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SIZE DIMORPHISM AND GROWTH RATES IN DISTINCT POPULATIONS OF BLANDING'S TURTLES (*EMYDOIDEA BLANDINGII*) IN NOVA SCOTIA IN RELATION TO ENVIRONMENT

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***Abstract.*—Sexual size dimorphism is common in turtles, with greater size in most species favoring females. However, in Blanding's Turtles, which are among the longest-lived freshwater turtles for which field data are available, males are slightly larger. Nova Scotia's three known populations are disjunct from those in the species main range in south central Canada and north central United States and occupy different habitats that may exert different environmental pressures on the turtles. We compared body size and sexual size dimorphism across four distinct populations to identify any patterns that might reflect divergent environments. Sexual size dimorphism was consistently male biased in all populations, but differed significantly in degree across populations, suggesting that the environment exhibits a significant effect on size and growth rate. Indeterminate growth was evident in both sexes pooled across populations. The growth rate of adult males exceeds that of adult females, and juvenile growth rate exceeds that of adults regardless of population.**

Key Words.—Blanding's Turtle; *Emydoidea blandingii*; sexual size dimorphism; indeterminate growth.

INTRODUCTION

Sexual size dimorphism (SSD), which occurs in most species of animals once they reach sexual maturity, at 22-25 years old in Nova Scotia, has been the subject of intense study and controversy (Blanckenhorn et al. 2006; Fairbairn et al. 2007; Dale et al. 2007; Cox and Calsbeek 2009; Stillwell et al. 2010). Two major hypotheses are proposed to explain SSD evolution and maintenance. The first involves sexual selection (Lovich and Gibbons 1992), which can arise from either intraspecific competition (usually among males) for mates or epigamic selection by females (Trivers 1972). The second proposes that SSD is caused by differential interactions of males and females with their environment and can be maintained through several ecological routes: dimorphic niche, bimodal niche, or intrasexual competition (Slatkin 1984; Shine 1989).

In several turtle species, SSD varies intraspecifically in degree and direction among populations (Tinkle 1961; Iverson 1985; Gibbons and Lovich 1990). These variances are associated, although not exclusively, with population-specific growth, size-specific mortality, and food availability (Lovich and Gibbons 1992). In turtles, SSD usually favors larger females, but a few species are known to have larger males (Gibbons and Lovich 1990; Congdon et al. 2001), and male-dominated SSD appears to be ancestral (Stephens and Wiens 2009; Gosnell et al. 2009).

In its continental range, which extends from south central Canada to the north central United States, the Blanding's Turtle (*Emydoidea blandingii*) exhibits slight male-biased SSD (Seburn and Bishop 2007; Stephens and Wiens, 2009). This species is among the longest-lived of freshwater turtles for which empirical field data are available (Brecke and Moriarty 1989) and exhibits late maturation with no sign of reproductive senescence (Congdon et al. 2001). In the disjunct populations of Blanding's Turtles from southwest Nova Scotia, some adult females are still reproductively active after 40 years (Herman, Unpubl. data). Three Nova Scotia populations are currently described as genetically distinct from each other (Mockford et al. 2005), and occupy divergent habitats, including rocky lakeshores with associated inflow brooks and meadows, and acidic bogs fed by slow-moving brooks. One sub-population also appears distinct based on recent molecular analysis and habitat divergence from the other populations (Toews 2005).

Indeterminate growth is documented in an array of reptiles (Stamps 1993), but remains controversial in Testudines. Congdon et al. (2003) demonstrated the presence of asymptotic growth after maturity in Painted Turtles (*Chrysemys picta*), but determined that Blanding's Turtles did not show that trait (Congdon and van Loben Sels 1993). The purpose of this study is to first confirm SSD pattern between males and females, and to explore body size-habitat patterns among populations. We also examined 40+ years of data for evidence of indeterminate growth in Nova Scotian Blanding's Turtles.

MATERIALS AND METHODS

The data used for this analysis came from the Blanding's Turtle Recovery Database (BTRD) which has been compiled since 1969, and includes captures and recaptures (McNeil, unpubl.data). We used size data from the BTRD for the three known and genetically distinguishable populations in Nova Scotia: Kejimkujik National Park (KP), McGowan Lake (ML), and Pleasant River (PR). We treated Barren Meadow (BM) as a discrete sub-population from Pleasant River (hereafter considered a distinct population for discussion purposes) for two reasons; preliminary data suggest it is genetically distinct (Toews 2005) and the habitat differs markedly from that of the other three populations (Lefebvre 2009). Barren Meadow consists of a sphagnum bog fed by two small brooks and contains few nesting sites compared with the other populations (BM = 3 sites, ML = 6 sites, KP = 10 sites, PR = 10 sites; Lefebvre 2009). The majority of the ML population occurs in West Bog, an 11 ha ombrotrophic bog that drains into McGowan Lake (McNeil 2002). The other two populations occur in more complex habitats consisting of a lake system (KP) and a river system (PR) both surrounded by wetlands, which contain more food and habitat resources (e.g. refuge, basking sites, nesting sites) than either ML or BM. Turtles hatched from eggs that were collected as part of a head start program were captive-reared for about two years under identical conditions, to provide early growth rate data. These turtles will be referred to as "hatchlings" to discriminate them from the other juveniles.

Blanding's Turtle data in the BTRD were from turtles hand captured during visual surveys along the shores of brooks and in flooded meadows, or by trapping with hoop traps. Each turtle was marked with unique carapace notch code for future identification upon recapture. If sexually mature, sex of individuals was determined using secondary sexual characteristics: concavity of plastron and length of tail pre-cloacae (Lefebvre 2009; Herman et al. 1995).

We calculated individual ages of captive-reared turtles from KP and ML from the hatch date. Absolute age of nearly one-fifth (60/332) of the marked individuals was known. A regression of plastron rings on absolute age, after Germano (1998), was significant ($r^2 = 0.979$, $F_{1,57} = 2656$, $P < 0.001$), with a slope (0.975) that did not differ significantly from 1. When absolute age was unknown, we estimated age of juvenile and adult turtles by counting the number of growth annuli on the plastron. Although this method is controversial in some species (Wilson et al. 2003), it is valid when growth rings are verified as being deposited annually and up to point of wear (see Germano and Bury 1998). We counted rings of known-age turtles (2 to 19 years old) and the relationship was accurate. To accurately count growth rings, we brought turtles into the lab and scanned their plastrons at a resolution of 600 dpi. If we captured an individual with a smooth (no rings) plastron, we assumed it to be 30 years old, and we added the number of years from the next capture. Capture-mark-recapture (CMR) allowed us to extend the known age of individuals.

We took morphometric measurements (strait line carapace length, plastron length, carapace height, mass) at first capture for all turtles using calipers. Upon recapture, we re-measured all juveniles and periodically re-measured adults to estimate growth. We chose carapace length (CL) measured with calipers to represent size in this study. It has been recorded consistently in the BTRD since the database was initiated. It is a reliable metric for size as it lacks the sex bias of plastron length (due to concavity of the plastron in males), and unlike mass, is not affected by reproductive events that can cause substantial mass increase (egg production) and subsequent decrease (egg deposition). We performed a preliminary sample size analysis (anova.power.test; R Development Core Team 2008) to verify that sample sizes were sufficiently large to perform analysis of covariance (ANCOVA) maintaining a statistical power of at least 0.95. Sample size analysis uses the means and variances of sex (males, females) or population (BM, KP, ML, PR) to verify that data meet the minimum sample size needed at a specified confidence level (0.95).

We performed four ANCOVAs with CL as the dependent variable and age as a covariate: (1) overall adult population and sex differences; (2) adult growth rate between sexes; (3) juvenile growth rate among populations; and (4) hatchling growth rate between two populations. We considered both sex and population fixed factors. Where necessary, we analyzed subsequent pairwise comparisons for population differences with Holm's test with the family-wise error rate set at $\alpha = 0.05$ (Holm 1977, 1979) with the glht function in package multcomp in R. We determined indeterminate growth by examining a fitted linear model. We used a homogeneity of slopes procedure to determine if growth rates differed between populations (hatchlings and juveniles) or sex (adults) with age as the covariate. In such an analysis, a significant interaction of the main factor and covariate equates to a difference in slopes. We calculated differences in juvenile population slopes with an F-test using a pooled variance. We visually scoped growth rates by plotting linear regressions comparing age and CL for hatchlings (separated by population), juveniles, and adults (separated by sex). We completed residual analysis by visualization and with a Breusch-Pagan test when sample sizes between females and males differed. All analyses were done with R version 2.6.2 (R Development Core Team 2008).

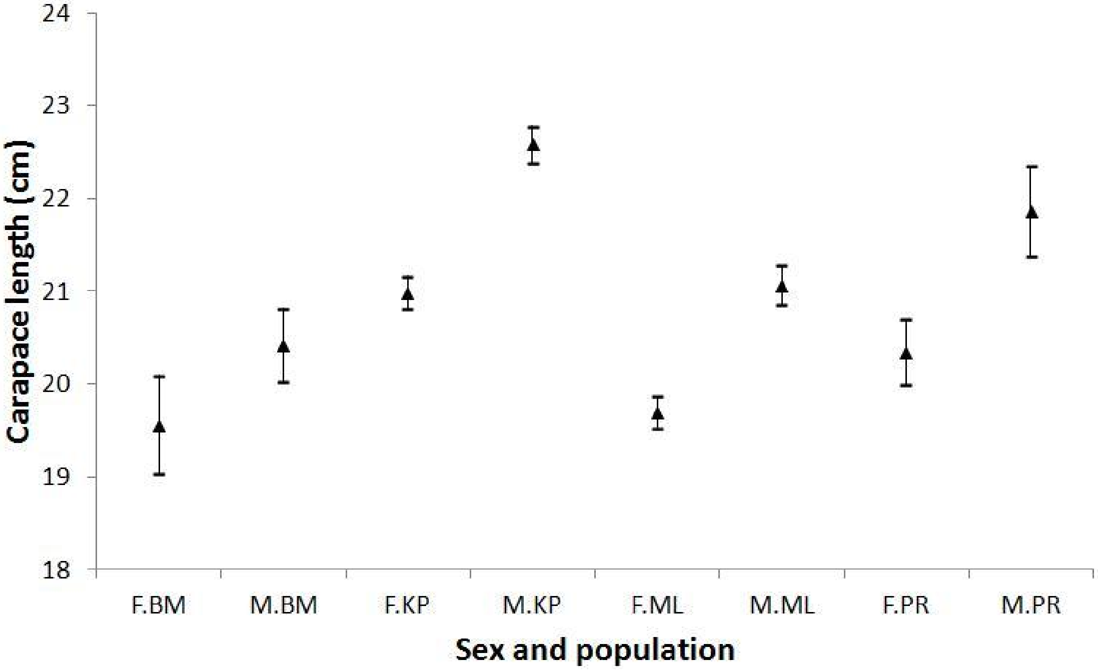

FIGURE 1. Plot of means with standard error of carapace length by sex (F = females, M = males) and population (KP= Kejimkujik National Park, ML=McGowan Lake, PR=Pleasant River, BM=Barren Meadow) for all adult Blanding's Turtles (*Emydoidea blandingii*) from Nova Scotia, Canada. Carapace length differed significantly among populations (by gender) and sex (by population; p value ≤ 0.04), except females from BM and ML (P = 0.623; N.S.). Circles are outliers. NS = not significant between sexes by site.

RESULTS

We included 1,000 measurements in the analyses (327 juveniles, 353 females, 320 males) from 332 individuals (144 juveniles, 93 females, 95 males). We calculated that we needed a minimum sample size of 34 individuals for sex differences and 20 for population differences. Population and sex both contributed to size differences with similar variability among populations and a general trend of higher median CL in males than in females within each population (Fig. 1). We confirmed the assumptions of the ANCOVA by visual inspection of residuals and equality of variance ($X^2 = 0.57$, df = 1, $P = 0.45$). An interaction between population and sex was not significant ($P = 0.58$; Table 1); therefore, main effects of population and sex can be interpreted directly and are controlled for age effects. Carapace length was significantly longer in males than females (Table 1). The omnibus p-value for population differences indicates that at least one population has a significantly different CL (Table 1). Pairwise comparisons among populations showed that CL differed significantly both among and within populations and sex combinations ($P < 0.04$ for all cases), except for females from ML and BM ($P = 0.62$). Among all populations, KP turtles were largest, PR turtles were larger than both ML and BM turtles within which females were equally the smallest, and BM males were smaller than ML males.

Initial visual inspection of the plot of males and females suggested that juveniles from different populations had different slopes and intercepts, and that differences were present between the adult sexes (Fig. 2). Both males and females continued to grow once they reach sexual maturity, but at a slower rate than juveniles. The growth rate (slope) of males differed significantly from that of females ($F = 4.99$, df = 1, $P = 0.026$) and both growth rates differ significantly from zero (males: $F = 38.7$, df = 1, $P < 0.001$; females: $F = 47.6$, df = 1, P

TABLE 1. ANOVA table for size variation in adult Nova Scotia Blanding's turtles (*Emydoidea blandingii*). Sex and Population are fixed factors; Age is a covariate. Asterisk (*) indicates significance at $P < 0.001$

	Df	*SS*	*MS*	*F*	*P* value
Population	3	267	88.8	63.8	< 0.001*
Sex	1	271	271	194	< 0.001*
Age	1	28.2	28.2	20.2	< 0.001*
Population:Sex	3	8.13	2.71	1.94	0.121
Residual	548	764	1.39		

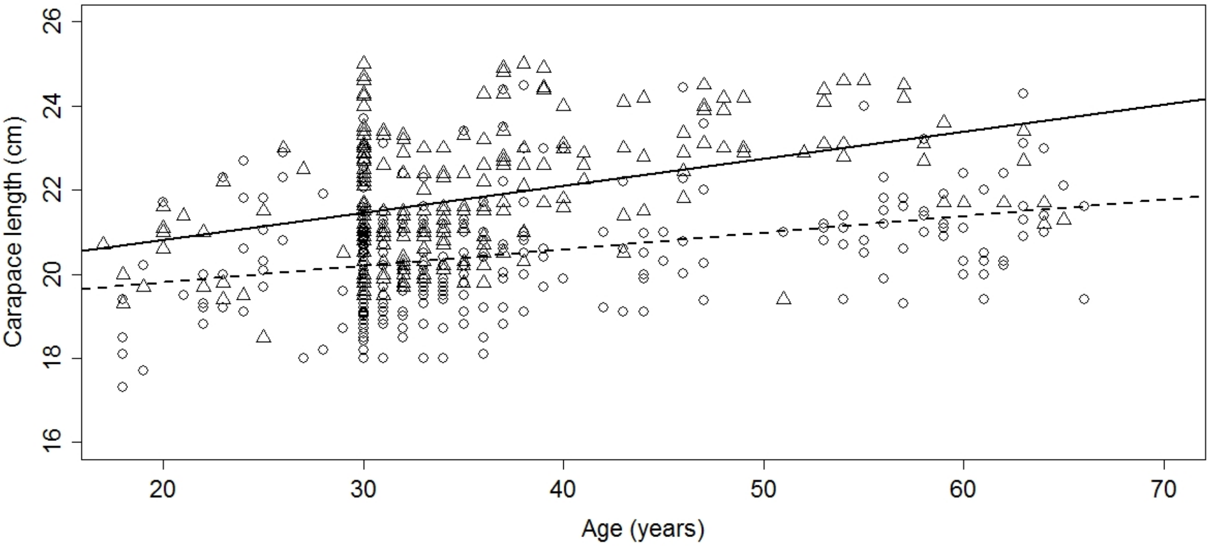

Figure 2. Relationship of carapace length by age (in years) for adult male (triangle, solid line) and female (circle, dashed line) Blanding's Turtles (*Emydoidea blandingii*) in Nova Scotia, Canada. Lines are least square linear regressions.

< 0.001). Combining the overall ANCOVA on population and sex, and non-homogeneity of slopes show that males are larger than females and have higher growth rates.

McGowan Lake had only one juvenile data point and was removed from the juvenile population analysis. A juvenile population interaction showed a significant differences in growth rates among populations ($F = 34.5$, df = 2, $P < 0.001$; Fig. 3). Growth rate was significantly higher in KP than in both PR ($T_{df = 329} = 28.33$; $P < 0.001$) and BM ($T_{df = 329} = 24.07$; $P < 0.001$), but growth rates in PR and BM were equivalent ($T_{df = 329} = 29.65$; $P = 0.53$). Preliminary results from hatchlings from KP and ML (the two most divergent populations in resource

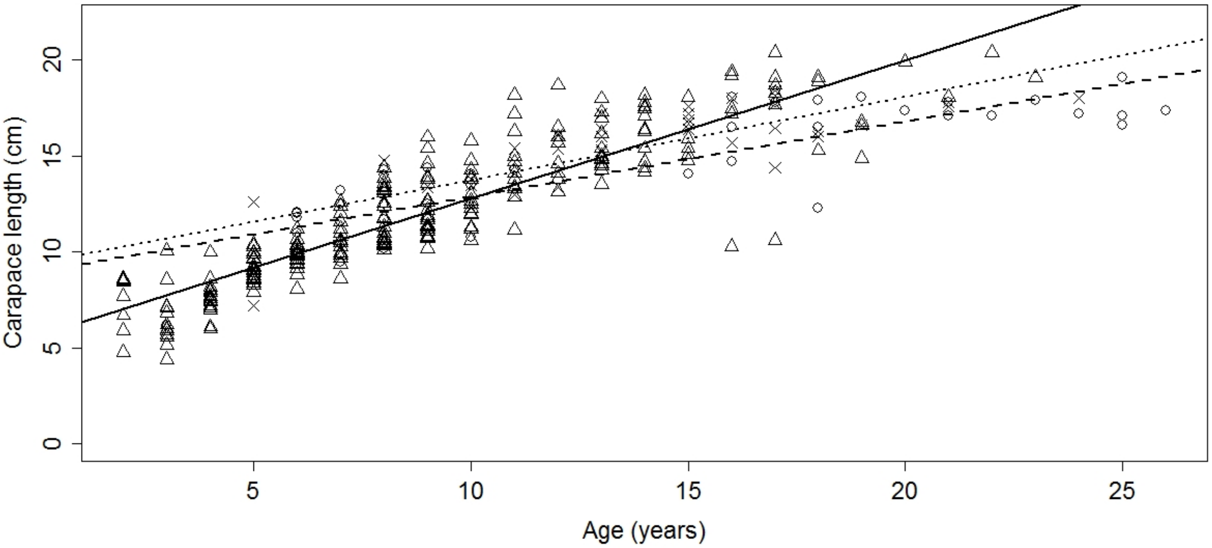

Figure 3. Relationship of carapace length by age (in years) for juvenile Blanding's Turtles (*Emydoidea blandingii*) from three populations, Kejimkujik National Park (triangle, solid line), Pleasant River (cross, dotted line), and Barren Meadow (circle, dashed line) in Nova Scotia, Canada. Lines are least square linear regressions.

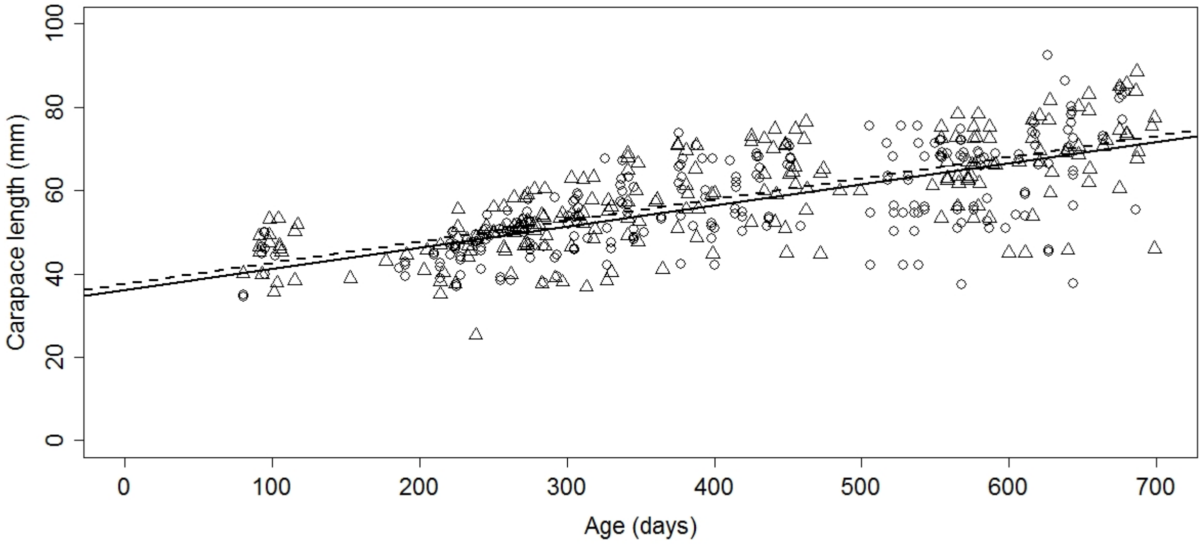

FIGURE 4. Relationship of carapace length by age (in days), for hatchling Blanding's Turtles (*Emydoidea blandingii*) raised in captivity from two populations in Nova Scotia, Kejimkujik National Park (circle, solid line) and McGowan Lake (triangle, dashed line), from hatch to 2 years. Lines are least square linear regressions.

availability) raised in captivity, showed no significant interaction (F < 0.001, df = 1, P = 0.99). Thus, population slopes were parallel and main effects were determined directly. Carapace Length did not differ between populations for adults (F = 1.66, df = 1, P = 0.20), but a significant difference in size at emergence existed between populations (F = 446, df = 1, P < 0.001; Fig.4).

DISCUSSION

The three populations vary in number of individuals. KP is largest, with approximately 132 adults (Herman et al. 1995). McNeil (2002) estimated the ML population at 79 adults. Data are insufficient to precisely estimate the size of the PR population, which was last to be discovered and includes the BM sub-population, but at least 70 individual adults have been captured to date, including 36 at BM (Lefebvre 2009). Therefore, with 353 females and 320 males measurements (including recaptures), and the smallest population sample size of 47 individuals, the analysis should yield robust results. Sexual size dimorphism is consistent with other studies (Berry and Shine 1980; Germano et al. 2000; Congdon et al. 2001; Stephens and Wiens 2009; Gosnell et al. 2009), in which male Blanding's Turtles were slightly larger than females.

The size-ratio between females and males appears smaller in Nova Scotia populations than in Nebraska. In Nebraska populations, the females were approximately 9% smaller than males. In Nova Scotia, females ranged from 7% (KP, ML, and PR) to 4% (BM) smaller than males.

Habitat type and CL appear correlated at the population level. Local environmental conditions have been shown to be major factors in size determination elsewhere (Fairbairn and Preziozi 1994; Stillwell et al. 2010), especially in species with asymptotic growth after maturity (Stamps 1993; Fairbairn 1997; Bonnet et al. 2010). Temperature, food, social status, local density, and other resources all play a role in determining sexual maturation and growth rates. The complex lake system (KP) and river system (PR) habitats in Nova Scotia have more resources, including more nesting habitat, overwintering sites, and higher productivity (i.e. food), and significantly larger individuals than do the acidic bog (ML and BM) habitats, which contain fewer resources and smaller individuals.

Bourque (2006), using water color as a proxy for productivity, reported low primary and secondary production in West bog (ML) and BM (< 250 Hazen units). According to his model (Bourque 2006), ML and BM habitats should be unsuitable for this species. Low pH and associated nutrient immobilization in sphagnum bogs limits primary production, and the unpalatability of the vegetation attracts few herbivores (Aerts et al. 1992). It has been suggested that in poor environments, energy allocation should be put towards earlier reproduction, resulting in a smaller adult size (Kenneth 1996; Dodd and Dreslik 2008). However, in the Nova Scotia's

Blanding's Turtle complex, evidence points to both later maturation and smaller adult body size in the less productive environments.

The availability of nutrients in systems with higher productivity allows individuals to maintain higher reserves. Additionally, the greater number of nesting and overwintering sites at KP and PR may exact less energy expenditure as distance to those areas critical to life history is shorter (Lefebvre 2009; Kydd 2010), leaving more energy for growth. KP turtles are the largest and have the highest growth rate, in both adults and juveniles. This is consistent with Bourque's (2006) assessment of the habitat, suggesting that resources are greater in KP, and growth is not dictated solely by genotype, but some combination of genotype and environment exists. The hatchling data supports this argument; growth rates were not significantly different under identical conditions. This suggests that differences in wild populations are a result of phenotypic plasticity (Ashton and Feldman 2003; Bonnet et al. 2010; Stillwell et al. 2010), where much of the differences among populations may be due in response to climatic or ecological variables. In a similar study with Snapping Turtles (*Chelydra serpentina*), Brown et al. (1994) found trends consistent with this study. However, their two sites were geographically distant resulting in different ambient temperatures, and they did not test for a genetic effect on size or growth rate. In our study, all individuals were raised in the same conditions and fed the same diet, suggesting an environmentally mediated effect (resources) on size, rather than a genetically determined one, although size differences (possibly genetically driven) could be ontogenetically controlled.

Blanding's Turtles in Nova Scotia show sexual size dimorphism similar to that reported across the main range of the species (Seburn and Bishop 2007; Ernst and Lovich 2009; Gosnell et al. 2009; Stephens and Wiens 2009). Our analyses suggest a correlation between habitat type occupied by turtles, using the assessment by Bourque (2006), and their size regardless of sex. Habitats in these four Nova Scotia populations vary greatly in type, productivity, and available resources. Body size differences among populations suggest an ecological link between body size and environment. Similar growth rates of individuals from the most divergent habitat types reared in captivity and under identical nutrient and environmental regimes support the ecological hypothesis. Finally, both sexes in the Nova Scotia populations show continuous (albeit slow) growth as adults, which is not concordant with the findings of Congdon et al. (2003). Growth rates are higher in juveniles than adults and appear to be environmentally driven for both, but overall, adult growth rates are slow. Females show significantly slower growth rates than do males, presumably due to investment of resources in egg production and nest excavation. We suggest that both mate choice and environmental hypotheses may explain the evolution and maintenance of size dimorphism and continuous growth in Blanding's Turtles in Nova Scotia. Sexual size dimorphism might arise evolutionarily from a benefit based on sexual selection of a mate, but the variation and degree appears to be influenced more strongly by environmental factors and phenotypic plasticity, especially before sexual maturation.

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José Lefebvre received his undergraduate degree in biology at Université du Québec à Rimouski (UQAR) (2007), and his M.Sc. in Conservation Biology at Acadia University (2009). He is currently pursuing a Ph.D. at Dalhousie University, in male reproduction dynamics of Blanding's Turtles, co-supervised by Stephen Mockford (Acadia University) and Christophe Herbinger (Dalhousie University), and was appointed Adjunct Professor at Acadia University (2010). He is also trained as a wildlife technician. (Photographed by Stephen Mockford)

Tom B. Herman received his Bachelor of Arts in Biology and Environmental Studies from Antioch College in 1972. He then moved to the Zoology Department at University of Alberta, earning his Master of Science in 1975 and his Ph.D. in 1979. He arrived at Acadia as a Sessional Lecturer in 1978 and was appointed an Assistant Professor in 1980. In addition to an extensive list of appointments to Acadia committees, both past and present, Dr. Herman is a Past President of the Canadian Society of Zoologists, President of the Science and Management of Protected Areas Association, and Vice-Chair of the Mersey Tobeatic Research Institute. He sits on several national and regional advisory committees on endangered biodiversity, as well as the Board of Directors of the Atlantic Environmental Science Network and the Offshore Energy Environmental Research Association. (Photographed by Stephen Mockford)

Trevor Avery is an Adjunct Professor and Instructor in the Department of Biology at Acadia University after completing a Ph.D. at Memorial University of Newfoundland. He is a Marine Biologist and Biostatistician (P.Stat.) studying aquatic ecology with foci on conservation and recreation of diadromous species (striped bass and American eels), freshwater invasive species such as smallmouth bass and chain pickerel, and early life history of cold-ocean marine fishes. He has increasing research interests in wetland conservation ecology. For kicks, Trevor dabbles in parasite infestations on fishes, and taxonomy of *Vaccinium* (blueberry) and sea scallops. (Photographed by Jose Lefebvre)