

The Blanding's Turtles (*Emydoidea blandingii*) of Weaver Dunes, Minnesota

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ABSTRACT.—The population of Blanding's turtles (*Emydoidea blandingii*) at Weaver Dunes, Wabasha County, Minnesota, may be the largest in the world. The Weaver Dunes complex is composed of Weaver Bottoms which is a 1620 ha shallow lake, the old Zumbro River Channel (1500 ha consisting of approximately 750 ha of wetland habitats), and Weaver Dunes (600 ha of stabilized dunes). Between 15 April 1974 and 1 June 1980 we marked a total of 2402 individuals and made 474 recaptures. An additional 49 females were marked in June 1998 and 25 recaptures were made of previously marked individuals. Clutch sizes were determined for 44 females during 1976 and 1977 and 70 females during 1998. Adult females averaged 197.0 mm carapace length (CL) and 1.08 kg in body mass; adult males averaged 213.6 mm CL and 1.29 kg in body mass. Compared to males of similar length, plastrons of females were wider and total shell width was narrower and higher. Of 598 reproductive females, fewer than 20% were captured on land during the nesting season in successive years, and some females appeared not to reproduce each year. Clutch size averaged 9.8 eggs and was positively related to body size of females. Eggs averaged 23.5 by 37.5 mm in width and length, respectively, and hatchlings captured in the field averaged 33.1, 36.7, and 15.4 mm in plastron and carapace length and shell height, respectively. Females matured at a minimum CL of 160 mm and minimum age of 14 yrs. Juveniles averaged 10 mm/yr increase in CL. The oldest adults in the population were a minimum age of 40 to 45 yrs. Adult growth averaged 0.46 mm/yr, with some adults exhibiting zero or negative growth. Juveniles comprised 35.1–55.7% of samples of turtles. Adult sex ratio was 1 male to 2.2 females. Emergence of adults from overwintering occurred between 13 March – 8 April. Nesting began between 26 May – 12 June, and nesting season duration averaged 17 days. Hatchling emergence averaged 27 days between mid-August and late September. Since 1.6% of hatchlings were captured on land in the spring following nest construction, some hatchlings apparently overwintered on land. First order estimates place the population size of Blanding's turtles at between 2500–4600 individuals on the west side of Weaver Dunes alone (the old Zumbro River Marsh area).

KEY WORDS.— Reptilia; Testudines; Emydidae; *Emydoidea blandingii*; turtle; ecology; growth; juveniles; morphology; population; demography; reproduction; sexual dimorphism; Minnesota; USA

Three decades ago the biology of Blanding's turtles (*Emydoidea blandingii*) was poorly known, with only one report on their ecology and population biology (Gibbons, 1968). However, growing concern about conservation and management (McCoy, 1973; Graham and Doyle, 1977), prompted interest in the species throughout its range (citations herein). As a result, the increased level of knowledge about ecology and life history of Blanding's turtle now makes it among the better known North American turtles. Blanding's turtle life history characteristics (delayed sexual maturity, extreme iteroparity, long reproductive life span, and extended longevity) can be described as extreme even when compared to turtles in general (Wilbur and Morin, 1988; Brecke and Moriarty, 1989; Congdon and van Loben Sels, 1991, 1993; Congdon et al., 1993). Some Blanding's turtle populations are notable in their apparent lack of

juveniles and highly biased adult sex ratios (Graham and Doyle, 1977; Congdon and van Loben Sels, 1991; Congdon et al., 1993). Despite increased interest in Blanding's turtles, data on variation in life history trait values within and among populations remain scarce. Consequently, design and implementation of conservation and management programs for Blanding's turtles have had to rely on composites of data from a variety of populations of different sizes and from different parts of their range.

Blanding's turtle populations are often characterized as small, low density, and fragmented throughout much of their range and the species is listed as threatened in Minnesota (Coffin and Pfannmuller, 1988). The present study reports on 6 years of observations on a large population of Blanding's turtles at Weaver Dunes, Minnesota (Fig. 1), a population that may be the largest in the world. We studied: (1) habitat-

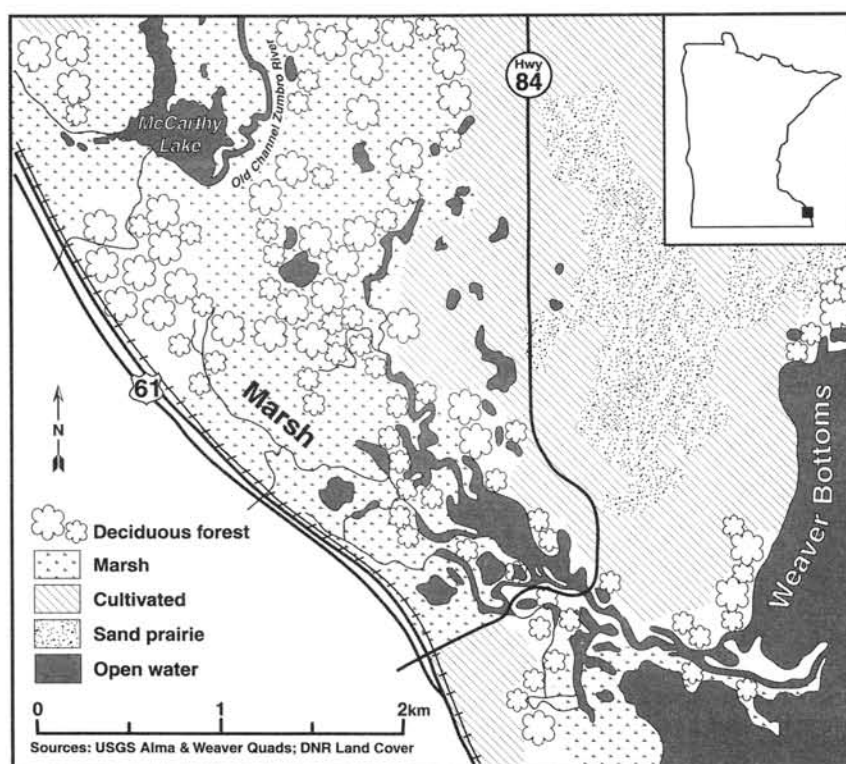


Figure 1. Map of the Weaver Dunes area of southeastern Minnesota.

specific adult body size, (2) sexual size and shape dimorphism, (3) reproductive characteristics, (4) growth rates of juveniles and adults, and (5) phenology of activity. In addition, we made two first order estimates of population size.

MATERIALS AND METHODS

Study Area. — The general area known as Weaver Dunes is located within the Upper Mississippi River floodplain in the southeast corner of Wabasha County, Minnesota (T 109 N, R 9 W, Minneiska Township). Weaver Dunes is an elevated (4.7–28.3 m above flood level) glacio-alluvial sand terrace of approximately 600 ha that is characterized by sand prairie and oak savannah plant communities that have stabilized many high dunes. Within the dune area are occasional active blowouts at dune crests and aeolian ponds occur in the deepest depressions. After a century of grazing by cattle, agricultural use of Weaver Dunes recently shifted to crop cultivation on the gentler slopes around the bases of the dunes (Galatowitsch, 1984). The herpetofauna of the area was surveyed by Moriarty (1985) and compared to that of a Wisconsin sand prairie by Cochran (1986). Lowland habitats consist of deciduous floodplain forest and extensive marshes, sedge meadows, ponds, and swales that border the sand prairie. Less than one third of the Weaver Dunes terrestrial habitat is protected through ownership by the Minnesota DNR and the Nature Conservancy.

West of Weaver Dunes, two old channels of the Zumbro River once flowed north and south and both channels emptied into the Mississippi River. The south-flowing channel emptied into Weaver Bottoms, an extensive backwater of

the Mississippi River. Sometime prior to 1920, farmers excavated an east-flowing channel through the sand terrace, diverting Zumbro River flows directly to the Mississippi River's main channel. In 1973, the diverted route of the Zumbro River (east of Kellogg, Minnesota, and 12 km north of the study area) was leveed and armored for flood control purposes by the US Army Corps of Engineers. Alterations to the Zumbro River channel did not totally eliminate riparian wetlands. The old southern Zumbro Channel is still fed by three creeks and numerous underground seeps and springs. The old Zumbro channel turns east and empties into Weaver Bottoms about 2.5 km north of Weaver, Minnesota (Fig. 1). The entire area of the old Zumbro River channel is approximately 1500 ha, of which roughly 750 ha is wetland habitat. West of the old Zumbro River channel the floodplain gives way to steep bluffs, comprising the western wall of the Mississippi River Valley. Most of the wetlands within the old Zumbro River bottomlands are under federal or state ownership.

East of Weaver Dunes is Weaver Bottoms, a 1620 ha former marsh area flooded in 1938 by impoundment of the Mississippi River by the US Army Corps of Engineers for commercial navigation. Approximately 90% of the Weaver Bottoms area is publicly owned and is within the Upper Mississippi River National Wildlife Refuge. Prior to impoundment, Weaver Bottoms consisted of a mosaic of wetland meadows, forest, and wetlands (marshes, channels, creeks, lakes, ponds, and sloughs). Before flooding, Weaver Bottoms was a diverse and dynamic ecosystem that in old photographs appeared to be excellent Blanding's turtle habitat. Since the area was flooded the area of aquatic vegetation has been reduced from approximately 1335 ha to 731 ha

between 1938 and 1975 and the loss of aquatic vegetation is now almost complete.

Although Blanding's turtles were captured over much of the Weaver Dunes area during the early years of the study, later field work was concentrated at specific sites chosen because of high seasonal densities of turtles or special features (e.g., overwintering sites, breeding locations, and staging areas used by females prior to nesting). In addition, low water levels made much of the aquatic habitat inaccessible by boat, and deep (>1 m) muck made many areas difficult to reach on foot.

Specific Study Sites. — Locations of specific sites are not identified in Fig. 1 due to conservation concerns. Site 1 is a shallow side channel (1.0–1.3 m deep, 1.5 ha) near the mouth of the old Zumbro River that is an overwintering site and spring breeding pond. It is dominated by coontail (*Ceratophyllum demersum*) and is bordered by deciduous floodplain forest. Site 2 is a small (0.25 ha) alder thicket (Curtis, 1959) dominated by closely spaced tussocks of speckled alder (*Alnus rugosa*) in shallow (<0.5 m) standing water with a muck bottom (0.2–0.6 m). Only juveniles (less than 6 yrs of age and less than 110 mm CL) were captured at Site 2 (Pappas and Brecke, 1992). Site 3 is a eutrophic pond (3.75 ha) about 1.0 m deep with thick (0.2–0.6 m) bottom sediments. It is bordered by a zone of emergent vegetation (3–25 m) dominated by bottlebrush sedge (*Carex comosa*). Dominant aquatic plants at this site are coontail (*C. demersum*), pondweed (*Potamogeton pectinatus*), and duckweed (*Lemna minor*). Site 4 is a swampy inlet of open floodplain connected to the old Zumbro River channel that is similar to Site 3 and bordered by emergent sedge and cattail (*Typha latifolia*). Site 5 is a eutrophic pond (0.65 ha and about 1.3 m deep) bordered by a marsh zone (3–10 m wide) of emergent vegetation dominated by sedges and surrounded by deciduous floodplain forest near Weaver Bottoms. Site 6 is nesting habitat consisting of stabilized sand dunes (0.1–1.0 ha) within an extensive rolling sand prairie. Vegetative cover is typical of sand prairies in southeastern Minnesota which corresponds closely to the "Sand Barrens" habitat of south-central Wisconsin (Curtis, 1959). Scattered stands of oak woodland habitat and introduced red pine (*Pinus resinosa*) provide windbreaks. Dominant understory near the rims of the dunes (nesting sites) consists of little bluestem (*Andropogon scoparius*) and prairie junegrass (*Koeleria cristata*).

Mark-Recapture Methods. — Adult turtles were individually marked by notching marginal and plastral scutes with a hasp file or bone saw. Hatchlings were individually coded by removing complete digits with small scissors and then cauterizing the cut with silver nitrate. In both procedures a unique alpha-numeric identification code was assigned (Cagle, 1939, 1946). In addition to their individual marks, numbers were painted on the carapace of adult turtles with Testor's white stove enamel to aid in identifying turtles at a distance without disturbing them. Paint numbers were legible with binoculars up to 100 m and remained for up to 3 yrs in some turtles.

Observations and collections were made during all months except December through February when aquatic habitats were ice-covered. Turtles were caught in aquatic habitats with baited traps (Lagler, 1943) and by muddling. We waded to the middle of ponds and used binoculars to search for the turtles' conspicuous yellow throats. When approached from the pond center, turtles often would not submerge until we approached within 10 m. At that distance their location was noted and then captured by muddling. Turtles were also captured on land and at drift fences during terrestrial movements.

In 1976, we constructed a 1575 m drift fence parallel to Wabasha Co. Hwy. 84 to intercept turtles moving from aquatic areas to elevated sand prairie to nest (Fig. 1). The fence was 0.5 m tall with 0.5 m wide gates placed at 30 m intervals. Two 20-liter plastic buckets were buried flush with the ground on each side of all gates (4 buckets per gate). Buckets were placed only on the dune side of the fence to allow females to move through the fence on the way to the nesting grounds; however, as females and hatchlings moved from dunes to wetlands they were captured in the drop buckets. The 1.5 km stretch of highway adjacent to the fence was patrolled each day and drift fence buckets were checked twice daily from 0800–1000 and 1500–1700 hrs (Central Daylight Time) during the nesting season and fall emergence of hatchlings. Data from the patrols and drift fence allowed daily frequency of movements of nesting females and hatchlings to be determined.

Data Recorded. — Data recorded for each turtle included date and site of capture, time of day, weather conditions, and activity. Ambient and soil temperatures were also recorded at the time of some captures. Scute abnormalities, growth annuli, injuries, and distribution of algae on the shell were recorded by drawings, photographs, or stencils.

Turtles were weighed on a triple beam balance to the nearest 5 g. The following straight line measurements were taken for each turtle: carapace length (CL), width of carapace at the widest point across the abdominal plate (CW), plastron length (PL), plastron width (PW) at the widest point across the abdominal plate inside the carapacial margin, and carapace height (CH) just posterior to the plastral hinge. Carapace length was used as the measure of body size in this study because it is less prone to measurement error than plastron length; however, plastrons of each individual were carefully straightened across the hinge before measurements were taken. Lengths of abdominal laminae were measured with a transparent plastic ruler to the nearest 0.5 mm in juveniles and some adults. Measurements were taken along the inter-abdominal seam from the pectoro-abdominal seam to the abdomino-femoral seam. Annuli were counted in juveniles and photographed or stenciled.

The sex of captured individuals was determined from morphological characteristics such as concavity of the plastron, size and length of the tail, location of cloacal opening in relation to the margin of the carapace, and the difference between carapace and plastron lengths. Based on observa-

Table 1. Mean morphometrics (mm) and masses (g) of adult Blanding's turtles (greater than 165 mm CL) captured at Weaver Dunes, Minnesota, between 1974–80. Data are: mean \pm SE, (range), *n*.

	Carapace Length	Plastron Length	Plastron Width	Carapace Width	Shell Height	Body Mass
Females	197.0 \pm 0.4 (164–229) <i>n</i> = 670	193.7 \pm 0.4 (163–224) <i>n</i> = 670	109.8 \pm 0.3 (94–130) <i>n</i> = 428	133.4 \pm 0.3 (111–157) <i>n</i> = 431	78.3 \pm 0.3 (65–95) <i>n</i> = 294	1079.0 \pm 8.6 (690–1790) <i>n</i> = 408
Males	213.6 \pm 1.8 (177–238) <i>n</i> = 59	201.1 \pm 1.6 (173–220) <i>n</i> = 58	112.6 \pm 1.1 (94–129) <i>n</i> = 58	144.2 \pm 1.2 (118–160) <i>n</i> = 59	82.3 \pm 1.0 (71–92) <i>n</i> = 35	1291.3 \pm 45.4 (750–1810) <i>n</i> = 43

tions of reproductive individuals of both sexes, individuals were classified as adults if they were greater than 164 mm CL. Five smaller individuals were classified as adult females because they were reproductive or observed in nesting areas (clutch size was not determined for these individuals). All other individuals were classified as juveniles.

Clutch size (CS) was determined for 44 females during the 1976 and 1977 nesting seasons. Clutch size and egg size were obtained from 6 dissected females, 2 excavated nests, and from 36 females that were induced to oviposit by injection of oxytocin (Ewert and Legler, 1978), and subsequently checked for the presence of eggs by palpation. In June 1998, 70 females were radiographed to determine their clutch size.

Statistical Analyses. — Parametric statistical tests were used when variables were continuous and assumptions of the

tests were met. Otherwise, non-parametric tests, such as Spearman's Rank Correlation (RHO) and Wilcoxon tests (Sall, 1982) were used. Since morphometric parameters are influenced by body size, shape differences were examined using analysis of covariance (ANCOVA) with CL as the covariate. Unless otherwise stated, levels of significance were accepted at $\alpha < 0.05$. Measures of central tendency and dispersion are presented as the mean \pm one standard error unless stated otherwise.

RESULTS

A total of 2402 individual Blanding's turtles were captured between 15 April 1974 and 1 June 1980. An additional 49 new females were captured in June 1998, and 67 turtles were recaptured in 1998–99 that had been initially marked in the 1970s.

Body Sizes of Adults. — Adult Blanding's turtle females and males at Weaver Dunes averaged 197.0 and 213.6 mm in CL and 1.08 and 1.29 kg body mass, respectively (Table 1). The relationship between CL and body mass (log transformed) was more variable for females ($r^2 = 0.62$; Fig. 2a) than for males ($r^2 = 0.94$; Fig. 2b). Within the Weaver Dunes complex (Fig. 1), adults of both sexes from the east side (Mississippi River and Weaver Bottoms) were larger (males, CL, ANOVA, $F_{1,96} = 75.2, p < 0.001$; females, CL, ANOVA, $F_{1,692} = 3253, p < 0.001$) than those from the west side (old Zumbro River marshes; Table 2) of Weaver Dunes.

Sexual Size Dimorphism. — Among all adults both measured and weighed, males were larger (CL, ANOVA, $F_{1,723} = 136.5, p < 0.001$) and heavier (ANOVA, $F_{1,449} = 49.5, p < 0.001$) than females (Table 1). However, the largest male (238 mm CL) was only 9 mm larger and the heaviest male was only 20 g heavier than the largest and heaviest females, respectively (Table 1).

During a single observation period during early spring at one overwintering and spring breeding pond, a minimum

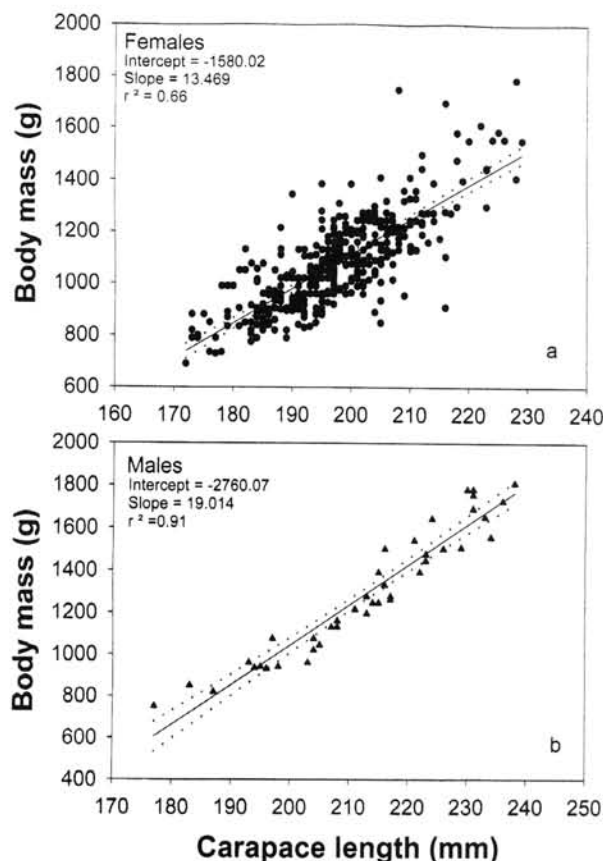


Figure 2. Relationship between body mass (log normal transformed) and carapace lengths of adult (a) female, and (b) male Blanding's turtles (solid line = predicted line from linear regression, dotted lines are 95% confidence intervals).

Table 2. Comparison of body size (CL) of Blanding's turtles from the east side (Mississippi River and Weaver Bottoms) and the west side (Zumbro River marshes) of Weaver Dunes between 1974–98.

Area	Sex	<i>n</i>	Mean CL \pm SE	Range
East Side	Female	60	205.9 \pm 1.11	189–228
	Male	38	222.3 \pm 1.58	188–238
West Side	Female	662	196.8 \pm 0.39	168–229
	Male	31	207.6 \pm 2.34	183–234

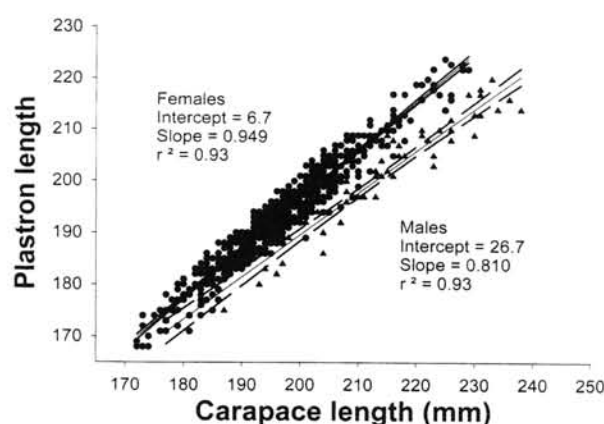


Figure 3. Relationships between the difference between carapace and plastron lengths and carapace lengths of males (triangles) and females (dots); (solid line = predicted from linear regression, dotted lines are 95% confidence intervals).

of 23 individuals and 3 mounted pairs of Blanding's turtles were seen in 2 hours of observation. Over the next 2 days, 16 turtles were captured by hand (7 males and 9 females). The mean body size of males ($n = 7$, CL = 221 mm, range = 214–230) was significantly larger than that of females ($n = 9$; CL = 208, range = 197–221; $t = -3.53$, $p = 0.003$). In another sample of 17 mounted pairs captured during the spring breeding season, the average CL of males was 13.0 mm greater than those of females (paired t -test, $t = 5.797$, $p = 0.001$). In two pairs, males (CL = 225 and 194 mm) were smaller by 3 and 10 mm, respectively, than the females (CL = 228 and 204 mm). Body masses of males and females in the sample were not significantly different ($p = 0.18$).

Sexual Shape Differences. — In addition to apparent sexual size dimorphism noted above, there were also differences in the shapes of adult male and females. Among all adults, the slope of the relationship between PL and CL was 0.95 and 0.81 for females and males, respectively. The average adjusted mean (ANCOVA, CL as covariate) difference in CL – PL (DIFF) of males was 11.7 (range = –1–24 mm) and females was 3.4 (range = –2–12 mm). Although DIFF was significantly related to CL for both sexes ($p < 0.01$), the relationship was approximately 3.8 times steeper in males than in females (Fig. 3).

A sample restricted to adults of both sexes within a common range of body sizes (CL = 177–229 mm; i.e., with the smallest females and largest males removed) revealed size-adjusted shape differences (Table 3). The adjusted mean (ANCOVA, CL as covariate) of plastron length of females was 7 mm longer than that of males, and females were 2 mm deeper in shell height and had plastrons 4 mm wider compared to males (Table 3). Surprisingly, however,

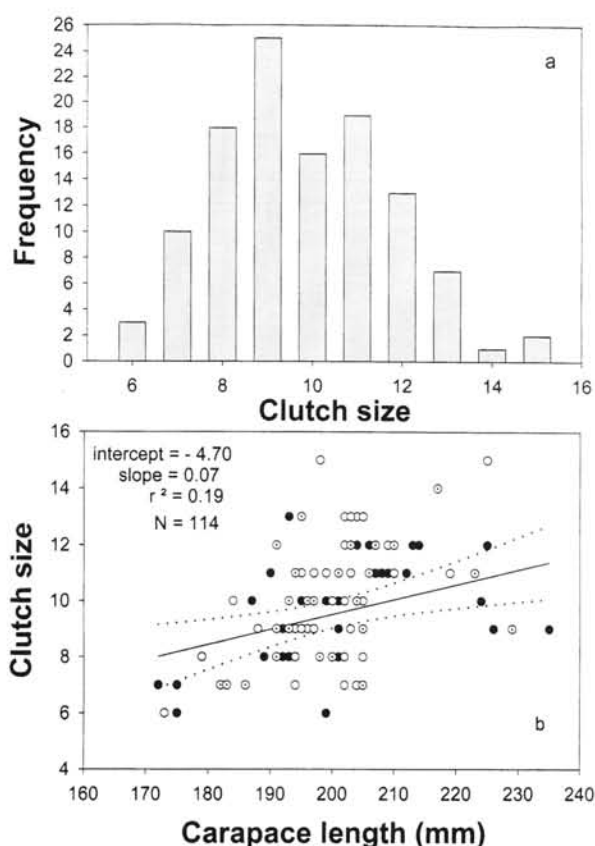


Figure 4. (a) Clutch size frequency distribution and (b) relationship of clutch size to body size in Blanding's turtles at Weaver Dunes (dots = 1974–80 samples; open circles = 1998 samples; open circles with center dots = 1974–80 turtles recaptured in 1998; solid line = predicted from linear regression, dotted lines are 95% confidence intervals).

despite the wider plastron of females, total shell width of males averaged 1.7 mm greater than that of females. Therefore, height and width differences of males and females appear to be related to differences in the morphology of the bridge marginals (i.e., compared to males, the increased shell height of females occurs because bridge marginals appear to grow more vertically and less laterally).

Reproductive Characteristics. — Clutch size of 114 females captured between 1974–76 and in 1998 averaged 9.8 eggs (SE ± 0.21 ; range = 6–15; Fig. 4a) and increased with body size of females (Fig. 4b). Body size and clutch size from the 1970s and 1998 samples were not significantly different (Wilcoxon p values > 0.5). For 25 females recaptured in 1998 after 21–24 yrs (mean = 22.6 yrs), clutch size was 9.9 eggs vs. 9.8 eggs in the sample from 1974–76.

Freshly laid eggs are ellipsoid in shape and 73 eggs from 8 clutches averaged 23.5 mm (range, 21.5–25.2) in width

Table 3. Mean carapace length and adjusted means of body size parameters of a sample of female and male Blanding's turtles with similar minimum and maximum carapace lengths (CL = 177–229 mm). All lengths are in mm.

	Mean Carapace Length	ANCOVA	Plastron Length	Plastron Width	Carapace Width	Shell Height
Females	197.8 \pm 0.4	adjusted mean	194.9 \pm 0.1	110.6 \pm 0.2	134.3 \pm 0.2	79.0 \pm 0.2
	$F_{1,723} = 69.4$; $p < 0.001$	p -value	$p < 0.001$	$p < 0.001$	$p = 0.002$	$p < 0.006$
Males	210.2 \pm 1.8	adjusted mean	187.2 \pm 0.4	106.3 \pm 0.6	136.0 \pm 0.5	77.1 \pm 0.7

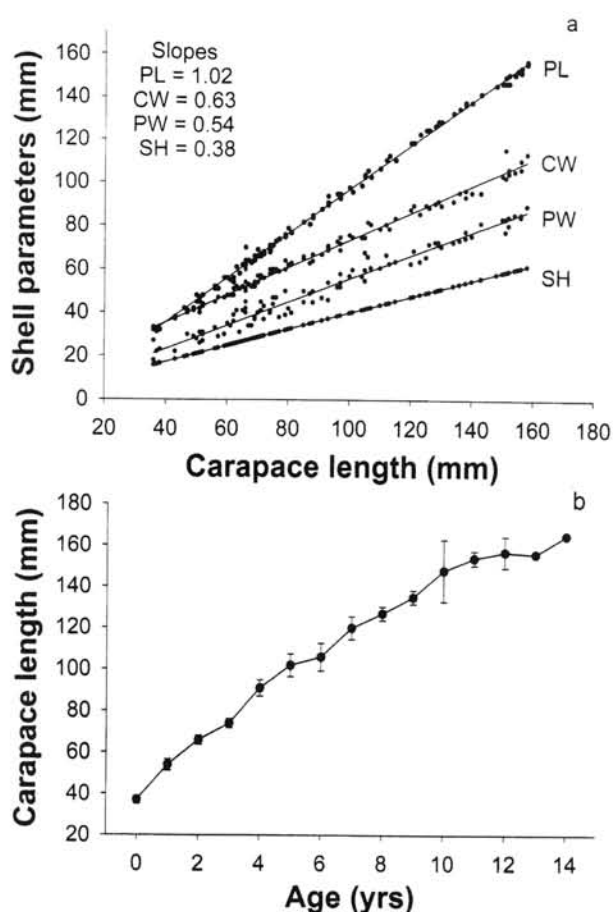


Figure 5. (a) Relationships between growth of shell parameters and carapace length of juveniles (PL = plastron length, CW = carapace width, PW = plastron width, and SH = shell height), and (b) relationship between carapace length and age of juvenile Blanding's turtles (error bars are ± 2 SE).

and 37.5 mm (range, 34.4–40.9) in length. Eggs from 13 clutches (115 eggs) averaged 12.7 g (range, 10.3–14.2) wet mass, and total clutch masses averaged 112 g (range, 78.9–164.4) wet mass.

Over all years of the study, no female was observed nesting more than once per year, and of 598 females registered as reproductive, 103 (17%) were known to nest in two, 90 (15%) in three, and one (0.2%) in four successive years (1974–77).

Hatchling Size and Growth of Juveniles. — Forty hatchlings from eggs incubated at constant temperature 25°C in the laboratory averaged 30.6 mm (SE ± 0.31) PL and 34.5 mm (SE ± 0.32) CL. Hatchlings ($n = 60$) captured in the field before they reached water averaged 33.1 mm (SE ± 0.18) PL, 36.7 mm (SE ± 0.19) CL, and 15.4 mm (SE ± 0.09) shell height.

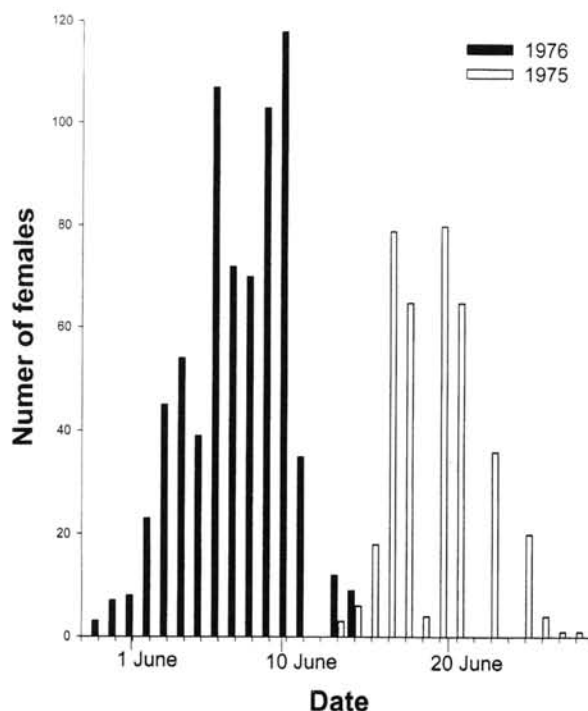


Figure 6. Daily frequency of female Blanding's turtles making nesting migrations during 1975 and 1976 at Weaver Dunes.

Among 45 juveniles, widths of the first growth ring on the abdominal scute (adjacent to the birth plate) ranged from 3.3–8.0 mm (mean = 5.0 mm). Four of these juveniles had narrow annuli adjacent to the birth plate that averaged 1.5 mm (range, 1.0–1.8) indicating that some growth may occur between emergence from nests and the hatchling's first winter.

Growth of shell parameters of 114 individuals between age 0 yrs (hatchling emergence) and 14 yrs were all essentially linear (Figs. 5a,b). Plastron length increased in proportion to CL of juveniles (slope = 1), whereas carapace width (slope = 0.63), plastron width (slope = 0.54), and shell height (slope = 0.38) increased at decreasing rates (Fig. 5a). As a result, the circular shape of hatchlings elongates into the oblong adult form as individuals grow. The carapace length of juveniles increased an average of 10 mm/yr from age 0 to 10 yrs.

Plastral Kinesis. — The size and age at which the plastral hinge becomes movable was examined in 52 juveniles ranging from 51–113 mm CL. Juveniles exhibited no plastral kinesis at ages 1–2 yrs ($n = 19$, mean PL = 57.6 mm, mean CL = 61.7 mm), developed partial kinesis between ages 2–3 yrs ($n = 22$, mean PL = 77.8 mm, mean CL = 81.0 mm), and complete kinesis by age 5 yrs ($n = 11$, mean PL = 101.3 mm, mean CL = 103.5 mm).

Table 4. Seasonal activity of adults and hatchlings (* spring emergence may have occurred 7–10 days earlier than field observations began).

Year	Spring Emergence of Adults	Days from Spring Emergence to Nesting	Nesting Season	Days from Nesting to Hatchling Emergence	Duration of Hatchling Emergence
1974	28 Mar–6 Apr	74–81	10–25 Jun	74–88	22 Aug–20 Sep
1975*	1–7 Apr	73–82	12–27 Jun	74–91	24 Aug–25 Sep
1976	15–21 Mar	77–87	30 May–15 Jun	76–89	12 Aug–11 Sep
1977	13–20 Mar	75–87	26 May–15 Jun	75–92	10 Aug–13 Sep

Table 5. The number of hatchling turtles captured moving away from nesting areas and toward wetlands. Hatchlings were captured at a drift fence or moving across Hwy. 84.

Species	Spring (May)	Fall (Aug–Sep)
<i>Emydoidea blandingii</i>	26	1564
<i>Chelydra serpentina</i>	7	49
<i>Chrysemys picta bellii</i>	117	28
<i>Graptemys geographica geographica</i>	38	7

Sexual Maturity. — The sex of juveniles could not be determined by external features. Based on observations of courting, the smallest known mature male at Weaver Dunes was 183 mm CL. However, a 171 mm CL (12 yrs old) male that was dissected had testes that appeared to be similar to those of adult males (R. Vogt, *pers. comm.*). Four immature females 152–158 mm CL (11–13 yrs old) were dissected and all had undeveloped ovarian follicles and lacked corpora lutea (M. Ewert, *pers. comm.*). Based on the dissections and observations of females moving to nest or nesting, we estimate minimum size and age at maturity of females at Weaver Dunes to be 160 mm CL and 14 yrs.

Ages and Growth Rates of Adults. — Two turtles recaptured between 1976–80 had dates carved on the carapaces (1958, a male, and 1965, a female). Both dates were carved by local residents (J. Scanlon, J. Schmoker, *pers. comm.*). Numbers on both turtles were worn, but not distorted by growth. Assuming that both turtles were adults and a minimum of 20 yrs old when the dates were inscribed indicates minimum ages at recapture of 35 and 40 yrs for the female and male, respectively. In addition, if a conservative minimum age of 20 yrs is assigned to the 67 adult turtles marked before 1980 and recaptured in 1998–99, they would all now be more than 40 yrs old.

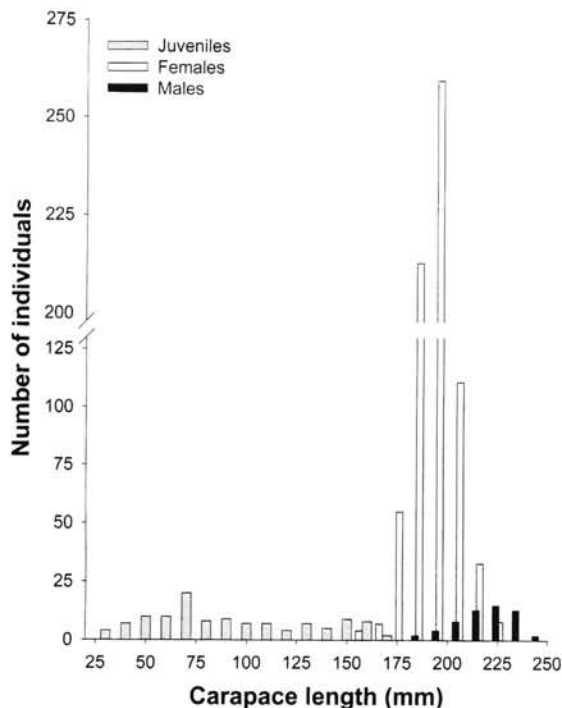


Figure 7. Body size distribution of Blanding's turtles at Weaver Dunes.

The mean growth rate of 98 adults recaptured after periods of 1–4 yrs was < 0.46 mm/yr (range = 0–0.6). In 1998–99, 67 adults that had been marked between 1974–80 were recaptured. The interval between captures ranged from 18–25 yrs (mean = 22.5 ± 0.18) and the change in measured CL ranged from -5 to 23 mm. After setting all negative changes in CL to zero, average annual growth rates were 0.11 mm/yr (SE ± 0.022).

Sex Ratio of Adults. — During the non-nesting portion of the field season, when bias in capture rates between the sexes should be reduced, we captured 59 males and 129 females ($n = 187$ adults), an adult sex ratio of 1 male to 2.2 females.

Seasonal Activity of Adults. — Over the four years from 1974–77 the onset and duration of activities varied (Table 4). Emergence of adults from overwintering occurred between 13 March and 8 April and the period between emergence and initiation of nesting averaged approximately 80 days (Table 4). Nesting seasons began between 26 May and 12 June and averaged 17 days (range = 16–20) in duration, with peak nesting activity during the first and second week in June in 1976 and 1975, respectively (Fig. 6).

Hatchling Emergence from Nests. — Hatchling emergence took place between mid-August and the end of September (approximately 27 days), and the interval between nesting and hatchling emergence activity averaged approximately 82 days (Table 4). Although the majority of Blanding's turtle hatchlings ($n = 1564$, 98.4%) were captured while moving towards wetlands in the fall, 26 individuals (1.6%) were captured on land in spring (Table 5). Of 56 snapping turtle (*Chelydra serpentina*) hatchlings, 87.5% were captured in the fall, whereas of 145 painted turtle (*Chrysemys picta*) and 45 map turtle (*Graptemys geographica*) hatchlings, 80.7 and 84.4%, respectively, were captured on land approximately 10 months later in the spring following nest construction (Table 5).

Population Body Size Distribution. — We collected 843 juvenile (excluding hatchlings) and adult turtles at Weaver Dunes during the course of the study. Mature females were sampled in much greater numbers than males, primarily due to collection bias caused by captures of nesting females on land. In a sample of 301 adult and juvenile Blanding's turtles collected during months that excluded nesting seasons, 114 (37.9%) were juveniles. At the most heavily sampled area (Site 3), 64 of 115 individuals were juveniles (55.7%). All body sizes of juveniles were represented (Fig. 7).

DISCUSSION

Body Sizes of Adults. — Overall mean body sizes of adults (males, CL = 213.6 mm; females, CL = 197.0 mm) at Weaver Dunes are intermediate in size compared to other populations: (1) southeastern Michigan (males, $n = 44$, CL = 198.5 mm; females, $n = 152$, CL = 191.8 mm; Congdon, unpubl. data), (2) Massachusetts (males, $n = 41$, CL = 215.6 mm; females, $n = 33$, CL = 204.2 mm; Graham and Doyle, 1979), (3) Ontario, Canada (females, $n = 11$, CL = 176.5,

MacCulloch and Weller, 1988), and (4) Nebraska (females, $n = 17$, CL = 214.8, Rowe, 1992). Blanding's turtles that occur northwest of Minneapolis-Saint Paul, Minnesota, are substantially larger than those in any other population studied (males, $n = 23$, CL = 260.3 mm; females, $n = 42$; CL = 244.6 mm; Sajwaj et al., 1998).

Adult males and females captured on the Weaver Bottoms (Mississippi River) side of the dune nesting areas averaged 14.7 and 9.1 mm larger, respectively, than adults of both sexes sampled on the old Zumbro River (marsh) side of Weaver Dunes (see Fig. 1). Differences in average body size between habitats are equal to the levels of difference found among many of the populations listed above. Although the causes of the apparent body size differences are not known, genetic differences between sites is not likely since potential for exchange of individuals is high. Historical and other causes may be difficult to document since the habitats on both sides of the dunes have been modified (creation of Weaver Bottoms in 1938 and diversion of the Zumbro River channel in 1973). Differences in body sizes between Weaver Bottoms and the old Zumbro River marsh area may be associated with habitat differences and resource levels.

Sexual Size Dimorphism. — Males are significantly larger and heavier than females within the entire Weaver Dunes population, within samples taken from the Weaver Bottoms and Marsh side of the dunes, and within smaller samples of breeding pairs and of individuals taken from pools during the spring breeding season. How important the apparent sexual size dimorphism (SSD) is in Blanding's turtles is open to question. In support of the biological significance of SSD is the observation that agonistic encounters were observed between males occupying vernal breeding ponds in early spring, and sexual differences in body size at breeding aggregations (13–14 mm) are similar to the differences between adults in the population at large (15.6 mm). In contrast are observations that differences in body sizes of male and female Blanding's turtles at Weaver Dunes are minimal compared to the degree found in many other species of turtles (Berry and Shine, 1980; Gibbons and Lovich, 1990; Lovich and Gibbons, 1992), and some other populations of *E. blandingii* have no apparent sexual size dimorphism (Gibbons, 1968; Kofron and Schreiber, 1985; Petokas, 1986; Congdon and van Loben Sels, 1991). However, minor size differences between males and females and differences in age structure or size specific migration between the sexes when coupled with small sample sizes, can influence detection of apparent or real SSD (Dunham and Gibbons, 1990).

Sexual Shape Dimorphism. — In addition to SSD, males and females in the Weaver Dunes population were shaped differently. For a given CL, females had longer and wider plastrons and higher shells; males were shorter but wider overall. The apparent mechanism for increasing shell width of females is wider plastrons and that for increasing shell height is higher bridge marginals. As a result, even though plastrons are wider in females than in males of the same CL, differences in shapes of bridge marginals between the

sexes result in males being wider overall. That the difference in height between the sexes is not apparently due to differences in lateral curvature of the carapace suggests that carapace curvature may function similarly in males and females.

Differences in body shapes of males and females found at Weaver Dunes was similar to that found in populations in Massachusetts and Nebraska (i.e., for a given length, females had higher shells than males). Males were found to be wider than females at Weaver Dunes and Massachusetts (Graham and Doyle, 1979), but not in Nebraska (Rowe, 1992). That females have wider plastrons and have higher shells for a given carapace length supports the hypothesis that total clutch volume in turtles may be constrained by the abdominal volume within the shell (since plastral kinesis is limited and the carapace cannot be expanded). Shell height of females is significantly correlated with clutch size in other species of turtles (Jackson and Walker, 1997; Zuffi et al., 1999).

At Weaver Dunes, the difference between CL versus PL of males (ANCOVA, CL as covariate, adjusted mean = 11.7 mm) was over three times that of females (adjusted mean = 3.4 mm). Sexual differences in PL have been reported in other populations of Blanding's turtles, and the difference is apparently associated with the concave shape of the plastron of adult males (Graham and Doyle, 1979; Congdon and van Loben Sels, 1991; Rowe, 1992). The shorter plastron of males is hypothesized to be caused by the concave shape around the midline which functions to aid males in mounting females. In addition, compared to females the larger gap between the posterior edge of the plastron and the posterior marginals of males may be associated with the enlargement of the tail and with allowing the penis to flex ventrally during copulation. The relationship between the difference in carapace and plastron length increased with body size in both sexes; however in males (slope = 0.19) the difference increased at approximately four times the rate of females (slope = 0.05).

Reproductive Characteristics. — Mean clutch size for the Weaver Dunes population (9.8 eggs) was most similar to a population in Michigan (10.2 eggs; Congdon and van Loben Sels, 1991) and one in Massachusetts (10.6 eggs; Butler and Graham, 1995), was greater than a population in Ontario (8.0 eggs; MacCulloch and Weller, 1988), and smaller than populations in Massachusetts (12.9 eggs, DePari et al., 1988) and Nebraska (14.9 eggs; Rowe, 1992). Clutch size of Weaver Dunes females is most different from the large-bodied females found at Camp Ripley in central Minnesota (17.7 eggs; Sajwaj et al., 1998). The slope relationship of CS to body size (0.07, $r^2 = 0.20$) for the Weaver Dunes population was slightly less than that found in populations in Ontario, Canada (0.11, $r^2 = 0.45$, $n = 11$; MacCulloch and Weller, 1988), and Michigan (0.10, $r^2 = 0.26$, $n = 280$; Congdon and van Loben Sels, 1991). In a Nebraska sample, no relationship between clutch size and body size was found ($n = 17$; Rowe, 1992).

Eggs of Weaver Dunes females were similar in length, width, and wet mass to those produced by females in Ontario

(MacCulloch and Weller, 1988) and Michigan (Congdon and van Loben Sels, 1991). Eggs were larger and heavier than those from a Nebraska population where average clutch size was about 5 eggs greater (Rowe, 1992) than clutch size at Weaver Dunes.

No observations at Weaver Dunes suggested that females produce more than a single clutch of eggs in a year. The among-year nesting observations suggest that some females reproduce annually whereas some reproduce less often. Less than annual reproduction by some females is similar to that found in other Blanding's turtle populations (Congdon et al. 1983; Petokas, 1986; DePari et al., 1987).

Hatchling Size and Growth of Juveniles. — Hatchlings captured while moving from nesting areas toward marshes averaged about 2 mm longer CL than those incubated in the laboratory and measured immediately after they emerged from eggs. When hatchlings emerge from eggs, their carapaces and plastrons are slightly curled, whereas hatchlings caught in the field have presumably been out of the egg long enough to allow their shells to straighten. Hatchlings captured in the field were similar in size to those from Michigan (Congdon and van Loben Sels, 1991) and Massachusetts (Butler and Graham, 1995).

Four of 45 juveniles captured had a growth annulus adjacent to the birth plate, indicating growth during the fall following emergence from nests. Hatchling growth in their first fall has not been reported for *E. blandingii*, but has been noted in *Terrapene ornata* (Legler, 1960) and *Clemmys guttata* (Ernst, 1976).

Growth rates of Weaver Dunes juveniles (10.0 mm/yr) correspond closely to the growth rate (10.4 mm/yr) found in a Michigan population, the one other study where carapace length was used as the measure of body size (Congdon and van Loben Sels, 1991). Juveniles from Weaver Dunes and Michigan grew at higher rates than the smaller-bodied population in Ontario (Petokas, 1986) and apparently at lower rates than the larger-bodied population in Massachusetts (Graham and Doyle, 1977).

Plastral Kinesis. — Juveniles at Weaver Dunes attain complete shell closure at approximately age 5 yrs and 101 mm CL. There are no other reports on the ontogeny of plastral kinesis in *E. blandingii*. Legler (1960) discussed the ontogeny of the movable hinge in *Terrapene ornata*, and found that juveniles were able to close their shells at 70 mm PL (the end of the fourth growing season).

Whether the degree of shell closure associated with a given body size results in a substantial upward step function in survivorship remains to be determined. However, juvenile Blanding's turtles with an average CL of 91 mm were found at the edge of open water in habitats more typical of those where adults are found (Pappas and Brecke, 1992).

Body Size and Age at Maturity. — Growth rings of juvenile and young adult Blanding's turtles are particularly distinct, and are considered a valid indicator of age (Graham, 1979; Congdon and van Loben Sels, 1991). Recaptures of 8 marked juveniles appear to verify that one major growth annulus is added per year prior to attainment of sexual

maturity. After maturity is reached and growth rates decline, later annuli become crowded together and less distinct.

The smallest female observed nesting at Weaver Dunes was 164 mm CL, a size almost identical to that of the smallest nesting female in southeastern Michigan (163 mm CL, Congdon and van Loben Sels, 1991). The smallest mature females from Massachusetts (181 mm PL; Graham and Doyle, 1977), and central Minnesota (228 mm CL; Sajwaj et al., 1998) were both larger than maturing females from Weaver Dunes or Michigan (Congdon and van Loben Sels, 1993).

Our estimate of minimum age at sexual maturity (14 yrs) for Weaver Dunes females corresponds fairly well with those of previous studies of 12–13 yrs, 14.1 and 14.2 yrs, and 14 yrs (Graham and Doyle, 1977; Petokas, 1986; Congdon and van Loben Sels, 1993). In Michigan, some female Blanding's turtles may not reach maturity for 20 yrs (Congdon and van Loben Sels, 1993), and in central Wisconsin some females mature at 18 yrs (Ross, 1989). Graham and Doyle (1977) suggested that sexual maturity in *E. blandingii* is probably more closely related to age rather than size. However, accumulating evidence suggests that substantial variation in juvenile growth rates, age and size at sexual maturity occurs within populations of Blanding's turtles, and that interactions among these traits determine the phenotypes of primiparous females (Stearns and Koella, 1986; Congdon and van Loben Sels, 1993).

Ages and Growth Rates of Adults. — Because adults cannot be accurately aged, the population age structure of Weaver Dunes *E. blandingii* is unknown. However, based on dates inscribed on their shells, two adults may have been at least 35 and 40 yrs old. The oldest known Blanding's turtle was at least 77 yrs old (Brecke and Moriarty, 1989) and a group of females marked on the E.S. George Reserve in Michigan in the 1950s (Sexton, 1995) are a minimum ages of 65 yrs (Congdon, unpubl. data). Combined, the observations suggest that Blanding's turtles may be among the longest lived emydid species in North America.

Some adult turtles at Weaver Dunes appeared to cease growth after reaching sexual maturity, whereas others continued to grow, a situation similar to that reported for adults in a Michigan population (Congdon and van Loben Sels, 1991). Over a four year period, the mean growth rate of Weaver Dunes adults (0.46 mm/yr) was slightly less than growth rates reported for a Michigan population (0.66 mm/yr, Congdon and van Loben Sels, 1991). However, since the growth rate reported for Michigan adults was restricted to individuals that showed positive growth, overall adult growth rates of the two populations may actually be more similar. In addition, growth rates will be influenced by the relative number of young adults in a sample of individuals. A recording of negative growth can result from measurement error or shell wear or shrinkage (Ream, 1967; Vogt, 1980).

Within a sample of adult turtles from Weaver Dunes recaptured after two decades, 49% exhibited negative or no growth, and 90% of the individuals grew an average of less than 0.3 mm/yr. In a sample of 12 adult turtles from

southeastern Michigan with recapture intervals averaging 20.5 yrs (11–26 yrs), growth rates averaged 0.10 mm/yr (Congdon, unpubl. data). One third of the individuals did not grow and the growth rate of only one individual exceeded 0.2 mm/yr.

Adult Sex Ratios. — The adult sex ratio (1 male to 2.2 females) at Weaver Dunes is female biased as are those of the Michigan (1:3.8; Congdon and van Loben Sels, 1991) and Wisconsin (1:2.5; Ross, 1989) populations. Adult sex ratios were not different from 1:1 in populations from Massachusetts (Graham and Doyle, 1977) and southwestern Michigan (Gibbons, 1968).

Biased sex ratios can result from temperature dependent sex determination (TSD) that occurs during development in *E. blandingii* (Gutzke and Packard, 1987), sex specific differential mortality, or migration patterns of juveniles or adults.

Proportion of Juveniles in the Population. — That juveniles comprise a large percentage of the total sample (35.1–55.7%) is in contrast to all previous observations of *E. blandingii* populations where an apparent lack of small juveniles is one of the notable features (Gibbons, 1968; Graham and Doyle, 1977; Congdon et al., 1983; Kofron and Schreiber, 1985; Petokas, 1986; Congdon and van Loben Sels, 1991; Butler, 1997). One reason for the large proportion of juveniles at Site 3 may be that it is located 75–100 m from a major nesting area, and many hatchlings move from nests to this site. The reason for the apparent scarcity of young animals in other populations is not clear. Suggestions by Gibbons (1968) and Graham and Doyle (1977) that sampling bias may have favored the capture of adults is supported by the Weaver Dunes trapping records in that we seldom collected juveniles in open water baited traps ($n = 7$) or by dip netting from a canoe. In addition, young individuals may be secretive and cryptic (Congdon et al., 1993; Butler, 1997), and juvenile Blanding's turtles exhibit habitat preferences that may contribute to sampling bias (Pappas and Brecke, 1992; Butler and Graham, 1995).

Seasonal Activity of Adults and Hatchlings. — Temporal variation in turtle activity can be influenced by weather conditions. Initiation of spring emergence, nesting, and hatchling emergence over four years all varied from 2 to 3 weeks. Warmer springs resulted in earlier nesting seasons for Blanding's turtles (Congdon et al., 1983) and for common snapping turtles (Congdon et al., 1987; Obbard and Brooks, 1987). Between 1974–77, durations of nesting seasons ranged from 16–20 days at Weaver Dunes, values that were similar to those reported for Blanding's turtles in southeastern Michigan (1976–81, 16–30 days, Congdon et al., 1983).

The predominant pattern is for Blanding's turtle hatchlings to emerge from nests in the fall (Congdon et al., 1983; Butler and Graham, 1995; Standing et al., 1997). Capture of hatchlings at drift fences occurred an average of 75 days after nest construction at Weaver Dunes. Time from nest construction to hatchling emergence from nests averaged 84 days in southeastern Michigan (Congdon et al., 1983) and 94 days in Nova Scotia (Standing et al., 1999).

That 1.6% of hatchlings at Weaver Dunes were captured at drift fences in the early spring indicates that overwintering in terrestrial environments is possible. Data from

other studies also indicate that some hatchlings remain on land (either in nests or at other sites) during their first winter (Congdon et al., 1983; Butler and Graham, 1995; Standing et al., 1997). In Nova Scotia, Blanding's turtle hatchlings have been observed to avoid water following nest emergence (Standing et al., 1997). Two other observations combine to indicate that overwintering on land is possible for Blanding's turtle hatchlings: (1) hatchlings can tolerate freezing at -2°C for at least 48 hours (Packard et al., 1999), and (2) snow cover provides enough insulation to prevent soil temperatures in southeastern Michigan from going below -2°C during some winters (Nagle et al., 2000).

Body Size Distribution. — The two major features of the body size distribution of turtles (excluding hatchlings) at Weaver Dunes is the relatively even distribution of juveniles across all size groups, and the large number of adult females compared to adult males. In a sample of turtles captured outside of the nesting season, approximately 38% were juveniles. The even distribution of size classes of juveniles combined with the large number of hatchlings captured between 1974–80 argues for relatively even recruitment over time. However, without a more comprehensive mark-recapture study, it is impossible to judge whether the number of recruits is large enough to result in a stable population.

Population Size Estimates. — Data are not adequate to base mark-recapture estimates with confidence intervals for the Weaver Dunes population of Blanding's turtles. However, the low mortality rates of Blanding's turtles combined with the number of individuals marked over the six years of this study result in a minimum population estimate of over 2000 individuals. In addition we can make two first order estimates of population size based on captures at the 1.5 km drift fence. Estimate 1 is based on the number of females initially captured, marked, released, and recaptured during the 1975 and 1976 nesting seasons. In 1975, 151 turtles were initially marked, and in 1976, 253 new females were captured and marked and 48 recaptures were made of females marked in 1975. A simple Lincoln Index resulted in an estimate of 1271 nesting females in the area of the old Zumbro River marshes sampled by the drift fence. Estimate 2 is based on the 731 females counted at the drift fence or crossing the road during a 15-day monitoring period in 1976 (a conservative number since the area was not monitored on all days of the nesting season). The number of females obtained by both methods were adjusted by a generous assumption that the drift fence samples one third of the total area of the old Zumbro River marshes (i.e., two thirds of the wetlands were not sampled by the fence). To obtain the total population estimate, the total number of males was calculated from estimated numbers of females and the known adult sex ratio (2.2 females per male = 0.45), and the number of juveniles was calculated (as 0.25 of the total number of adults). Based on estimates 1 and 2, the total population was between 2500 to 4600 individuals, respectively, on the old Zumbro River Marsh (west) side of Weaver Dunes alone. Currently data are not available to estimate the population on the Weaver Bottoms (east) side of Weaver Dunes.

Based on an estimate of the wetlands only within the old Zumbro River area and population size results in densities of 3 to 6 Blanding's turtles per ha compared to 9 individuals per ha of wetland in southeastern Michigan (Congdon et al., 1986); a comparison that suggests the estimated population size on the west side of Weaver Dunes is low.

Why are there so many Blanding's turtles at Weaver Dunes? The large population may be the result of the extensive mosaic of aquatic habitats (Old Weaver Bottoms wetland and the old Zumbro River Marsh area total over 3000 ha with over 2000 ha of wetland) coupled with close proximity to extensive nesting areas (Weaver Dunes = 600 ha). Another striking characteristic of the Weaver Dunes population is the relatively large numbers of juveniles which suggest that nest success and hatchling recruitment may be high, presumably due to the large nesting area that predators need to search. Weaver Dunes may represent the preferred habitat of Blanding's turtles. Fossil Blanding's turtles have been found in what had been prairie marshes south and west of existing populations (Preston and McCoy, 1971). Prairie marsh habitats have retreated from the central plains toward the Great Lakes region of the United States since the last glacial maximum (Preston and McCoy, 1971) and have been substantially reduced since European settlement.

Large losses of habitat such as Weaver Bottoms must certainly have impacted the overall population size or, if the turtles from Weaver Bottoms moved into adjacent habitats, caused a substantial increase in turtle density. Such an increase in density would have the potential to reduce per capita resources which could reduce: (1) juvenile growth rates, (2) clutch sizes and reproductive frequency of females, and (3) survivorship of juveniles and adults.

If the combination of large wetlands and nesting areas are the reason for the large population at Weaver Dunes, then, from the perspective of Blanding's turtles, the area seems to be unique. With the growing interest in Blanding's turtles over the past 30 years, it is unlikely that an unknown site could exist with a population the size approaching or exceeding that at Weaver Dunes.

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