Does sexual bimaturation affect the cost of growth and the operational sex ratio in an extremely size-dimorphic reptile?¹

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Abstract: Sexual bimaturation, an intersexual difference in age at maturity, is a consequence of sexual size dimorphism (SSD). Sexual bimaturation arises through intersexual differences in growth trajectories. In theory, differences in growth trajectories should bias the operational sex ratio in favour of the early-maturing sex. In addition, in animals with sexual bimaturation, the late-maturing sex always maintains a lower intrinsic rate of growth (k) that may be linked to the metabolic cost of growth. We studied growth, its relation to the operational sex ratio, and its metabolic cost in the extremely size-dimorphic northern map turtle. We found that females take twice as long as males to reach maturity and that females maintain higher absolute rates of growth but have a lower k. The estimated operational sex ratio was even in our study population, and estimates of annual mortality were similar between adult males and females. Based on respirometry, we found no evidence that fast-growing females incur a metabolic cost compared to non-growing males.

Keywords: body size, cost of growth, Graptemys geographica, growth model, sexual size dimorphism, standard metabolic rate.

Résumé : Une différence intersexuelle dans l'âge à la maturité est une conséquence du dimorphisme sexuel de taille. Cette différence entre les sexes dans l'âge à la maturité est causée par des trajectoires de croissance différentes selon le sexe. En théorie, les différences de trajectoires de croissance devraient causer un biais du rapport effectif entre les sexes en faveur du sexe à maturité hâtive. De plus, chez les animaux ayant des différences intersexuelles dans l'âge à la maturité, le sexe à maturité tardive maintient toujours un taux de croissance intrinsèque (k) inférieur qui peut être associé au coût métabolique de la croissance. Nous avons étudié la croissance, sa relation avec le rapport effectif entre les sexes et son coût métabolique chez la tortue géographique, une espèce qui présente un dimorphisme sexuel de taille extrême. Nous avons constaté que les femelles prennent deux fois plus de temps pour atteindre la maturité que les mâles et qu'elles maintiennent des taux de croissance absolue plus élevés, mais qu'elles ont un k plus faible. Le rapport effectif estimé entre les sexes était égal dans notre population d'étude et les estimations de mortalité annuelle étaient similaires entre les mâles et les femelles adultes. En utilisant la respirométrie, nous n'avons trouvé aucune évidence que les femelles à croissance rapide ont un coût métabolique plus élevé que celui des mâles qui ne sont pas en croissance.

Mots-clés : coût de la croissance, dimorphisme sexuel de taille, Graptemys geographica, modèle de croissance, taille corporelle, taux métabolique standard.

Nomenclature: Le Sueur, 1817.

Introduction

In most animals, males and females differ in body size (Blanckenhorn, 2005). Evolutionary causes of sexual size dimorphism (hereafter SSD) are typically linked to the reproductive roles of each sex: sexual selection favours larger size in males, and fecundity selection favours larger size in females (Andersson, 1994). At the proximate level, SSD is realized via intersexual differences in growth trajectory (Shine, 1990).

Sexual bimaturation (intersexual difference in age at maturity) is a consequence of SSD in animals with asymptotic growth after maturity, such as fishes, amphibians, and reptiles (Stamps & Krishnan, 1997). In size-dimorphic animals, the larger sex virtually always matures later (Stamps & Krishnan, 1997). Among tetrapods, SSD reaches an extreme in emydid turtles, in which females can be twice the size of males (Fitch, 1981; Gibbons & Lovich, 1990). Large body size in female turtles confers a reproductive advantage because reproductive output typically increases with body size (Iverson, 1992; Bulté, Irschick & Blouin-Demers, 2008). In contrast, body size in male emydid turtles is not as tightly linked to reproductive success because access to mates does not seem to depend on fighting ability in this group (Berry & Shine, 1980). It was therefore suggested that in aquatic emydid turtles, males mature at a size at which most aquatic predators can be escaped, while females delay maturity to attain an optimal body size for egg production (Wilbur, 1975; Gibbons et al., 1981). Because growing to a large size requires time, females thus tend to mature later than males (Dunham & Gibbons, 1990; Jones & Hartfield, 1995; Lindeman, 1999).

Sexual bimaturation has important implications for the ecology of animals, including effects on population parameters and on energetics. At the population level, sexual

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bimaturation can bias the sex ratio of adults strongly in favour of the early-maturing sex. In emydid turtles with pronounced female-biased SSD (and thus bimaturation), adult sex ratios tend to be heavily biased towards males (Gibbons, 1990; Lovich & Gibbons, 1990). Sexual bimaturation also seemingly affects energetics of size-dimorphic animals. In many dimorphic reptiles, the larger sex maintains higher absolute growth rates than the smaller sex (Roosenburg & Kelley, 1996; Brown & Weatherhead, 1999). Elevated growth rates in the larger sex bring numerous benefits. Growing fast can reduce the age differential at maturity (Roosenburg, 1996) and decrease the probability of death before maturity (Congdon, Dunham, & Sels, 1993). In addition, maturing early may increase the reproductive experience of females and in turn increase their long-term reproductive success (Paitz et al., 2007). Thus, the larger sex is expected to grow fast to incur those benefits. Growing fast may, however, involve a metabolic cost (Wieser, 1994; Nagy, 2000). Indeed, in addition to the energetic cost of maintenance, growing life stages (*i.e.*, juveniles) must allocate energy to the physiological machinery responsible for biosynthesis as well as to activities associated with energy acquisition and energy processing (Wieser, 1994; Nagy, 2000). Thus, the sex growing faster (*i.e.*, the larger sex) should theoretically have higher mass-specific metabolic demands than the other sex. In birds and mammals, the metabolic cost of growth can be substantial (Wieser, 1994). In reptiles, there is little empirical evidence that fast growth is costly (Nagy, 2000; but see Peterson, Walton & Bennett, 1999), but few studies have attempted to measure the metabolic cost of growth in reptiles (Nagy, 2000). Moreover, to our knowledge, no study has investigated the metabolic cost of growth in the context of sexual bimaturation. Interestingly, despite often maintaining higher absolute growth rates, the larger sex virtually always approaches its asymptotic size (a) more slowly (*i.e.*, higher k value for the von Bertalanffy growth model) (Stamps, 1993). The metabolic cost of growth could provide a mechanistic explanation for this commonly observed intersexual difference in k (Stamps, 1993).

We studied growth in a population of northern map turtles (*Graptemys geographica*) from Ontario. We first built a growth model based on data from marked individuals to estimate age at maturity in each sex and to compare growth rates between males and females. We then examined whether sexual bimaturation biases the sex ratio towards males as predicted by Lovich and Gibbons (1990). Finally, we used respirometry to test if fast-growing juvenile females incur a metabolic cost compared to non-growing adult males of similar body size.

Methods

STUDY SITE

We conducted this study from 2003 to 2007 at the Queen's University Biological Station ($44^{\circ} 34' \text{ N}$, $76^{\circ} 19' \text{ w}$) approximately 100 km south of Ottawa, Ontario, Canada. We captured northern map turtles in Lake Opinicon with basking traps, by snorkelling, and by surveying nesting areas. Captured turtles were brought back to the laboratory where we measured maximum plastron length using

a forestry calliper (\pm 0.5 mm). We marked turtles captured for the first time by drilling a unique combination of small holes in their marginal scutes. Turtles were released at their capture location within 24 h. We determined sex based on external sexual characteristics. Males have long tails and their cloacal openings are located past the posterior margin of the carapace. In contrast, females have short tails and their cloacal openings are at the margin of the carapace. In addition, females have wider heads than males (Bulté, Irschick & Blouin-Demers, 2008).

GROWTH RATES AND GROWTH MODEL

To compare growth rates between males and females, we calculated growth rate (GR) as

$$GR = PL_r - PL_c / t_r - t_c$$
^[1]

where PL_r is the plastron length at recapture, PL_c is the plastron length at first capture, and $t_r - t_c$ is the time in days spent growing between the measurements of PL_c and PL_r . Because temperate turtles spend most of the year hibernating and do not grow during that period (Litzgus *et al.*, 1999), we subtracted the number of days spent hibernating in the calculation of $t_r - t_c$. We determined the hibernation period in Lake Opinicon from radio-telemetry data on 53 individuals (Bulté, Gravel & Blouin-Demers, 2008). For the model, we assumed that turtles in our study population hibernate from 1 October to 1 May (212 d·y⁻¹).

We estimated growth parameters of males and females by fitting our growth data to the von Bertalanffy growth equation (Fabens, 1965; Frazer, Gibbons & Greene, 1990):

$$PL = a(1 - be^{-kt})$$
^[2]

where PL is plastron length, a is the asymptotic PL, b is a parameter related to hatchling size, k is the intrinsic rate of approach to a, and t is the age in years. In northern map turtles, *PL* is a good measure of overall size. Indeed, at overlapping PL values (75 to 130 mm), the difference in the predicted mass of males and females does not exceed 1.5% (G. Bulté, unpubl. data). Compared to other growth curves (e.g., logistic, Gompertz), the von Bertalanffy curve fits the growth data of emydid turtles best (Lindeman, 1997; Litzgus & Brooks, 1998), including that of Graptemys (Jones & Hartfield, 1995; Lindeman, 1999). The von Bertalanffy equation requires knowledge of the age (i.e., t)of each individual, however, which is seldom possible with wild animals. To circumvent this limitation, we used the growth-interval model derived from the von Bertalanffy equation by Fabens (1965):

$$PL_r = a - (a - PL_c)e^{-kd}$$
^[3]

where PL_r and PL_c are as in equation [1], where *a* and *k* are as in equation [2], and where *d* is the time in years spent growing between captures. Parameter *b* is absent from the Fabens model, but once *a* is estimated, *b* can be calculated as

$$1 - (PL_h/a)$$
 [4]

where PL_h is the size at hatching (Schoener & Schoener, 1978). We set PL_h to the mean PL (28.4 mm) of 514

hatchlings from our population (Bulté, Irschick & Blouin-Demers, 2008). The Fabens model has been shown to provide reliable estimates of growth parameters in turtles of unknown ages (Frazer, Gibbons & Greene, 1990).

We estimated parameters a and k by fitting PL_c , PL_r , and d to equation [2] with the nonlinear modelling platform of JMP (5.0.1a). We calculated 95% support-plane confidence intervals (SPCI; Schoener & Schoener, 1978) around estimates of a and k to compare parameter estimates between males and females. We calculated d as the number of days (then converted to years) spent growing between captures. We estimated d from the number of activity days. In our study population, map turtles are active from 1 May to 1 October (d = 153 d). To satisfy the assumption of independence, we included only the first and last capture of each individual in the growth model (*i.e.*, a single growth interval per individual). We included measurements of PL separated by at least 90 active days because preliminary observations indicated that this interval was sufficient for juveniles to grow markedly.

We estimated age at maturity (t_m) from size at maturity as follows:

$$t_m = [[LN(1 - PL_m) / a] / b] / -k$$
[5]

where a, b, and k are as in equation [1], and PL_m is plastron length at maturity. In females, we estimated PL_m from the smallest gravid female captured in our population. For males, we estimated PL_m from the smallest male exhibiting an enlarged and elongated tail, a secondary sexual character in map turtles (Lindeman, 2005). We concede that external sexual characteristics may not be an exact measure of sexual maturity. Thus, the minimum age at maturity estimated from the minimum size at maturity should be interpreted with some caution. To generate confidence intervals around our estimates of age at maturity, we conducted a Monte Carlo simulation. Using equation [5], we generated a theoretical distribution of age at maturity (t_m) . For each calculation of t_m , a and k were drawn randomly with replacement from a normal distribution with a mean of μ and a standard deviation of σ , where μ was our estimate of the parameter from the non-linear regression and σ was its standard deviation. Parameter b was calculated from the mean hatchling size. Preliminary simulations showed that using the maximum or the minimum hatchling size to calculate b had only a minor effect on estimates of age at maturity. The distribution of t_m was generated from 1000 simulations. For each sex, the 2.5 and 97.5 percentiles of the distribution were used as the 95% confidence limits around our estimate of age at maturity.

SEX RATIO AND SURVIVAL

We independently estimated population size of adult males and of adult females for each time interval by fitting the POPAN formulation of the Jolly–Seber model (Pollock *et al.*, 1990) in program MARK (White & Burnham, 1999). We used a sampling interval of 1 y in the model. For each sex, we first evaluated the goodness of fit of the global model (*i.e.*, the model with the most parameters) by examining the variance inflation factor (\hat{c}). In both sexes, the value of \hat{c} was close to 1 (males = 0.5, females = 1.51). We then fitted simpler models and compared their fit with biascorrected Akaike's Information Criteria (AIC_c) to select the best model to estimate population size. With 5 y of data, we generated 3 estimates of population size for each sex. We tested whether the mean population sizes of males and females deviated from 1:1 with a χ^2 test.

The effect of sexual bimaturation on adult sex ratio can be offset by intersexual differences in survival. Thus, we estimated annual survival (ϕ) and recapture rate (p) with Cormack-Jolly-Seber model (Lebreton et al., 1992) in the program MARK. We fitted a set of candidate models and compared their fit with AIC_c. We confirmed that the global model fitted the data well with a bootstrap goodness-offit test of 1000 iterations (Cooch & White, 1998). To test whether survival differed between the sexes, we compared the models' AIC_c values. Annual survival can be considered to differ between the sexes if models with sex-specific survival fit the data substantially better (based on AIC_a) than models without sex-specific survival. We corrected for the lack of fit by adjusting the \hat{c} to its estimated value (1.34). We estimated annual survival rate with model averaging to account for uncertainty in model selection.

RESPIROMETRY AND THE COST OF GROWTH

In ectotherms, the energetic cost of maintenance is referred to as the standard metabolic rate (SMR), which is the amount of energy expended by a post-absorptive, resting animal (McNab, 2002). We predicted that this cost would be higher in juvenile females with high growth rates relative to non-growing adult males of equal body size. We estimated SMR by measuring oxygen consumption (VO_2) on resting, post-absorptive turtles with open-flow respirometry. We measured VO₂ at 26 °C in 6 males (mean mass = 177 g, SE = 18) and 8 females (mean mass = 188 g, SE = 11). Mean mass did not differ between males and females (*t*-test: $t_{12} = 0.552, P = 0.59$). We compared juvenile females and males to control for the effect of mass on SMR. To allow gut clearance, we fasted turtles in outdoor basins for at least 2 d prior to measurements. We equilibrated the turtles in water at 26 °C and then moved them to an opaque respirometry chamber lined with a moist cloth to prevent desiccation. We left the turtles undisturbed in the respirometry chamber for at least 2 h before beginning the measurements. During VO₂ measurements, exterior air was pumped through a drierite[®] column to absorb water and then sent to the chamber. The flow of air entering the chamber was adjusted between 100 and 200 mL·min⁻¹ depending on the size of the turtle. A subsample of air exiting the chamber (50% of the flow entering the chamber) was desiccated through a second drierite® column and sent to a gas analyzer (Sable Systems FC-1, Henderson, Nevada, USA). The concentration of O_2 in the chamber was measured every 20 s for 220 min, and baseline measurements were taken at the beginning and at the end of each trial to correct for instrument drift. All VO₂ measurements were made between the hours of 1800 and 2400, a period during which these diurnal turtles are normally resting. To eliminate bouts of activity from our estimates of SMR, we calculated SMR from the lowest 25th percentile of the data for each individual (165/660 measurements). This approach provides a good estimate of SMR

in reptiles (Litzgus & Hopkins, 2003; Hopkins *et al.*, 2004). We calculated SMR from VO_2 using the software Datacan (Sable Systems Datacan V, Henderson Nevada, USA) following Withers (1977).

Results

We marked 978 northern map turtles (551 females, 400 males, and 27 unsexed individuals) between 2003 and 2007. The smallest gravid female captured (n = 130) had a *PL* of 193 mm. The largest mature female captured had a *PL* of 257 mm. The mean *PL* of all the mature females was 217 mm (SE = 0.67). The smallest male with a clearly elongated tail had a *PL* of 75 mm, while the largest male captured had a *PL* of all the mature males was 99 mm (SE = 0.61).

GROWTH RATES

We were able to obtain 2 measurements of *PL* separated by at least 90 active days for 173 males and 208 females. *GR* of males and females decreased with increasing *PL* (Figure 2). There was evidence, especially in males, that the relationship between *PL* and *GR* slightly deviated from linearity. We thus tested whether a second-order polynomial fitted the data significantly better than a linear regression. In females, the quadratic term was not significant ($F_{1, 205} = 0.248$, P = 0.62, $R^2 = 0.0003$), showing



FIGURE 1. Size distributions of male and female northern map turtles from Lake Opinicon, Ontario, Canada (n = 551 females, 400 males). Arrows indicate the estimated sizes at maturity.

that adding curvature to the line did not improve the fit significantly. In males, the quadratic term was significant $(F_{1,169} = 49.55, P < 0.0001, R^2 = 0.067)$ but increased the unexplained variance by less than 7% compared to the linear regression. We used ANCOVA to compare GR between males and females, but because the relationship between PL and GR was non-linear in males (Figure 2), we restricted our analysis to smaller turtles (PL < 95 mm, 113 individuals: 39 females and 74 males; Figure 3) to satisfy the requirement of linearity of ANCOVA. The ANCOVA was significant $(F_{3,109} = 94.75, P < 0.001, R^2 = 0.72)$ and indicated that growth rates decreased with increasing PL in both sexes $(F_{1,109} = 19.44, P < 0.001, R^2 = 0.05)$ and that females had higher growth rates than males ($F_{1, 109} = 262.37$, P < 0.001, $R^2 = 0.67$). The interaction between sex and age was not significant ($F_{1, 109} = 2.43$, P = 0.12), indicating that the slopes of the relationships between growth rate and PL did not differ between the sexes.

GROWTH MODEL

Estimates of the growth parameters of the von Bertalanffy model are presented in Table I and the fitted model in Figure 4. Asymptotic plastron length (a) was 228 mm for females and 111 mm for males and, not surprisingly, the



FIGURE 2. Growth rates as a function of initial plastron length in male and female northern map turtles from Lake Opinicon, Ontario, Canada.

95% SPCI did not overlap (Table I). In contrast, the 95% SPCI of the rate of approach of a(k) overlapped slightly (by 0.007; Table I).

From our estimates of minimum *PL* at maturity, females require 11.7 y (95% CI = 10.5 to 13.0 y) to mature and males 4.5 y (95% CI = 3.9 to 5.5 y). The von Bertalanffy model predicts a linear relationship between *PL* and *GR*, and this relationship deviated slightly from linearity in males. To ensure that using the von Bertalanffy model did not lead to spurious estimates of *GR*, we examined the distribution of the residuals of the *GR* values. The mean deviation (in absolute value) of the predicted values was 1.18 mm·y^{-1} (SE = 0.1), with 90% of the *GR* estimates being less than 2.5 mm·y⁻¹ from the actual values. Thus, the von Bertalanffy equation does perform well at predicting growth rate in males, even if the relationship between *PL* and *GR* deviated slightly from linearity.

Adult sex ratio and survival

Between 2003 and 2007, we captured 330 adult females and 374 adult males. For females, the AIC_c weight of the best model estimating population size received 97% percent of the support. We thus used only this model to estimate population size. In males, however, the top 2 models fitted the data equally well (52 and 48% of the support). We consequently averaged the estimates of population size of these 2 models. Our estimated adult male population size was 335 (95% CI = 281–391) compared to 317 (95% CI = 243–391) for adult females. The operational sex ratio (male:female) was 1:0.94 and was not significantly different from 1:1



FIGURE 3. Female northern map turtles from Lake Opinicon, Ontario, Canada maintain higher growth rates than males at overlapping body sizes.

(Pearson's $\chi^2 = 0.44$, P = 0.50). For the survival analysis, the top model received 80% of the support, and all 4 of the top candidate models (receiving collectively 100% of the support) included sex-specific survival (Table II). Mean annual survival rate was 87.3% in females, compared to 82.6% in males (Table III).

COST OF GROWTH

The mean SMR of juvenile females was 23% higher than that of males (0.098 mL $O_2 \cdot h^{-1} \cdot g^{-1}$ compared to 0.075 mL $O_2 \cdot h^{-1} \cdot g^{-1}$), but this difference was not statistically significant (*t*-test: $t_{12} = 0.85$, P = 0.41). Our modest sample size provided us with low statistical power, so we conducted *a posteriori* power analyses to determine the minimum detectable difference with our sample size and the necessary sample size to detect a significant difference given our effect size. The analyses indicated that we had sufficient power to detect a difference of 0.06 in SMR (80%) and that we would have needed 77 individuals to detect a significant difference given the observed effect size.

Discussion

Sexual size dimorphism is realized by intersexual differences in growth and maturation patterns (Shine, 1990). In northern map turtles, we found marked differences in growth and maturation parameters that are concordant with those reported for other size-dimorphic reptiles (*e.g.*, turtles: Lindeman, 1999; snakes: Brown & Weatherhead, 1999). In particular, we found that females need more than twice as long as males to reach sexual maturity (11.7 *versus* 4.5 y).

Based on the early maturation of males, we expected a male-biased adult sex ratio (Lovich & Gibbons, 1990).



FIGURE 4. Fitted von Bertalanffy growth models for female (solid line) and male (dash line) northern map turtles from Lake Opinicon, Ontario, Canada.

TABLE I. Mean parameters (95% SPCI) of the von Bertalanffy growth model¹ and estimated age at maturity (95% CI) for male and female northern map turtles from Lake Opinicon, Ontario, Canada. a is the asymptotic size, b is a parameter related to hatchling size, k is the intrinsic rate of approach of a, and t is the age in years. MSE is the mean squared error, and RMSE is the standard deviation of the residual error.

Sex	п	а	k	b	MSE	RMSE	R^2	Age at maturity
Males	178	111.6 (109.1–114.1)	0.18 (0.15-0.21)	0.74	7.03	2.65	0.95	4.5 (3.9–5.5)
Females	217	228.3 (222.2–234.5)	0.15 (0.14-0.16)	0.87	33.93	5.82	0.98	11.7 (10.5–13.0)

¹ $PL_t = a(1 - be^{-kt})$, where PL_t is the plastron length at age t.

TABLE II. Candidate models estimating annual survival (ϕ) rates and recapture rates (*p*) of northern map turtles in Lake Opinicon, Ontario, Canada. *t* represents time dependence and sex represents sex dependence. Models with lower AIC_c and higher AIC_c weights fit the data better.

φ	р	AIC _c	ΔAIC_{c}	AIC _c weight	Number of parameters
sex	$t \times sex$	1545.84	0.00	0.80	10
$t \times \text{sex}$	t	1550.20	4.36	0.09	11
$t \times \text{sex}$	sex	1550.37	4.53	0.08	10
$t \times \text{sex}$	$t \times \text{sex}$	1552.91	7.07	0.02	14

TABLE III. Estimates of annual survival in northern map turtles from Lake Opinicon, Ontario, Canada. Numbers in parentheses indicate 95% confidence intervals.

Year	Females	Males		
2003 to 2004	0.88 (0.58 to 0.97)	0.81 (0.51 to 0.95)		
2004 to 2005	0.87 (0.7 to 0.95)	0.87 (0.68 to 0.87)		
2005 to 2006	0.87 (0.65 to 0.96)	0.80 (0.67 to 0.88)		

We found that the sex ratio in our study population was not statistically different from an even ratio. Population sex ratio can be affected by sampling bias, intersexual differences in mortality, uneven hatchling sex ratio, or any combination of these factors (Lovich & Gibbons, 1990). We have no reason to think that our sampling was biased towards females, and estimating population size for each sex independently should control for any potential sex bias in sampling. Incubation temperature may contribute to the even operational sex ratio. In map turtles, higher incubation temperatures produce females and lower incubation temperatures produce males (Ewert, Jackson & Nelson, 1994). Thus, it is plausible that females are overproduced in our population via selection of warmer nesting sites. We also detected evidence of differential survival between males and females. These differences certainly account, at least in part, for the lower than expected proportion of males. The cause of this difference in survival is, however, unclear. Anthropogenic mortality has the potential to bias population sex ratio (Dorcas, Wilson & Gibbons, 2007). It is possible that because of their much smaller size, males are less likely to survive collisions with boats. This would explain why the prevalence of traumatic injuries caused by boats is higher in females in highly dimorphic turtles (Roosenburg, 1991; Galois & Ouellet, 2007). The smaller body size of males may also make them more vulnerable to a wider range of predators. Alternatively, the lower survival rate in males may also reflect intersexual differences in longevity. Overall, the most likely explanations for the higher proportion of females than expected from the pattern of bimaturation are the overproduction of females via temperaturedependent sex determination and a slightly higher mortality rate in males.

In size-dimorphic reptiles, the larger sex almost always has a smaller k and approaches its asymptotic size (a) at a slower rate (e.g., turtles: Lindeman, 1999; snakes: Brown& Weatherhead, 1999) than the smaller sex. These patterns were also apparent in northern map turtles. In females, our estimate of k was similar to those reported for other species of *Graptemys* (Jones & Hartfield, 1995; Lindeman, 1999). In contrast, in males, our estimate of k was smaller than those for 3 species of *Graptemys* reported by Lindeman (1999) but was similar to the k reported for male *G. oculifera* (Jones & Hartfield, 1995). A lower value of k in the larger sex appears to reflect a constraint on energy acquisition (Stamps & Krishnan, 1997). Thus, the relatively smaller k in male *G. geographica* (this study) and *G. oculifera* (Jones & Hartfield, 1995) may indicate that male growth is relatively more constrained by energy acquisition in these species.

Despite a smaller dimorphism in k in northern map turtles compared to other Graptemys, sexual dimorphism in absolute growth rates was still very important. Indeed, we estimated that females grow on average 2.1 times faster than males before sexual maturity. We thus expected females to have higher SMR than males due to the metabolic demands imposed by tissue synthesis (Wieser, 1994). Although females tended to have higher SMR per unit of body mass, this difference was not statistically significant. It seems probable that our low statistical power prevented the detection of a significant difference. Yet, our power analyses indicate that a sample size much larger (n = 77)than that typically used in respirometry studies is required to detect significant differences. The only other test of the cost of growth in chelonians also failed to detect a metabolic cost of growth under both standard and field conditions (Brown, Nagy & Morafka, 2005), suggesting that such a cost may be difficult to detect in animals with intrinsically low metabolic rates such as turtles. Therefore, we cannot conclude that the metabolic cost of growth accounts for the lower value of k typically found in the larger sex. Our test was, however, limited to the metabolic cost of biosynthesis, which represents only a fraction of the overall energetic cost of growth. Growing also requires the allocation of energy to foraging, to processing and digesting food, and to behavioural thermoregulation (Nagy, 2000). All of those processes contribute to the overall metabolic cost of growth (Nagy, 2000) and may explain the sexual differences in k found in most sexually dimorphic animals with indeterminate growth (Stamps, 1993).

Studies investigating intersexual variation in thermoregulatory behaviour and its relationship to growth rates would provide important insights into the proximate determinants of age at maturity and SSD. In addition, studies investigating intersexual variation in physiological performance and in thermoregulatory behaviour should shed light on the mechanisms responsible for sexual bimaturation.

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