site 2 had 58 houses and 12.3 km of roads.

A base map of the study area was delineated from aerial photographs (1:9600) and entered into a geographic information system (GIS) using ARC/INFO. Road intersections, whose coordinates were obtained from the Global Positioning System (GPS), were used to georeference the map. Temperature and rainfall data were obtained from the Sanford Water District, approximately 25 km from the study area.

Capturing, Measuring, and Marking. — Turtles were captured by hand or hoop net during 1991–93 at Site 1 and during 1991 and 1993 at Site 2. Captured turtles were marked (Ernst et al., 1974), measured, aged, sexed, and checked for obvious abnormalities. Temporary numbers providing unique identification were also painted on the carapace of each turtle with Testor™ markers to aid in identification from a distance. Straight-line plastron length (PL), carapace length (CL), carapace width, and shell height were measured to the nearest 1 mm. Mass was measured to the nearest 20 g using a Pesola scale. The minimum age of each turtle was determined by counting plastral growth rings. Turtles were sexed based on morphological characteristics (Graham and Doyle, 1977; Ernst et al., 1994) and females were palpated to determine if they were gravid.

Radio-transmitters (AVM Type SB2, Livermore, California) were attached to the carapace of turtles using dental acrylic. Five and four females were radiotagged at Site 1 during 1992 and 1993, respectively. Three of these were radiotagged both years. One juvenile found on land was dusted with fluorescent powder and tracked using an ultraviolet light (Butler and Graham, 1993).

Reproductive Data. — We located nests by observing gravid radiotagged turtles in the evenings, and by searching roadsides and yards for nesting turtles or destroyed nests. Nesting females were observed with binoculars from a distance to minimize disturbance. Observations of females usually ended before nest completion. Nests were marked by placing painted rocks next to nesting females or by documenting surrounding landmarks. Raised (approx. 9 cm) cages of 1.3 x 1.3 cm galvanized wire mesh were positioned over nests to trap hatchlings and were held in place with small rocks or sticks (i.e., they were not buried in the ground). Nests were monitored periodically for predation or other disturbance until the first hatchling emerged, and daily thereafter. Hatchling carapace length and plastron length were measured to the nearest 0.1 mm and mass was measured to the nearest 1 g. Nests were excavated in the fall or the following spring to determine clutch size. Unhatched eggs were opened.

In some cases we identified probable nest sites of radiotagged females (for nests that went undetected) based

on female locations, gravidity checks, and abandoned nest sites. Incidental observations of matings were recorded.

Population size was estimated by the Petersen and Schnabel methods (Krebs, 1989) using capture data from 1991–93. Sex ratios were tested against a 1:1 ratio using the Log-likelihood Ratio Goodness of Fit Test. Measurements of males and females were compared using the Mann-Whitney Test. Nonparametric methods were used for multiple comparisons between geographic regions (Zar, 1984). Statistical analyses were performed using SYSTAT (Wilkinson, 1990) and significance was accepted at the 0.05 level.

RESULTS

Population Size and Structure. — We captured 34 turtles; 18 (8 females, 8 males, and 2 juveniles) at Site 1 and 16 (9 females, 6 males, 1 juvenile) at Site 2 (Table 1). Eleven of 31 (35%) adults showed signs of injury (missing limbs, 4 turtles; shell fractures, 1; shell scars/chips, 6). We also captured two turtles that subsequently died. One radiotagged female at Site 1 drowned when the antenna of her transmitter became entangled in vegetation. The antenna had apparently been partially detached from her carapace during a predator attack. An unmarked 4-yr-old juvenile (CL = 64 mm, PL = 59 mm) with a cracked shell was also found near death on a paved road at Site 2. The female was not included in counts or population estimates because mark-recapture methods assume a closed population.

In addition to the juvenile that died, three of 34 (9%) captured turtles were juveniles. They had CL of 51, 95, and 146 mm and based on annuli counts were aged 1, 5, and 9 yrs old, respectively. Most of the juveniles were located in or near habitat types not frequently used by adults. The dead juvenile was found during June next to a large forested swamp, while the 9-yr-old, radiotagged late in 1991, remained in a scrub-shrub swamp from August until hibernation. We found the 1-yr-old during August in a puddle formed by a tire rut and tracked it for 12 days using fluorescent powder. During that time it traveled 359 m in a convoluted path through upland forest and a dry scrub-shrub swamp.

The Petersen population estimate for Site 2 was 25 adults, but the 95% confidence interval was large (15–163). Using the Schnabel method, the population estimate for Site 1 was 16 adults with a 95% confidence interval of 11–25. This estimate equals the number of adults actually captured at Site 1 and translates into 1.8 turtles/km² of study area or

Table 1. The number of adult Blanding's turtles captured each year from 1991–93 at two southern Maine sites. Unmarked turtles are the subset of captured turtles that were unmarked (never captured before) at first capture each year.

	Site 1		Site 2	
	No. captured	No. unmarked	No. captured	No. unmarked
1991	14	14	9	9
1992	15	2	-	-
1993	13	0	8	6

Table 2. Body mass (g) and shell measurements (mm) of adult Blanding's turtles at a study area in southern Maine.

	Sex	Mean	SD	Min	Max	Median	n	p ^a
Non-gravid mass	F	1298	179	980	1580	1310	12	
	M	1387	185	1080	1620	1420	11	0.207
Plastron length	F	202.3	11.2	189	221	204.0	9	
	M	200.3	10.2	183	214	204.0	11	0.790
Carapace length	F	206.2	9.6	192	224	208.0	11	
	M	212.3	9.9	195	223	218.0	9	0.171
Carapace width	F	139.2	8.4	127	152	139.0	11	
	M	143.6	10.1	130	154	145.0	9	0.342
Shell height	F	82.2	3.7	76	89	83.0	11	
	M	80.4	4.9	73	88	79.5	8	0.431

^a Mann-Whitney Test probabilities.

0.3 turtles/ha of wetland area. This wetland area, however, consisted mostly (>90%) of forested or scrub-shrub swamps which were used for periods of dormancy, but were not a large component of the habitat of active Blanding's turtles (Joyal, 1996). Including only pools (and ponds), where individuals spent the majority of their time (Joyal, 1996), the density of Blanding's turtles was 3.9 turtles/ha of available pools or 5.9 turtles/ha of occupied pools.

The observed sex ratio was not significantly different from 1:1 at Site 1 or Site 2, or when the data were pooled ($p > 0.50$). We also did not detect any significant differences in body measurements between sites or sexes (Table 2). The smallest gravid female had a CL of 192 mm (PL = 191 mm, mass = 980 g), and the smallest adult male had a CL of 195 mm (PL = 183 mm, mass = 1080 g). The plastron of both individuals were worn and growth rings could not be counted. For adults, the number of countable rings ranged from 21–32, but plastral rings could not be counted in 14 of 31 adults due to plastral wear.

Reproductive Ecology. — Although Blanding's turtles occupied several discrete wetlands at Site 1, the population seemed to be panmictic. Turtles frequently traveled between wetlands and, at a minimum, each turtle shared wetlands with an average of 4 turtles of the opposite sex during this study. This figure is probably conservative given that the

three females radiotagged during both years shared wetlands with 6–8 males. Blanding's turtles mate from March to November (Ernst et al., 1994), so these encounters represent potential breeding opportunities. Copulation (Graham and Doyle, 1979; Baker and Gillingham, 1983) was observed twice during June and three times during July. Although Sites 1 and 2 were located close together, turtles did not seem to move regularly between sites; only one female (#11) was observed traveling between the two sites. She traveled 1.33 km from Site 1 to Site 2 where she mated with at least one male before returning to Site 1 two weeks later. Thus, she provided a pathway for potential genetic interchange between sites.

At least five of six radiotagged females became gravid. The sixth female (#57) made an overland excursion in June 1992 to a forested wetland, but a nest was not located and we were unable to confirm that she was gravid. In 1993, the nests of two radiotagged females went undetected: one due to the great distance (>1 km) the female (#18) traveled, the other was missed because the female (#60) exhibited unusual behavior by unsuccessfully attempting to nest on several different evenings. No nesting turtles or destroyed nests were found during road and yard searches.

We located six nests from five individual radiotagged females over two years (Table 3). Nesting dates ranged from 13–20 June. Turtles nested in the evenings and did not

Table 3. Nest data from five Blanding's turtles radio-monitored during 1992 and 1993 at Site 1 in southern Maine.

Turtle ID	Year	Clutch size	Number hatched	Nest date	Enclosed date ^a	Emergence date (n)	Days to emergence	Egg failure ^b (n)	Nest site/ ?Probable site?
18	92	8	5 ^c	17 Jun	18 Jun	2 Oct (1) 3 Oct (1) 5 Oct (1) ? Oct (1)	107 108 110	A (3)	gravel road
18	93			18 Jun	-				?forest opening? ^d
19	92	5	3	15 Jun	27 Jun	10 Oct (3)	117	A (2)	dirt in horse pen
19	93	10	9	13 Jun	15 Jun	16 Sep (8) 27 Sep (1)	95 106	A (1)	dirt in horse pen
55	92	9	1	14 Jun	14 Jun	10 Oct (1)	118	P (8)	dirt/brush pile
60	92	8	0	20 Jun	22 Jun	-		P (6) A (2)	crack in bedrock
60	93			after 24 Jun	-				?crack in bedrock? ^e
11	93	11	7	18 Jun	25 Aug	25 Aug (5) 1 Sep (1) 4 Sep (1)	68 75 78	A (4)	crack in bedrock

^a Date that the nest was covered with hardware cloth.

^b A = arrested development or infertility, P = invertebrate predation.

^c One hatchling did not emerge and was dead when the nest was excavated the following spring.

^d Exact nest location not known but >1500 m from 1992 nest.

^e Female attempted to nest in soil on bedrock 15, 18, 20, 22, 23, and 24 June.

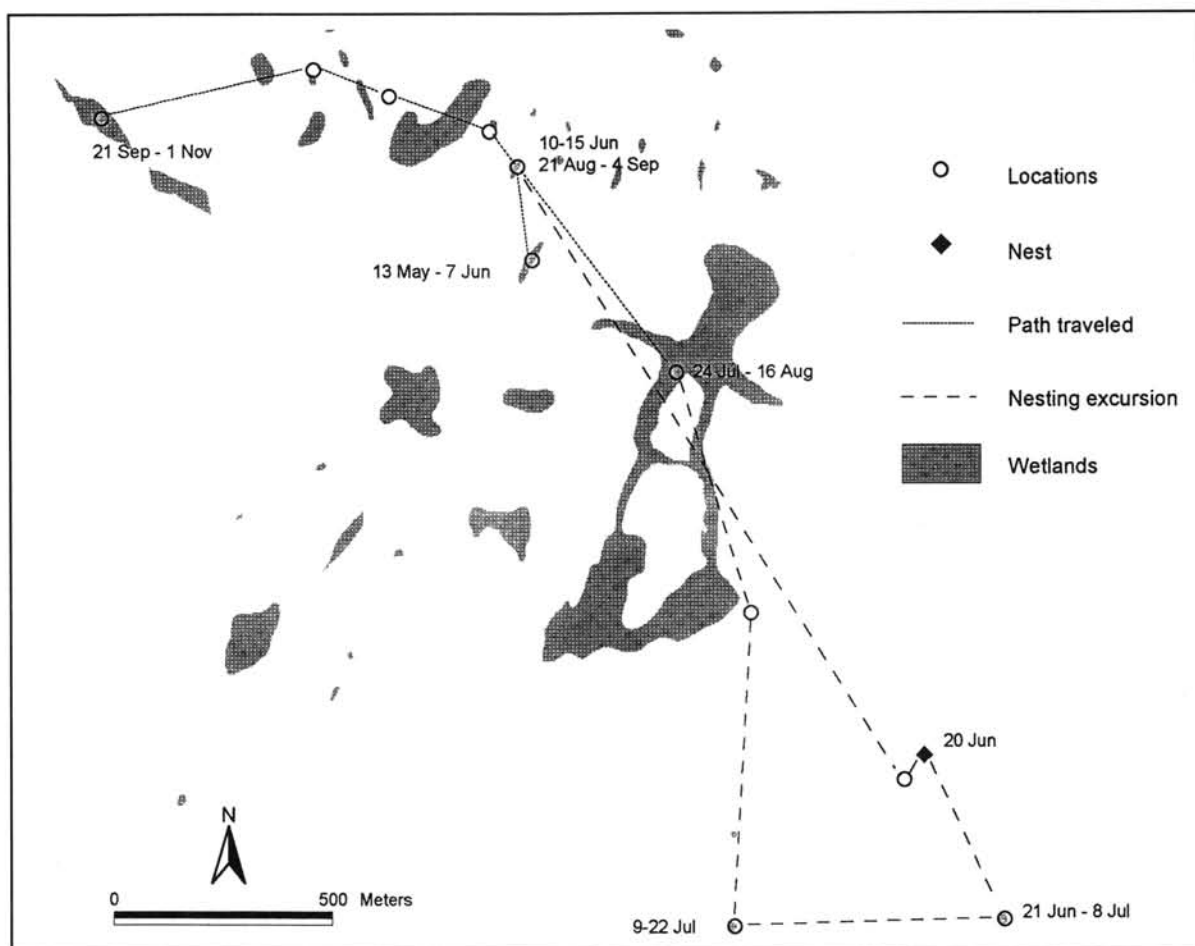


Figure 1. Movements of a radiotagged female (EB60) in southern Maine during 1992. The dashed lines represent her nesting excursion and demonstrate the great distance Blanding's turtles will travel to nest. Her locations and movements have been simplified to reduce cluttering the figure.

complete their nests before dark. Females, especially those nesting in soil on bedrock outcroppings, occasionally abandoned incomplete nesting cavities. New nests were usually initiated shortly thereafter during the same evening, but the females apparently would not begin excavating a new nest after dark. Subsequent nest attempts were usually in the same vicinity as the first attempt.

Four of the six nests were located in human-altered sites (Table 3). The other two nests were located in soil-filled cracks in bedrock, one near the top of a 160 m hill. Two females (#19, #60) exhibited nest substrate and site fidelity (<50 m) while another female (#18) nested over 1500 m from her previous nest.

The distance from the nest to the nearest wetland ranged from 70–410 m (mean = 242 m, SD = 138 m, $n = 6$). The distance from the nest to the wetland used by the female prior to nesting ranged from 100–1620 m (mean = 633 m, SD = 587 m, $n = 6$). After attempted or completed nesting, females spent the night under leaf litter or returned to a nearby wetland, but usually did not return to their previous wetland. Distance from the nest to the next wetland entered by the female ranged from 180–1010 m (mean = 682 m, SD = 325 m, $n = 6$). Round-trip nesting excursions ranged from 3–17 days in length.

One radiotagged female (#60) traveled out of the study area to nest during 1992 (Fig. 1). She left her pre-nesting wetland on 15 June and traveled 1620 m to nest in soil on bedrock 5 days later near the top of a 160 m hill. After nesting, she traveled 420 m to a small vernal pool on the far side of the hill. She remained near this pool for 17 days and then traveled 620 m down the hill to a small scrub-shrub wetland where she remained for 13 days. She then traveled 1170 m and was back at the original site by 24 July. This female made the same trek in 1993. Her itinerant behavior, however, was apparently not anomalous as another marked female (not radiotagged) from the same study area was found in the same vernal pool.

Clutch size ranged from 5–11 eggs (mean = 8.50, SD = 2.07, $n = 6$) (Table 3), and clutch sizes of individual turtles varied between years. One turtle (#19) laid 5 eggs in 1992 and 10 in 1993. Another turtle (#18) laid 12 eggs in 1991 (J. Haskins, unpubl. data) and 8 eggs in 1992.

Five nests (83%) produced young. Of 51 eggs, 24 (47%) produced hatchlings that successfully emerged from the nest and one (2%) produced a hatchling that did not emerge. Fourteen eggs (27%) from two nests had small (2–4 mm wide) holes in the shells, suggesting invertebrate predation, and the remaining 12 eggs (24%) failed to develop or did not

develop completely. No evidence of actual or attempted mammalian predation was observed.

In 1992, hatchlings emerged 107–118 days (early Oct) after egg deposition (mean = 113.4, SD = 4.9, $n = 7$ hatchlings from 3 nests). In 1993, hatchlings emerged 68–106 days (late Aug – late Sept) after oviposition (mean = 84.9, SD = 13.7, $n = 16$ hatchlings from 2 nests). The one hatchling that emerged in 106 days, however, may not have emerged at all if it had not been disturbed the day before when the nest was excavated to determine hatching success. Maximum daily temperatures from July through August were significantly lower during 1992 (mean = 26.27°C, SD = 3.43) than 1993 (mean = 28.49°C, SD = 3.44) (Mann-Whitney Test, $p = 0.003$). Only six days were above 29°C in 1992 while 23 days were above this temperature in 1993.

Hatching was asynchronous in three of the four nests that produced more than one young. In 1992, one hatchling had not emerged from its nest by 2 November. It was dead when the nest was excavated the following spring.

Hatchling PL ranged from 26.9–30.2 mm (mean = 28.27, SD = 1.03, $n = 10$) and CL ranged from 29.7–33.6 mm (mean = 32.69, SD = 1.20, $n = 9$). The mass of each hatchling was 6 g ($n = 9$).

DISCUSSION

Population Size and Structure. — The population we studied was very small compared to most other populations reported in the literature. Our density estimates (maximum 5.9 turtles/ha of occupied pools and ponds) were also low compared to other population densities of 8.8–10.0 turtles/ha (Michigan; Congdon et al., 1986) and 27.5 turtles/ha (Wisconsin; Ross, 1989). Habitat differences may explain the higher densities. Unlike the Maine population, these other populations were in or near marshes, which is considered the species' ancestral habitat (Cahn, 1937; Smith, 1961 as cited in Preston and McCoy, 1971; Van Devender and King, 1975).

The sex ratio in our small population was not significantly different from 1:1, and we did not detect any differences in body size between males and females. Although equal sex ratios are considered normal among turtle populations (Bury, 1979), Congdon and van Loben Sels (1991) documented a significant bias toward females in a long-term study of Blanding's turtles. Male and female Blanding's turtles also tend to be similar in size (Rowe, 1987; Congdon and van Loben Sels, 1991; Rowe, 1992), although some populations exhibit dimorphism (Graham and Doyle, 1979; Sajwaj et al., 1998). Body measurements of Blanding's turtles from Maine were smaller than those from Minnesota (Sajwaj et al., 1998), similar to those in Massachusetts (Graham and Doyle, 1979) and Nebraska (Rowe, 1992), and larger than those in Ontario (Petokas, 1987; MacCulloch and Weller, 1988) and Michigan (Congdon et al., 1986). Size difference between populations may be due to differences in food quality and availability (Quinn and Christiansen, 1972; Graham and Doyle, 1977).

Our counts of plastral growth rings represent minimum ages for adults and do not reveal much about the actual distribution of ages within the adult population. Although counting growth lines may be an inaccurate and biased method of estimating age of adult turtles (Galbraith and Brooks, 1987; Brooks et al., 1997; Litzgus and Brooks, 1998a), it provides good estimates for sexually immature turtles (Galbraith and Brooks, 1987; Congdon and van Loben Sels, 1993; Germano and Bury, 1998).

Female Blanding's turtles mature at 14–20 years of age (Congdon and van Loben Sels, 1993), while males mature at approximately 12 years (Graham and Doyle, 1977). We only found three juveniles in our study area. Other studies have also noted an apparent scarcity of juveniles (Gibbons, 1968; Graham and Doyle, 1977; Congdon et al., 1983; Kofron and Schreiber, 1985; Petokas, 1987; Ross, 1989) which has been attributed to sampling bias (Ream and Ream, 1966; Gibbons, 1968; Graham and Doyle, 1977; Kofron and Schreiber, 1985), and the secretive nature and differential habitat use of juveniles (Ross, 1989; Pappas and Brecke, 1992; Congdon et al., 1993). In the current study, the paucity of juveniles may be due to a combination of all three factors. Trapping efforts and surveys were concentrated on open areas of wetlands and peripheral habitat types were not searched intensively (see Pappas and Brecke, 1992). Furthermore, the few encounters with juveniles suggest that forested or scrub-shrub swamps may be an important component of their habitat. If this behavior is representative of juvenile Blanding's turtles, it would help to explain their apparent scarcity. Similar ontogenetic change in habitat use has been described for snapping (*Chelydra serpentina*) and painted (*Chrysemys picta*) turtles (Congdon et al., 1992). Juveniles may choose shallower waters to find suitable prey, avoid predation, reduce competition, or develop swimming abilities (Congdon et al., 1992; Pappas and Brecke, 1992). While it is known that hatchlings may spend several days upland when dispersing from the nest to water (Butler and Graham, 1995; Standing et al., 1997), this is the first study to suggest extensive terrestrial activity of juvenile Blanding's turtles. Terrestrial activity by juveniles may not seem that unusual in light of the increased knowledge of adult terrestrial activity (Joyal, 1996).

Reproductive Ecology. — Although adults occupied several discrete wetlands, the population seemed to be panmictic. The travels of one female suggest that it may not only be males that go on lengthy journeys to procure mating opportunities (Morreale et al., 1984; Lovich, 1990).

Females nested during June, as documented for other populations (Congdon et al., 1983; Petokas, 1987; MacCulloch and Weller, 1988; Rowe and Moll, 1991). Blanding's turtles nest in a variety of human-altered sites (Petokas, 1987; Linck et al., 1989; Ross and Anderson, 1990; Standing et al., 1997). "Natural" nest sites include grasslands (Ross and Anderson, 1990), sandy beaches (MacCulloch and Weller, 1988), cobble lakeshores (Standing et al., 1997), beaver lodges (Petokas, 1987), and soil-filled cracks on bedrock (this study). Nesting in soil-filled cracks on

Table 4. Geographic variation in clutch size, nesting season, and time to emergence of Blanding's turtles.

Clutch Size				Nest Date	Days to Emergence			Geographic Location	Source
Mean	SD	Range	n		Mean	Range	n		
7.6	1.82	5-12	27	mid-Jun to early Jul				Long Point, Ontario	Petokas, 1987
8.0	1.81	6-11	12					Long Point, Ontario	MacCulloch & Weller, 1988
8.3			8	Jun				southwestern Michigan	Gibbons, 1968
9.4 ^a	3.47	1-15	23	15-24 Jun	97	85-110	35	Nova Scotia	Power, 1989
9.8 ^a	2.54	5-13	9	10-20 Jun	94	68-118	23	York County, Maine	Graham & Forsberg, 1986; J. Haskins (unpubl. data); this study
10.2 ^a	2.51	3-19	280	23 May-4 Jul	84	73-104	16 ^c	southeastern Michigan	Congdon et al., 1983; Congdon & vanLobenSels, 1991
10.6	2.40	4-15	37	10 Jun-5 Jul	93	80-128	13 ^c	Nova Scotia	Standing et al., 1999
10.6		8-13	14		77	69-90	14	east-central Massachusetts	Butler & Graham, 1995
12.6 ^b	1.92	8-18	74	3 Jun-1 Jul				Grenadier Island, Ontario	Petokas, 1987
13.0 ^b	1.80	9-17	21					Concord, Massachusetts	Graham & Doyle, 1979; DePari et al., 1987
14.9	4.54	8-22	17					western Nebraska	Rowe, 1992
17.7		11-24	31	10 Jun-11 Jul	83	77-89		central Minnesota	Sajwaj et al., 1998

^{a,b} Distributions compared using Kruskal-Wallis Test, $p < 0.0005$. A significant difference exists between populations with different letters.

^c $n = 16$ nests, not individuals.

bedrock has not been previously documented for Blanding's turtles, although it has for snapping (Petokas and Alexander, 1980) and spotted turtles (Litzgus and Brooks, 1998b).

At our study area, the closed canopy of the surrounding forest apparently precluded nesting and the available alternatives were areas cleared by humans, rock outcrops, and, perhaps, open-canopy swamps. The hatchlings of the successful bedrock nest emerged much earlier than those from other nests (Table 3). The high heat capacity and low heat loss of the bedrock probably kept this nest at a higher and more constant temperature than the other nests. Cracks in bedrock, however, may not always provide adequate drainage; some of the eggs in both of the natural nest sites were moldy. Although areas cleared by humans may offer good drainage and solar exposure, nests placed in these sites are also at a higher risk of disturbance by humans, vehicles, and perhaps predators.

Female Blanding's turtles travel long distances to nest and most exhibit nest site fidelity, although some may nest >1 km from previous nests (Congdon et al., 1983; Standing et al., 1999). In this study, females traveled 100–1620 m to nest. Similarly, females in Michigan nested 200–1200 m from their resident area (Congdon et al., 1983), females in Illinois nested 650–900 m from their home ponds (Rowe and Moll, 1991), and females in Nova Scotia nested up to 2900 m from their hibernaculum (Standing et al., 1999).

Females often nest a good distance from the nearest body of water (2–1115 m, mean = 135, Congdon et al., 1983; 70–410 m, mean = 242, this study). This habit of nesting far from water implies long journeys for emerging hatchlings, if they seek water prior to hibernation (Butler and Graham, 1995; Standing et al., 1997). Hatchlings have been documented to travel up to 450 m in 9 days (Butler and Graham, 1995).

The mean clutch size in this study was 8.5 eggs. If three additional clutches from York County, Maine (12 and 13, Graham and Forsberg, 1986; 12, J. Haskins, unpubl. data)

are included, the average clutch size for this geographic area is 9.8 eggs (SD = 2.54, $n = 9$). Clutch sizes of Blanding's turtles vary among populations (Table 4). Distributions of clutch sizes were reported by DePari et al. (1987), Petokas (1987), Power (1989), and Congdon and van Loben Sels (1991), permitting statistical comparisons. Clutch sizes in Maine are similar to those in Nova Scotia and southeastern Michigan, but smaller than those on Grenadier Island, Ontario, or in Massachusetts (Kruskal-Wallis, $p < 0.0005$) (Table 4). Within a turtle species, clutch size often increases with latitude (Tinkle, 1961; Moll, 1973; Petokas and Alexander, 1980; Gibbons, 1983), but Blanding's turtles do not appear to follow this pattern.

Over a period of six years, Congdon et al. (1983) found 67% nest predation, 11% whole clutch failure due to infertility, and 22% survivorship among unprotected, natural nests. Protecting nests from mammalian predators, however, does not ensure a high rate of hatching success. While Butler and Graham (1995) reported a high percentage (87%) of eggs hatching from protected nests, only 47% of the eggs in this study and 43% of the eggs reported by Standing et al. (1999) produced hatchlings that emerged. Caged nests are also still susceptible to non-mammalian predators. In this study, 27% of the eggs were apparently consumed by invertebrates. Predation of Blanding's turtle nests by ants has been documented by Congdon et al. (1983) and Butler and Graham (1995), and was also suspected in Nova Scotia (Weller as cited in Herman et al., 1995).

Mammalian predation did not seem to be a problem in this study. Although most nests were enclosed in hardware cloth, these enclosures were probably more effective at marking the nest and trapping hatchlings than deterring predators. In other studies, mammalian predators successfully removed or tunneled under nest covers (Petokas, 1987) or left signs of unsuccessful attempts (Herman et al., 1995). To effectively discourage predators, Butler and Graham

Table 5. Geographic variation in carapace length (CL, mm) and mass (g) of hatchling Blanding's turtles.

	Hatchling Size					Geographic Location	Source
	Mean	SD	Min	Max	n		
CL	32.7	1.20	29.7	33.6	9	York County, Maine	this study
Mass	6	0.00	6	6	9		
CL	33.0	1.82	29.7	35.9	35	Nova Scotia	Power, 1989
Mass	7.8	1.31	5.2	10.0	32		
CL	33.5	1.90			100	Nova Scotia	Standing et al., 1997
CL	33.9	1.30	31.5	36.0	27	Grenadier Island, Ontario	Petokas, 1987
Mass	8.3	1.02	6.7	9.7	27		
CL	34.6	1.69			235	east-central Massachusetts	Butler & Graham, 1995
CL	35.2	0.53	30.0	38.8	28 ^a	southeastern Michigan	Congdon & van Loben Sels, 1991
Mass	9.2	0.37	6.0	13.0	28 ^a		

^a n = 28 nests, not individuals.

(1993) buried cages 30–45 cm. In addition, in areas of high predation, unprotected nests were often destroyed within 24 hrs of oviposition (Congdon et al., 1983; Ross and Anderson, 1990; Herman et al., 1995). All but two of our nests were left uncovered for more than a day and one was left uncovered until hatchling emergence. None of the nests had evidence of attempted predation by mammals. Intensity of predation increases with density of nests (Hammer, 1969; Wilbur, 1975; Burger, 1977) so populations without concentrated nesting areas, such as the one we studied, may be at a lower risk of mammalian predation.

Annual predation rates of turtle nests can be high (Petokas and Alexander, 1980; Congdon et al., 1983; Congdon et al., 1987), but vary considerably among years (Burger, 1977; Congdon et al., 1983; Congdon et al., 1987) and habitats (Burger, 1977). Because Blanding's turtles have a long reproductive period (Congdon and van Loben Sels, 1993), high nest predation in a given year may be tolerable to a population.

Hatchlings emerged in early October during 1992 and from late August through September during 1993. Significantly cooler temperatures during the summer of 1992 probably explain this difference. Hatchlings also emerged from August to October in Michigan (Congdon et al., 1983) and from September to October in Nova Scotia (Standing et al., 1997). Although it may be tempting to infer a geographic trend in the time to emergence (Table 4), variation in this factor within populations is high. Time to emergence depends not only on geographic location, but also on local nest site conditions and annual weather conditions. In some years a few hatchlings may not emerge from the nest before winter freeze-up. One hatchling (2% of the eggs) in this study did not emerge during the fall and was found dead in the nest the following spring. Congdon et al. (1983) found indirect evidence of overwintering in the nest and several nests in Nova Scotia contained dormant hatchlings in the fall (Herman et al., 1995). Although hatchling *Chrysemys picta* normally overwinter in the nest at northern latitudes and can survive

subzero temperatures (Packard et al., 1989; Packard et al., 1997), survival of overwintering *E. blandingii* hatchlings is unknown. If overwintering is caused by cool temperatures (which is questioned by Gibbons and Nelson, 1978) and if overwintering hatchlings die, then cool temperatures may limit the northern range of Blanding's turtles. Hatchlings that emerge later in the fall may also be at a disadvantage in finding suitable hibernacula before winter freeze-up.

Hatchling size was comparable to other studies (Table 5). Hatchling mass, however, was low compared to elsewhere (Table 5), but we only weighed nine hatchlings from two nests.

CONSERVATION IMPLICATIONS

Blanding's turtles are rare in Maine, and this combined with their delayed maturity makes it difficult to detect population trends. Low densities and apparent skewed age/size structure raise concerns regarding the viability of the population we studied. The population is reproducing, but the paucity of juveniles or other documentation of ongoing recruitment are cause for concern for long-term population persistence and stability. Future research should include dedicated searches for juveniles and the documentation of juvenile habitat. Locating and protecting nests is time-consuming, costly, and may not greatly increase hatching success in populations which are little affected by mammalian predation. Indeed, nest protection by itself, without a concurrent reduction in adult mortality, is an insufficient conservation strategy (Congdon et al., 1993). Greater emphasis should be placed on protecting adults and on protecting habitat that supports all life stages. Due to the long distances females travel, the great distances they place their nests from the nearest wetland, and the use of upland and swamp habitat by juveniles, habitat conservation will need to take place on a landscape scale.

The population we studied is relictual in Maine, with the distribution having been wider in the past. Compared to

other *E. blandingii* populations, our Maine population does not inhabit large emergent marshes which are considered ancestral for the species and which support large populations elsewhere in the species' range. Our population also occurs at a lower density, and has a smaller mean clutch than reported elsewhere. The life history dynamics of *E. blandingii* make them intrinsically sensitive to chronic perturbation or high mortality (Congdon et al., 1993) and this population may be particularly vulnerable due to its relatively low density, age-shifted population structure, and smaller clutch size. Although Blanding's turtles in Maine may be naturally rare and on the periphery of their geographic range, they nonetheless merit conservation, especially because peripheral populations that use different habitats may be important as evolutionary units (Hunter and Hutchinson, 1994; Lesica and Allendorf, 1995).

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