

## Nesting Ecology and Embryo Mortality: Implications for Hatchling Success and Demography of Blanding's Turtles (*Emydoidea blandingii*)

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**ABSTRACT.** – A 23-year study (1976–98) of Blanding's turtle nesting ecology was conducted concurrently with a mark-recapture study on the University of Michigan's E.S. George Reserve in southeast Michigan. Nesting seasons averaged 28 days duration with the earliest beginning and latest ending on 15 May and 9 July, respectively. Females generally began nesting forays in the evening and completed nests after dark. A total of 451 nests were located, including: 1) intact observed nests associated with a known female ( $n = 296$ ), 2) intact observed nests not associated with a specific female ( $n = 16$ ), and 3) unobserved nests found after they were destroyed by predators ( $n = 139$ ). In the sample of observed nests, 182 were monitored until subsequent destruction by predators, hatchling emergence, or nest inspection for evidence of egg and embryo mortality in late fall. In total, 78% of observed nests were destroyed by surface predators (mainly raccoons), 1% were apparently destroyed by burrowing mammals, and 4% failed entirely due to abiotic and other causes (i. e., soil erosion, flooding, desiccation of eggs, root intrusion into nests). Approximately 10% of the observed nests were partially successful (produced at least one hatchling), and 8% were considered as total success (all eggs produced hatchlings). Adding embryo mortality to nest predation rates reduced embryo survival ( $S_x$  age 0) by about 30% (from 0.261 to 0.176). We recalculated the previously published life table (age 0 mortality based on nest predation rates only) that indicated a stable population. Lower embryo survival resulted in a population that would decrease by 50% in 78 years. To compensate for the increased embryo mortality, adult and juvenile survival estimates would have to increase by 1.5 and 2.2%, respectively; these compensatory increases in survival are certainly within the errors of estimates based on mark-recapture data. Because the vast majority of embryo mortality is caused by nest predators, additional embryo mortality in nests surviving predation does not appear to have a major impact on the population dynamics of Blanding's turtles as long as survivorship of older juveniles and adults is not reduced from present levels.

**KEY WORDS.** – Reptilia; Testudines; Emydidae; *Emydoidea blandingii*; turtle; demography; embryo mortality; nesting; nest predators; reproduction; Michigan; USA

As presently practiced, conservation ecology is primarily a reactive and crisis-driven discipline (Soule, 1985). Conservation strategies often involve immediate management solutions for desperate and complex environmental problems, requiring awareness of perturbing forces (e.g., habitat degradation, overexploitation) and careful consideration of the biology of the target organism. Management plans which fail to incorporate adequate ecological information due to time or financial constraints can be ineffective, and under certain circumstances, detrimental to survival of the target species (Frazer, 1992, 1997; Heppel et al., 1996). Considering the investment in time and money, populations at high risk, in decline, and those fragmented or small in size

do not make good models for long-term studies of life history and demography. As a result, relevant life-history data derived from long-term studies of stable populations are valuable resources as models for the design of species maintenance and recovery plans (Congdon et al., 1993; Frazer, 1997).

Most long-term mark-recapture studies have focused on concepts and hypotheses related to the evolution of life history traits. Traits of importance in life history and demographic studies are also those essential for accurately predicting population-level responses to acute and chronic sources of mortality, and for identifying temporal scales and factors associated with recovery (Brooks et al., 1991; Iverson, 1991; Congdon et al., 1993; Dunham, 1993; Dunham and

Overall, 1994; Galbraith et al., 1997). For example, in long-lived organisms, traits such as high adult and juvenile survivorship, delayed sexual maturity, low annual fecundity, and low embryo survivorship limit the ability of populations to respond to chronic, high levels of adult mortality (Brecke and Moriarty, 1989; Congdon et al., 1993; Congdon et al., 1994).

Growing concern about the status of Blanding's turtles (*Emydoidea blandingii*) is prompted by substantial habitat loss and fragmentation, and population declines (Kofron and Schreiber, 1985; Herman et al., 1995; Kiviat, 1997; Butler, 1997). High adult and juvenile mortality rates and chronically low nest survival, often found in areas characterized by human development (Kiviat, 1997; Wood and Herlands, 1997), are inconsistent with overall Blanding's turtle life history trait values, and have the potential to cause rapid population declines (Congdon et al., 1993). Periods with increased risk of mortality are those associated with extended overland nesting movements of females, particularly in areas with high vehicle traffic (Ashley and Robinson, 1996; Boarman et al., 1997).

To determine the magnitude, range of variation, and impact of natural sources of embryo mortality on the demography of Blanding's turtles, long-term field studies are required. The 34-year study of turtle nesting ecology and demography on the E.S. George Reserve in southeast Michigan (Congdon and Gibbons, 1996) has resulted in published life tables for populations of three turtle species (*Chrysemys picta*: Wilbur, 1975; Tinkle et al., 1981; *Emydoidea blandingii*: Congdon et al., 1993; *Chelydra serpentina*: Congdon et al., 1994). All three life tables were constructed with mortality of embryos (age class 0) based only on rates of nest predation. However, additional sources of embryo mortality within nests have not been reported and may be substantial enough to alter previous demographic descriptions.

The major goals of the present study were to: (1) describe the nesting ecology of a population of Blanding's turtles in southeastern Michigan, (2) document levels of embryo mortality that occur in nests not destroyed by predators, and (3) determine the relative impact of additional embryo mortality on the demography and population stability of Blanding's turtles.

## MATERIALS AND METHODS

The University of Michigan's E.S. George Reserve (ESGR) encompasses about 650 hectares of wetland and terrestrial habitats that are protected from human disturbance, a factor critical for conducting long-term research on natural populations. Descriptions of the aquatic and terrestrial habitats of the ESGR have been published previously (Cantrall, 1943; Sexton, 1959, 1995; Wilbur, 1975; Congdon and Gibbons, 1996). Blanding's turtles on the ESGR have been studied for 34 of the past 46 years (1953 to 1957 by O. Sexton, 1968 to 1973 by H. Wilbur, 1975 to 1979 by D. Tinkle and J. Congdon, and from 1980 to 1998 by J. Congdon). Intensive mark-recapture and nesting ecology studies began in 1975 and 1976, respectively, and have continued through the 1998 nesting season. The population

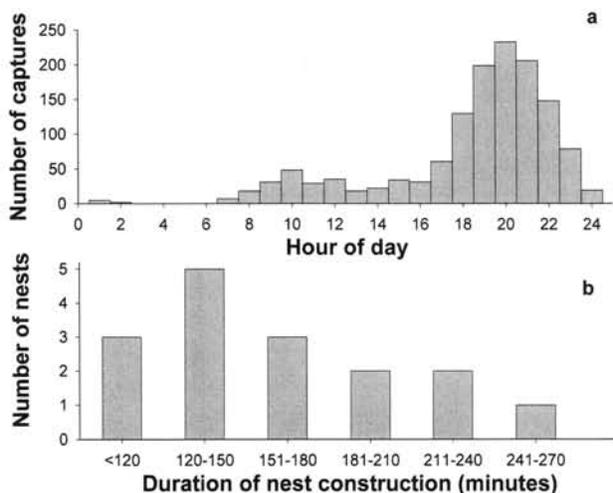
of adult Blanding's turtles has remained essentially stable at approximately 180 to 200 adults between 1975 and 1994 (Congdon and Gibbons, 1996).

Each year from 1975 to 1986 and from 1991 to 1995, intensive aquatic trapping was carried out from early May through early September, and drift fences were monitored from April through June, and usually during September and October. From 1987 to 1990, and 1996 to 1998, the study was conducted only from early May to early July. A total of 4385 recaptures of 1280 individuals (including 633 hatchlings marked at nests or terrestrial drift fences) have been made in aquatic areas and on land (for capture methods see Congdon et al., 1983). At first capture, all juvenile and adult turtles were individually marked by notching margins of the carapace, hatchlings were assigned an age (year of life) of 1, and when possible ages of juveniles were determined by counting annuli. We measured body mass and straight line plastron and carapace length, then released individuals at their point of capture.

All females captured during the first week in May through the end of each nesting season were palpated to determine if they were carrying oviductal eggs. From 1978 to 1998, radiographs were taken of all females known or suspected to be carrying eggs (Gibbons and Greene, 1979; Hinton et al., 1997). We recorded data related to reproduction by females that included clutch size, timing and duration of terrestrial activities, observations on nesting behavior, and nest survivorship.

Prior to capture of the first gravid female each year, all drift fences were activated and routine searches of nesting areas were made each day. After the first gravid female was captured, systematic searches of all nesting areas were initiated, and drift fences were checked approximately every 30 minutes (usually between 0600–2000 hrs or cessation of turtle activity). Searches of nesting areas were conducted on all days that females were active on land throughout nesting seasons (all years = 15 May – early July). The beginning of the nesting season each year was defined as the first day a female with eggs was found on land, and the end was defined as the date of the last nest or observation of a gravid female on land, followed by three days of searches without detecting females on land. All nests observed by us were identified and marked either with a stake placed 2 meters from the nest or with flagging tied to nearby vegetation. When females were captured immediately after nesting, they were palpated to determine if they had retained eggs. If eggs were palpated, an additional radiograph was taken to determine how many eggs were retained. Straight line distance from the nest to nearest water was measured with a meter wheel for a sample of 263 nests.

Active nests (those not destroyed by predators) were monitored daily for signs of predation until the end of the nesting season. When the field work continued throughout summer, surviving nests were checked weekly, and during the last week in August nests were encircled with an 0.3 m aluminum fence buried to a depth of 15 cm. Fenced nests were monitored twice per day until hatchlings began to emerge, and then more frequently during the period of actual emergence. In years that field research ended shortly after



**Figure 1.** a) Timing of overall nesting activities (i.e., exiting marshes, overland nesting migrations, and nest construction), and b) duration of construction of 17 Blanding's turtle nests.

the nesting season, nests were excavated and inspected in late August or early September.

Hatchling emergence and nest inspections yield data on the dates, timing, and synchrony of hatchling emergence, and on egg and embryo mortality. All live hatchlings were marked (individually or as a nest cohort), weighed and measured, and released at the nest site or directly into marshes. Failed eggs and dead hatchlings remaining in nests were counted and categorized as: (1) no development (infertile eggs, or those that died early in development; such eggs were desiccated and intact rather than rotted), (2) partial development (eggs in which embryo development was partially advanced, usually enough to cause rotting), or (3) total development (pipped eggs or hatchlings out of eggshells). We compared estimates of the number of eggs in nests (i.e., clutch size) based on nest inspection data vs. egg counts from radiographs to determine the reliability of nest inspections near the time of hatching. We also examined whether early vs. late hatchling emergence, or synchronous vs. asynchronous hatchling emergence were indicators of nest quality.

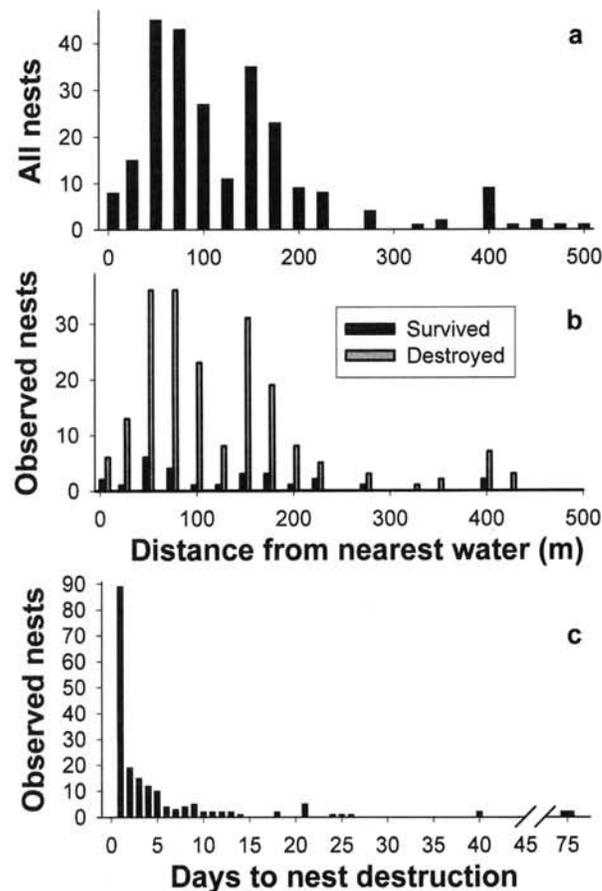
Life tables were constructed using values described by Congdon et al. (1993) for age at maturity, fecundity, and juvenile and adult survivorship. Life tables were modified using values for nest and embryo survivorship obtained from data accumulated on the ESGR *E. blandingii* population. Fecundity ( $m_x$ ) was defined as the number of female eggs produced annually, calculated as mean clutch size / 2 (to adjust for production of males by making an assumption of an equal primary sex ratio) multiplied by clutch frequency.

**RESULTS**

*Nesting Activities.* — Between 1976 and 1998, the duration of nesting seasons averaged 28 days with the earliest beginning and latest ending on 15 May and 9 July, respectively. Females generally left their resident marshes and began nesting forays before sundown (Fig. 1a); some arrived at nesting areas on the same evening, whereas others

remained on land for several days before nesting activities were observed. After leaving their marsh of residence and prior to nesting, females often were found in terrestrial habitats covered with leaves or under bushes or in small wetlands adjacent to nesting areas.

Most females committed to a nesting site and began construction before dark, then completed nesting after dark (Fig. 1a,b). Overall nesting activities were concentrated between 1700–2300 hrs; however, on warm rainy mornings and those following rain, some nesting activity occurred as early as 0700 hrs and occasionally continued throughout cloudy days (Fig. 1a). We recorded the beginning and end times for 17 nests. The majority of nests ( $n = 14$ ) were constructed within 3 hrs (mean = 149 min, range = 95–195 min). As a result of rapidly dropping temperatures after sundown, four other nests took over 4 hrs to complete (mean = 273 min). Nests were usually constructed in sandy soils in open-canopy areas with little vegetation. Although the maximum distance of nests from the nearest water was over 500 m, less than 1% of the 263 nests measured exceeded 400 m from water (Fig. 2a). Surviving nests were evenly distributed across all distances from water and did not appear to be a function of the number of nests present at a given distance (Fig. 2b); however, at larger distances from water, samples of observed nests were small.



**Figure 2.** a) Distance from nearest water for all nests, and b) observed nests that survived (black bars) and those that were destroyed by predators (gray bars). c) The number of days from nest construction to nest destruction by predators.

**Table 1.** *Emydoidea blandingii* nests on the E.S. George Reserve and their fate ( $n$  = number of nests followed that hatchling success could be determined with certainty; — = missing data). Causes of embryo failure other than incomplete development include flooding, erosion, and live hatchlings in nests becoming encapsulated with roots. Some nests were protected from predators.

Year	Annual Nest Production and Depredation				Causes of Embryo Mortality (%)				
	Total No. Nests	No. Monitored	Percent Survived	Percent Destroyed	$n$	Development			Other
						Total Nest Success	Partial Nest Success	Total Nest Failure	Total Nest Failure
1976	13	8	37.5	62.5	3	0.0	33.3	66.7	0.0
1977	20	14	50.0	50.0	7	28.6	71.4	0.0	0.0
1978	21	13	53.8	46.2	7	42.9	28.6	28.6	0.0
1979	20	13	30.8	69.2	4	25.0	0.0	75.0	0.0
1980	19	13	23.1	76.9	3	33.3	66.7	0.0	0.0
1981	16	13	7.7	92.3	1	0.0	100.0	0.0	0.0
1982	23	14	50.0	50.0	11	27.3	45.5	27.3	0.0
1983	21	14	50.0	50.0	8	50.0	25.0	25.0	0.0
1984	13	5	60.0	40.0	3	100.0	0.0	0.0	0.0
1985	19	15	0.0	100.0	0	—	—	—	—
1986	17	13	0.0	100.0	0	—	—	—	—
1987	26	9	0.0	100.0	0	—	—	—	—
1988	11	7	0.0	100.0	0	—	—	—	—
1989	20	11	0.0	100.0	0	—	—	—	—
1990	12	6	33.3	66.7	2	100.0	0.0	0.0	0.0
1991	14	6	0.0	100.0	0	—	—	—	—
1992	26	12	0.0	100.0	0	—	—	—	—
1993	21	12	0.0	100.0	0	—	—	—	—
1994	20	4	0.0	100.0	6	16.7	83.3	0.0	0.0
1995	20	10	40.0	60.0	10	30.0	50.0	0.0	20.0
1996	23	6	33.3	66.7	8	62.5	37.5	0.0	0.0
1997	28	16	31.3	68.8	4	0.0	50.0	50.0	0.0
1998	28	4	0.0	100.0	20	30.0	55.0	10.0	5.0
Total	451	182			97				
Mean			21.7	78.2		35.1	45.4	16.5	3.1

Over 23 years of study, we located a total of 451 nests that we classified in 3 ways: (1) observed active nest associated with known female ( $n = 296$ ); (2) observed active nest but female not known ( $n = 16$ ); and (3) nests found recently destroyed by predators ( $n = 139$ ).

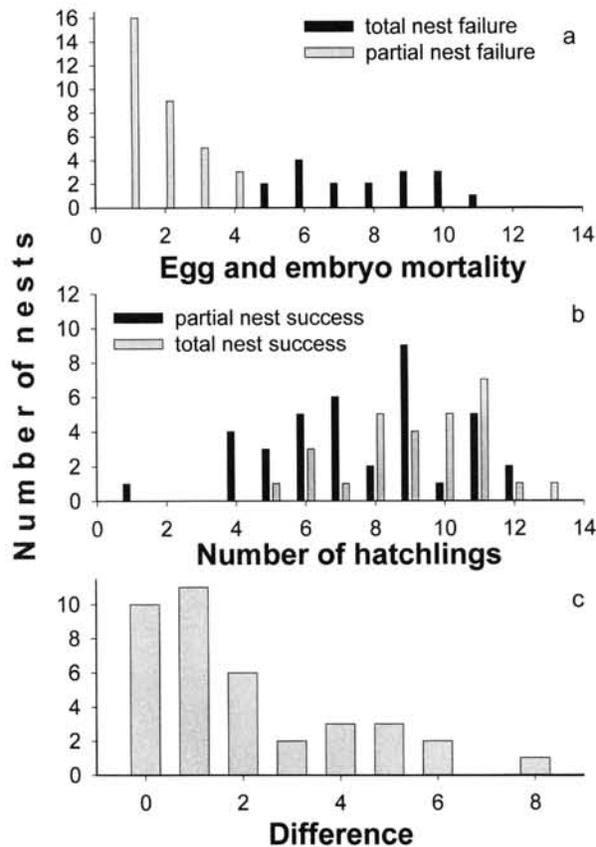
**Destruction of Nests by Predators.** —A sample of 182 observed nests over 23 years were monitored from nest construction to subsequent destruction by predators or through fall hatchling emergence. Nest destruction by predators averaged 78.2% (range = 40–100%; Table 1). Predation rates averaged 59.7% from 1976 to 1984, and 73.9% from 1995 to 1998. During the period from 1985 to 1994, predators destroyed 100% of observed nests in 9 of 10 years (mean = 94.5%; Table 1). Raccoons were the primary nest predator, and were frequently seen patrolling nesting areas.

Nests were most at risk during the first full day following construction (Fig. 2c). Many nests were destroyed the night they were constructed, and cases of destruction while the female was still at the nest were observed every year. By day 5, the risk of nest destruction had reached a relatively low and constant level (Fig. 2c). Destruction of nests after 10 days occurred during or just following rain. In the sample of 112 nests destroyed by predators, distance of the nest from water was not correlated with the number of days to destruction by predators (Spearman's  $Rho = 0.021$ ,  $p = 0.83$ ). The period of hatchling emergence was also associated with some risk of predation (represented by day 75 in Fig. 2c). Hatchling mortality associated with emergence from nests, although infrequent, occurred most often in nests with

asynchronous emergence (i.e., the emergence hole created by the first hatchlings to leave the nest exposed those that remained in the nest to increased risk of discovery by predators).

**Embryo Mortality in Nests not Destroyed by Predators.** — Among nests escaping predation, 19.5% failed to produce any hatchlings. In nests that produced no hatchlings, the number of failed eggs or embryos ranged from 5 to 11 (Fig. 3a). Limited or no development was responsible for the majority (16.5%) of total nest failures among nests surviving predation. One known cause of developmental failure was selection of nest sites with substantially reduced or absent insolation (i.e., areas with closed vegetation canopy) that resulted in low nest temperatures (Fig. 4). Soil temperatures at 60 mm depth in full sun averaged 16.5, 21.2, and 25.9°C for the last two weeks in May, and all of June and July, respectively, whereas temperatures at the same depth in a fully shaded area averaged 10.8, 15.2, and 19.0°C, respectively. On average the soil temperature in the shaded area was 6.3°C lower over the entire period.

A second factor causing total or partial failure of nests during prolonged dry periods was extremely dry soil. Dry soils caused two problems. First, females were not able to construct nest flasks because the soil collapsed into the nest cavity and the resulting nest cavity was funnel shaped (resembling an ant lion pit). Most females aborted these nesting attempts; however, when eggs were deposited in the funnel shaped nest, some were broken during covering and some remained uncovered when the female left the nest. In addition, dry soils caused desiccation of some eggs (prima-



**Figure 3.** Distributions of number of nests: **a)** categorized as “total failure” (no hatchlings) or “partial failure” (at least one egg or embryo failed during development) based on total egg and embryo mortality based on evidence obtained at nest inspection; **b)** categorized as “partial success” (at least one hatchling survived) or “total success” (all hatchlings thought to be in the nest survived); and **c)** categorized as “total success” (no evidence of egg failure) and for which clutch size was determined by radiography of the female prior to nesting (x-axis = difference in observed clutch size determined from radiographs minus egg counts based on nest inspection).

rily those closest to the surface). Additional total failure of nests surviving predation (3%) were due to: (1) flooding of nests placed in low areas, (2) erosion associated with summer thunder storms, and (3) root encapsulation of nests placed too close to vegetation. Root encapsulation also caused partial failure of some nests.

Among the remaining 80.5% of the total nests that escaped predators, 35.1% were totally successful (all eggs in the nest produced hatchlings) and 45.4% were partially successful (they produced at least one hatchling). Among partially successful nests, we found the majority of nests contained only 1 or 2 failed eggs or embryos (range = 1–4; Fig. 3a). As expected, the number of hatchlings emerging from individual nests was generally higher for those nests with no evidence of egg or embryo failure (Fig. 3b) compared to nests with evidence of partial egg or embryo failure.

We inspected nests around the time of hatchling emergence in the fall. To determine how accurate nest inspections were in detecting failed eggs or embryos, we compared clutch size determined from radiographs to the number of hatchlings emerging from individual nests categorized as

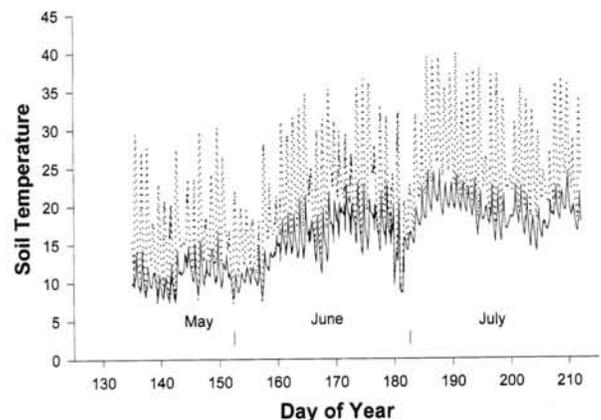
totally or partially successful. Clutch size determined from nest inspection detected an average of 2 fewer eggs (SE ± 0.34) in nests compared to clutch size determined from radiographs (Fig. 3c). In addition, we compared estimates of clutch size based on nest inspection data to egg counts from radiographs. Our ability to categorize nests as totally successful based on nest inspection after hatching was not consistent. Of all nest and radiograph pairs, 58% had differences of 0 or 1 egg and 42% had differences from 2 to 8 eggs when compared to the number of eggs females produced (Fig. 3c). The frequency of egg retention by females over all years of this study appears to be too low (4 individuals detected) to account for the differences between egg counts from radiographs and those from nest inspections.

**Hatchling Emergence.** — In a sample of 59 surviving nests, hatchling emergence took place between 65 and 110 days (mean = 85 d) following nest construction (Fig. 5a). Hatchlings emerged during all hours of daylight with about 75% emerging before 1300 hrs (Fig. 5b). All hatchlings emerged on the same day in 70% of nests, but emergence ranged from one to four days in other nests (Figs. 5c,d). We found no relationship between days to emergence and total hatchlings emerging (Spearman Rho = 0.188,  $p = 0.34$ ), or between days to emergence and number of failed eggs within nests (Spearman’s Rho = 0.023,  $p = 0.82$ ).

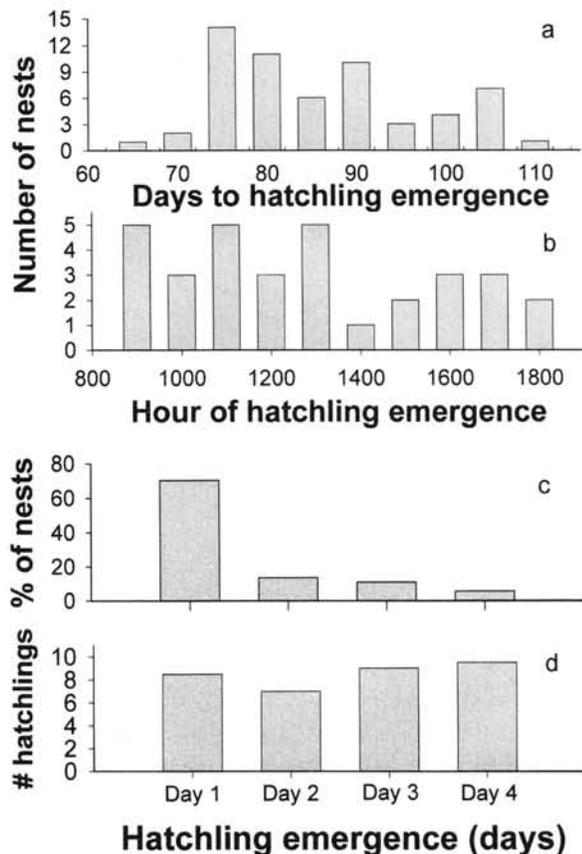
**Hatchling Recapture Rates.** — Of 286 hatchlings marked between 1976 and 1984, 25 (8.8%) were subsequently recaptured. Minimum recapture intervals averaged 9.2 years and ranged from 1 to 21 years (Fig. 6).

**Life Tables.** — Data used to construct life tables were obtained from the present study and from published studies of ESGR Blanding’s turtles (Table 2). We used values described by Congdon et al. (1993) for adult and juvenile survivorship and age at maturity. Variation in alpha was included in the life table by increasing fecundity ( $m_x$ ) values between ages 14 and 17 yrs. Annual fecundity ( $m_x$ ) was based on the grand mean of clutch size, adjusted for an equal hatchling sex ratio and an annual reproductive rate of 0.85.

Including sources of embryo mortality in addition to nest predation, long-term mean embryo survival ( $S_x$ ) de-



**Figure 4.** Soil temperatures at 60 mm depth (approximate depth of the top of Blanding’s turtle nests) on the E.S. George Reserve from 15 May – 31 July 1993. Temperatures were recorded in areas of full sun (dotted line) and full shade (solid line) every 15 minutes.

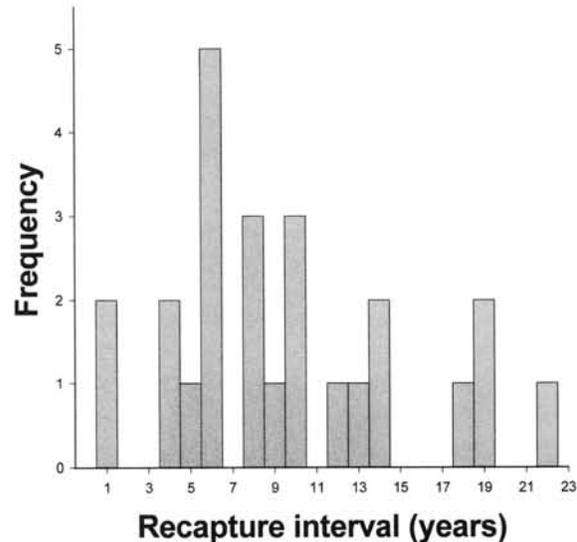


**Figure 5.** a) The number days from nest construction to hatchling emergence, and b) the hour of day that hatchlings emerged from nests. c) Number of nests from which hatchlings emerged over 1 to 4 days, and d) mean number of hatchlings produced for nests having hatchlings emerge over 1 to 4 days.

creased by 0.085 from 0.261 (Congdon et al., 1993) to 0.176. Embryo survival of 0.176, combined with all other demographic parameters used in the previous life table for ESGR Blanding's turtles (Congdon et al., 1993) resulted in a cohort that would decrease by half in 78 years (Table 3a). Increasing annual adult survival by 2% resulted in a cohort that would double in 142 years (Table 3b).

## DISCUSSION

**Nesting Activity.** — The onset of nesting in Blanding's turtles occurs earlier in years with greater numbers of warm days in early spring (Congdon et al., 1983). Blanding's turtles increase their body temperatures by basking on grass tussocks, muskrat mounds, and woody debris, particularly on sunny days when air temperatures are high in spring (Dobson, 1971; Sexton, 1995; Sajwaj, 1998). Higher body temperatures apparently promote enlargement of follicles and attainment of conditions necessary for ovulation earlier in the year (Ganzhorn and Licht, 1983; Obbard and Brooks, 1987; Congdon, 1989). The end of nesting seasons in dry years was later than those with frequent, warm rainy periods. In nesting seasons with more frequent rainfall, the frequency of nesting activity was higher during and following rain, and



**Figure 6.** Distributions of minimum recapture intervals of 25 individuals (8.8% of 286 hatchlings marked at nests or at drift fences) marked prior to 1984 on the E.S. George Reserve.

more females were successful at constructing nests on their first attempt. One factor prolonging nesting during dry seasons was a high frequency of aborted nesting attempts due to excessively loose, dry soil. Many excavations in dry soil were aborted, and under extremely dry conditions resulted in funnel-shaped depressions instead of typical flask-shaped holes. In an apparent attempt to avoid dry soil conditions during a drought year, one female repeatedly attempted to nest in open areas and then retreated under a pile of fallen leaves near the edge of a woods to nest. Because the soil under the leaf pile retained some moisture, she was able to construct a flask-shaped nest there, lay eggs, and cover; however, embryo development was not completed before winter and the nest failed completely.

Major factors influencing nest construction appear to be soil moisture and ambient temperature. Although most nesting activity occurred during the evening (Congdon et al., 1983; Linck et al., 1989; Rowe, 1992), nesting was observed during warm rains regardless of the time of day. Two potential advantages associated with nesting during rain include a softened nesting substrate and reduction of the olfactory cues used by predators to locate nests. Water transported to nests by females is clearly an essential component of nesting for the sympatric painted turtle (*Chrysemys picta*) and may be important for softening soil at the nest site

**Table 2.** Characteristics of Blanding's turtles on the ESGR in southeastern Michigan (Congdon and van Loben Sels, 1991, 1993; Congdon et al., 1993) used to construct life tables.

This Study:	
% of observed nests that survived predation	21.8
% of surviving nests producing hatchlings	80.4
Congdon et al., 1993:	
Average clutch size	10.1
Clutch frequency	0.85
Minimum age at maturity (yrs)	14
Average annual juvenile survivorship	0.783
Average annual adult survivorship	0.96

**Table 3.** Life tables for *Emydoidea blandingii* on the E.S. George Reserve. Data are long term means for the population. Life Table A uses all values used in Congdon et al. (1993), but incorporates embryo mortality from this study ( $S_x$  for age 0 reduced by 0.085 from 0.0261 to 0.0176). Life Table B uses all values used in Life Table A, but increased annual adult survivorship by 0.02 from 0.96 to 0.98. Annual fecundity (4 eggs) is based on a mean clutch size of 10 eggs, reproductive frequency of 0.85, and one half of all eggs produce daughters.  $S_x$  is probability of survival from age  $x$  to age  $x + 1$ ,  $l_x$  is the probability of survival from birth to age  $x$ ,  $m_x$  is the expected fecundity of a female at age  $x$ ,  $r$  = the intrinsic rate of population increase or the implicit solution of  $1 =$  the sum of  $l_x m_x e^{-rx}$ , and  $T_c$  is the cohort generation time for the population, and  $R_0$  is reproductive rate for females discounted by probability of mortality. Population parameters for Life Table A are  $R_0 = 0.713$ ;  $r = 0.0087$ , and  $T_c = 36.1$  years, time for population to be reduced by one half = 78 years; and for Life Table B are  $R_0 = 1.248$ ;  $r = 0.0049$ , and  $T_c = 47.0$  years, years for population to double = 142.

Age	Life Table A				Life Table B			
	$S_{(x)}$	$l_{(x)}$	$m_{(x)}$	$l_{(x)}m_{(x)}$	$s_{(x)}$	$l_{(x)}$	$m_{(x)}$	$l_{(x)}m_{(x)}$
0	0.17600	1.00000	0	0.00000	0.17600	1.00000	0	0.00000
1	0.78260	0.17600	0	0.00000	0.78260	0.17600	0	0.00000
2	0.78260	0.13774	0	0.00000	0.78260	0.13774	0	0.00000
3	0.78260	0.10779	0	0.00000	0.78260	0.10779	0	0.00000
4	0.78260	0.08436	0	0.00000	0.78260	0.08436	0	0.00000
5	0.78260	0.06602	0	0.00000	0.78260	0.06602	0	0.00000
6	0.78260	0.05167	0	0.00000	0.78260	0.05167	0	0.00000
7	0.78260	0.04043	0	0.00000	0.78260	0.04043	0	0.00000
8	0.78260	0.03164	0	0.00000	0.78260	0.03164	0	0.00000
9	0.78260	0.02476	0	0.00000	0.78260	0.02476	0	0.00000
10	0.78260	0.01938	0	0.00000	0.78260	0.01938	0	0.00000
11	0.78260	0.01517	0	0.00000	0.78260	0.01517	0	0.00000
12	0.78260	0.01187	0	0.00000	0.78260	0.01187	0	0.00000
13	0.78260	0.00929	0	0.00000	0.78260	0.00929	0	0.00000
14	0.96000	0.00727	4	0.02910	0.98000	0.00727	4	0.02910
15	0.96000	0.00698	4	0.02790	0.98000	0.00712	4	0.02850
16	0.96000	0.00670	4	0.02680	0.98000	0.00698	4	0.02790
17	0.96000	0.00643	4	0.02570	0.98000	0.00684	4	0.02740
18	0.96000	0.00617	4	0.02470	0.98000	0.00671	4	0.02680
19	0.96000	0.00593	4	0.02370	0.98000	0.00657	4	0.02630
20	0.96000	0.00569	4	0.02280	0.98000	0.00644	4	0.02580
21	0.96000	0.00546	4	0.02190	0.98000	0.00631	4	0.02520
22	0.96000	0.00524	4	0.02100	0.98000	0.00618	4	0.02470
23	0.96000	0.00503	4	0.02010	0.98000	0.00606	4	0.02420
24	0.96000	0.00483	4	0.01930	0.98000	0.00594	4	0.02380
25	0.96000	0.00464	4	0.01860	0.98000	0.00582	4	0.02330
26	0.96000	0.00445	4	0.01780	0.98000	0.00570	4	0.02280
27	0.96000	0.00428	4	0.01710	0.98000	0.00559	4	0.02240
28	0.96000	0.00411	4	0.01640	0.98000	0.00548	4	0.02190
29	0.96000	0.00394	4	0.01580	0.98000	0.00537	4	0.02150
30	0.96000	0.00378	4	0.01510	0.98000	0.00526	4	0.02100
31	0.96000	0.00363	4	0.01450	0.98000	0.00516	4	0.02060
32	0.96000	0.00349	4	0.01390	0.98000	0.00505	4	0.02020
33	0.96000	0.00335	4	0.01340	0.98000	0.00495	4	0.01980
34	0.96000	0.00321	4	0.01290	0.98000	0.00485	4	0.01940
35	0.96000	0.00308	4	0.01230	0.98000	0.00476	4	0.01900
36	0.96000	0.00296	4	0.01180	0.98000	0.00466	4	0.01860
37	0.96000	0.00284	4	0.01140	0.98000	0.00457	4	0.01830
38	0.96000	0.00273	4	0.01090	0.98000	0.00448	4	0.01790
39	0.96000	0.00262	4	0.01050	0.98000	0.00439	4	0.01750
40	0.96000	0.00252	4	0.01010	0.98000	0.00430	4	0.01720
45	0.96000	0.00205	4	0.00820	0.98000	0.00389	4	0.01550
50	0.96000	0.00167	4	0.00670	0.98000	0.00351	4	0.01410
55	0.96000	0.00136	4	0.00550	0.98000	0.00318	4	0.01270
60	0.96000	0.00111	4	0.00440	0.98000	0.00287	4	0.01150
65	0.96000	0.00091	4	0.00360	0.98000	0.00259	4	0.01040
70	0.96000	0.00074	4	0.00300	0.98000	0.00235	4	0.00940
75	0.96000	0.00060	4	0.00240	0.98000	0.00212	4	0.00850
80	0.96000	0.00049	4	0.00200	0.98000	0.00192	4	0.00770
85	0.96000	0.00040	4	0.00160	0.98000	0.00173	4	0.00690
90	0.96000	0.00033	4	0.00130	0.98000	0.00157	4	0.00630
95	0.96000	0.00027	4	0.00110	0.98000	0.00142	4	0.00570
100	0.96000	0.00022	4	0.00090	0.98000	0.00128	4	0.00510
105	0.96000	0.00018	4	0.00070	0.98000	0.00116	4	0.00460
110	0.96000	0.00014	4	0.00060	0.98000	0.00096	4	0.00390

and hydrating eggs (Kinney et al., 1998). Blanding's turtles also transport water to nests (> 50 ml measured for one female) and when females voided substantial amounts of water when captured or during aborted nesting attempts, they always returned to marshes before reinitiating nesting activity.

Most nests were constructed in relatively open areas in old fields or disturbed areas along road banks and firelanes. The majority of nests were constructed from 2 to 400 m from nearest water (Fig. 2a), and less than 1% of all nests were more than 500 m from the nearest water. Females moved much farther in selecting nest sites than is reflected by the distance of nests to nearest water. The distance from nest to water is most relevant to hatchlings emerging from nests and moving to water, particularly if there is a high risk of being killed by predators or other causes of mortality such as desiccation (Janzen, 1993; Butler and Graham, 1995; Congdon et al., 1999). Nests constructed a long distance from the maternal female's marsh of residence (and possibly the male's residence as well) would reduce the probability that a hatchling would establish residence in the same marsh. Because adult Blanding's turtles can have reproductive lives of over 20 years, having few adult offspring in proximity should reduce the probability of inbreeding.

*Destruction of Nests by Predators.* — Nest predation over the 23 years of study averaged 78.2% and was highly variable and apparently unpredictable among years. Nests are at highest risk of predation during the first 48 hours, but smaller periods of increased risk occur in older nests in association with rainfall and again at nest emergence (Fig. 2c). The timing of Blanding's turtle nesting activity on the ESGR coincides with the activity period of crepuscular mammalian predators. During peak nesting times, raccoons (and less frequently foxes, coyotes, opossums, and skunks) patrol nesting areas and destroy most nests shortly after completion. Raccoons have even been observed to remove eggs from the nest chamber while being deposited by females.

Most predator attacks on adult Blanding's females in nesting areas are not fatal (e.g., live females have been found upside down at nest sites). However, some attacks resulted in life threatening injuries (e.g., live individuals found with legs chewed off) or death (e.g., carcasses found eviscerated with head and limbs missing).

Population densities of furbearing mammals may be the major factor influencing rates of nest predation. Nest predation rates were lower during years when fur trapping was widespread (mid-1970s to early 1980s) compared to years following the collapse of the fur market (mid-1980s to mid-1990s; Congdon et al., 1993). The pattern of increased nest predation coincident with the collapse of the fur market was not observed for nest predation rates for the common snapping turtle, *Chelydra serpentina*, on the ESGR (Congdon et al., 1994). In general, compared to Blanding's turtle nests, snapping turtle nests are constructed closer to water, and the nest flask is larger and more disturbed soil is left on the surface after nest covering. Such characteristics, coupled with the musky odor of snapping turtles, may contribute to

high nest mortality by predators (Congdon et al., 1987). We know of no population data on nest predators that could be used to substantiate the association between predator densities and rates of nest destruction.

Although it occurs rarely, unidentified burrowing mammals (e.g., chipmunks, ground squirrels, voles, shrews, moles) also destroy some Blanding's turtle nests. We observed mammal tunnels through nests and subsequent nest inspection revealed no eggs or egg shells. Lack of external evidence at the nest site certainly limits our ability to detect incidences of subterranean predation; however, differences in egg counts from radiographs vs. at nest inspection may be partially explained by predation by burrowing mammals.

*Embryo Mortality in Nests not Destroyed by Predators.* — Among nests escaping predation, about one third (35.1%) were considered as total success (all eggs produced hatchlings) and 45.4% were partially successful nests (produced at least one hatchling). The majority of partially successful nests contained either 1 or 2 failed eggs or embryos (Fig. 3a).

Total failure of 16.5% of nests that survived predation apparently resulted from deposition of infertile eggs (or eggs that died early in development) or placement of nests in areas with reduced insolation. The one constant for all turtle species on the ESGR (*E. blandingii*, *Chrysemys picta*, and *Chelydra serpentina*) is that nests placed in complete shade (closed canopy areas) fail to produce hatchlings. When closed canopy nests are inspected in late fall, they contain eggs that are unpipped and contain almost fully developed embryos. In a laboratory study of Blanding's turtle eggs incubated at a constant 22°C, development to pipping did not occur (Gutzke and Packard, 1987; see also Fig. 4). One other observed cause of failure was desiccation of eggs due to extremely dry soil, a condition that appeared to affect the upper eggs in the nest most frequently.

Total embryo failure in nests in a Nova Scotia population of Blanding's turtles averaged almost twice as high (37.4%, Standing et al., 1999) as that observed for ESGR Blanding's turtles (16.5%). However, Standing et al. (1999) reported substantial variation in the range of total embryo failure (6.7–81.9%); values for two of the three years of their study were similar to those of the ESGR population. Annual variation in environmental conditions may have more profound consequences for hatching success in the most northerly populations.

Failure of a smaller proportion (3%) of those nests not destroyed by predators was due to erosion, flooding, or root invasion. Blanding's turtles, like most freshwater turtles, tend to select nesting sites with little vegetation, substantial exposure to sunlight, and well-drained soils (Ross and Anderson, 1990). As a result, nests are often constructed in disturbed areas such as roadsides or trails (Butler, 1997; Standing et al., 1997) that expose adults to danger associated with vehicles. In addition, some roadside and firelane sites are prone to runoff from torrential summer thunderstorms. On the ESGR, several such nests were washed out, inundated, or buried with soil to a depth that inhibited embryo

development. Some nests constructed in areas with vegetation were encapsulated by roots of weeds and grasses; hatchlings in some of these nest cavities were unable to dig through the root mat and emerge.

*Hatchling Emergence.* — Most hatchlings on the ESGR emerge from nests on the same day as their siblings (Congdon et al., 1983), whereas in Massachusetts (Butler and Graham, 1995) and Nova Scotia (Standing et al., 1997) hatchling emergence typically occurred over 2 or more days. Early vs. late fall emergence or the number of days over which hatchlings emerged were not related to the total number of hatchlings emerging from nests, or to the number of failed eggs found within nests. Therefore, our results do not support the ideas that the length of time from nest construction to hatchling emergence or whether hatchling emergence is synchronous or asynchronous are indicators of nest quality. We caution, however, that our data are limited because predators do not leave large samples of surviving Blanding's turtle nests for study.

Across their range, Blanding's turtle hatchlings primarily emerge from nests during the fall following egg-laying (Congdon et al., 1983; Butler and Graham, 1995; Standing et al., 1997). It remains unclear, however, whether or not hatchlings always move to aquatic habitats before their first winter. Captures of hatchlings at our drift fences in the fall indicate that many hatchlings move to wetlands adjacent to nesting areas shortly after emergence from nests. However, a few hatchlings on the ESGR have been captured entering wetlands during early spring (Congdon et al., 1983). Several observations combine to support the possibility that overwintering in terrestrial environments is possible in some years. Soil temperatures on the ESGR during many winters remain above  $-2^{\circ}\text{C}$  due to insulation afforded by snow cover (Nagle et al., 2000), and Blanding's turtle hatchlings can tolerate  $-2^{\circ}\text{C}$  for at least 48 hours (Packard et al., 1999). In addition, hatchling Blanding's turtles in Nova Scotia may avoid water altogether following nest emergence (Standing et al., 1999), and hatchlings apparently do not utilize cues such as slope, open horizon, and vegetation silhouettes for orientation (Butler and Graham, 1995; Standing et al., 1999).

*Hatchling Recapture Rates.* — Minimum recapture intervals of Blanding's turtle hatchlings suggest that: (1) they do not occupy the same habitats as other hatchling turtles on the ESGR, or (2) they are very cryptic and hard to find. That all individuals recaptured by age 10 were found in shallow areas of wetlands occupied by adults suggests that some young individuals do occupy habitats similar to those of adults. In comparison to the 8.8% recapture rate for Blanding's turtles, 33% of a sample of painted turtles (*Chrysemys picta*) were recaptured over approximately the same time period (unpubl. data). The low number of young juveniles captured is characteristic of one other study (Graham and Doyle, 1977), whereas at Weaver Dunes in southeastern Minnesota hatchlings are relatively abundant (Pappas and Brecke, 1992; Pappas et al., this volume).

*Life Tables.* — In total, 78% of nests were destroyed by predators, 4% failed entirely due to abiotic and other non-

predator sources, 10% produced at least one hatchling, and about 8% were completely successful. Although embryo mortality in addition to that caused by nest predators is relatively low, it may have important consequences for recruitment and demography of Blanding's turtles. Earlier life tables for Blanding's turtles were constructed without including data on embryo mortality that occurred in nests surviving predation (Congdon et al., 1993). Including additional sources of embryo mortality reduced the survivorship of age class 0 (time in nests) by 8.5% (Age 0  $S_x = 0.176$ ; Table 3) compared to the previous value (Age 0  $S_x = 0.261$ ) used by Congdon et al. (1993).

New life table calculations indicate that the ESGR population would decline by 50% in 78 years, compared to the stable population indicated by the earlier life table (Congdon et al., 1993). To obtain a stable population with age 0  $S_x$  of 0.176, average annual adult survivorship would have to increase by 1.5% (from 96 in the 1993 life table to approximately 97.5%), or juvenile survival between ages 1 and 13 yrs must increase by 2.2% (from 78.3 to 80.5%) compared to previous life table parameters (Congdon et al., 1993). Increasing adult survivorship by 1.5% increased the cohort generation time (the sum of  $x_l m_x / R_0$ ; or, in a general sense, the average age of mothers of neonates in a population with a stable age distribution) by about 10 yrs (from 36 to 47 yrs).

Existing demographic data on the ESGR Blanding's turtles indicate that the population is stable with the estimated change in number of adults of  $\pm 10$  individuals between 1975 and 1995 (Congdon and Gibbons, 1996). To obtain a stable cohort, the compensatory increase in adult or juvenile survival (alone or in some combination) to offset embryo mortality in nests surviving predation is almost certainly within the measurement error from mark-recapture data. Because embryo mortality during incubation was relatively low compared to that caused by predation, its minimal impact on demography and population stability was not unexpected. Most models and analyses of long-lived turtles indicate that population stability is most affected by changes in mortality of adults and older juveniles than it is by changes in egg or early juvenile mortality (Crouse et al., 1987; Congdon et al., 1993, 1994; Heppel et al., 1996).

Historically, several factors have contributed to the population stability of ESGR Blanding's turtles. Human (and vehicular) access to the ESGR has been restricted since 1930 (currently by means of a 4 m high chainlink fence and locked gates). In addition, the ESGR is contiguous with the Pinckney Recreation Area that contains wetlands that may provide recruits into the ESGR population. Until recently, private lands surrounding the ESGR have remained rural and relatively undeveloped. However, since some resident females leave the ESGR to nest, recent housing developments near the ESGR, and resulting exposure to increased vehicular traffic, are of concern. Additional mortality of nesting females would be expected to have greater impact on the population than the levels of observed post-predation embryo mortality.

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