Sexual dimorphism in northern map turtles (*Graptemys geographica*):

Ecological causes and consequences.

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ABSTRACT

Sexual dimorphism in traits such as colour, size, and shape is very ubiquitous in animals. The direction and intensity of sexual dimorphism, however, varies between species and understanding the causes for the evolution and maintenance of sexual dimorphism has been a central quest in evolutionary biology. The purpose of my thesis was to explore the ecological causes and consequences of sexual dimorphism in northern map turtles. I integrated a variety of approaches to test hypotheses associated with sexual size dimorphism (SSD) as well as sexual dimorphism in trophic morphology.

In my first chapter provided evidence through dietary and functional analysis that dimorphism in feeding structures has evolved to increase the energy intake of females to fuel egg production. In my second chapter, I investigated factors contributing to sex differences in diet and habitat use. I found no sex differences in habitat despite marked differences in prey distribution. Using stable isotopes analysis and fecal analysis, I found a large dietary overlap between males and females, indicating no intersexual competition for food. Patterns of prey selection in females, however, were again concordant with the reproductive role hypothesis. In my third chapter, I studied SSD from an ontogenetic perspective. I investigated sexual bimaturation (sex differences in age at maturity) and its relation to the operational sex ratio. Females take twice as long as males to reach sexual maturitd but the estimated operational sex ratio was even in my study population contrary to a male bias sex ratio as predicted by the pattern of maturation in this species. I also tested if fast growing juvenile females incur the metabolic cost of growth compared to similar size non-growing males. Based on respirometry, I found no evidence of such metabolic cost. In my fourth chapter, I investigated the thermoregulatory implications of sexual size dimorphism. I

showed that large females have a more limited range of daily body temperature than small turtles. This difference appears to lead to a lower accuracy of thermoregulation in large females. Maturation in males, however, does not appear to involve a thermoregulatory cost that could lead to a decrease in growth rate..

RÉSUMÉ

Le dimorphisme sexuel est très répendus chez les animaux. Toutefois, la direction et l'intensité du dimorphisme sexuel varient beaucoup entre les espèces. Comprendre les causes de l'évolution et du maintien du dimorphisme sexuel est une quête centrale en biologie évolutive. Le but de ma thèse était d'investiguer les causes et les conséquences écologiques du dimorphisme sexuel chez la tortue géographique. J'ai intégré différentes approches pour tester des hypothèses relatives au dimorphisme sexuel dans la taille corporelle (DST) et dans la taille de la tête.

Dans mon premier chapitre, j'apporte des évidences fonctionnelles que le dimorphisme sexuel dans la taille des structures trophiques a évolué en réponse à une sélection pour accroître l'allocation d'énergie à la reproduction chez les femelles. Dans mon second chapitre, j'ai examiné les facteurs qui affectent les différences intersexuelles dans la diète et l'utilisation des habitats. Je n'ai trouvé aucune évidence de différence intersexuelle dans l'utilisation des habitats. De surcroît, les patrons d'utilisation des habitats étaient inconsistants avec la distribution des proies. À l'aide d'analyse de la diète j'ai démontré qu'il y a un chevauchement de diète important entre les sexes dans ce qui suggère une faible compétiotion intersexuel pour la nourriture. Dans mon troisième chapitre, j'ai le DST du point de vue ontogénique. Le femelles de ma population cible prennent le double du temps des mâles pour atteindre la maturité sexuelle mais le ratio sexuel opérationnel était uniforme contrairement à biasé en faveur des mâles tel que prédit par le patron maturation. Avec de la respirométrie, j'ai aussi tester si la croissance rapide chez les jeunes femelles impliquent un coût métabolique mais je n'ai détecter aucune évidence d'un tel coût. Dans mon quatrième chapitre, j'ai exploré les conséquences pour la thermorégulation du DST. J'ai démontré que la plage quotidienne de températures corporelles chez les grosses femelles est plus restreinte que les petites tortues (mâles et femelles). Cette différence semble diminuer la précision de la thermorégulation chez les grosses femelles. J’ai aussi testé l’existence d’un conflit entre la reproduction et la thermorégulation chez les mâles. Je n’ai trouvé aucune évidenced’un tel conflit.

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LIST OF ABBREVIATIONS

CHAPTER 1.

HW	head width (turtle)
OL	Operculum length (snail)
PL	Plastron length (turtle)
RRH	Reproductive roles hypothesis
SL	Shell length (snail)
SSD	Sexual size dimorphism
TMD	Trophic morphology dimorphism

CHAPTER 2.

HW	head width (turtle)
OL	Operculum length (snails)
PL	Plastron length (turtle)
SL	Septum length (mussels)
SSD	Sexual size dimorphism
TMD	Trophic morphology dimorphism

CHAPTER 3.

ϕ	Annual survival rate
AIC_c	Akaike’s Information Criteria
GR	Growth rate
p	Recapture probability

PL	Plastron length
SMR	Standard metabolic rate
SSD	Sexual size dimorphism
VO_2	Oxygen consumption

Variables associated with the von Bertalanffy growth model

a	Asymptotic size
b	Parameter related to hatchling
d	Time in years spent growing between captures
k	Intrinsic growth rate
PL_h	Plastron length at hatchling
PL_c	Plastron length at first capture
PL_m	Plastron length at sexual maturity
PL_r	Plastron length at recapture
t	Age in years
t_m	Age at sexual maturity
$t_r - t_c$	Time in days spent growing between the measurements of PL_c and PL_r

CHAPTER 4.

d_b	Accuracy of body temperature
S_{mean}	Mean surface temperature of the water
S_{max}	Maximum surface temperature of the water
T_b	Body temperature
T_{gain}	Thermal gain accrued while basking

T_{range}	Daily range of body temperature
T_{set}	Preferred body temperature
T_{set}	Daily maximum body temperature
UVM	Upper voluntary maximum in a thermal gradient or basking arena

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GENERAL INTRODUCTION

Body size is the most physiologically and ecologically important traits in animals. Indeed, body size directly affects key processes such as metabolic rate (Schmidt-Nielsen 1984) and physiological thermoregulation (Dzialowski and O'Connor 2004). Ecologically, body size influences processes such as predator-prey interactions (Robb and Abrahams 2003), habitat selection (Werner and Gilliam 1984), and intraspecific competition (Heiling and Herberstein 1999). Because of its physiological and ecological importance, body size is under intense sexual and natural selection (Price 1984, Janzen 1993, Janzen et al. 2000, Wikelski 2005). Of particular interest in the study of body size is the intersexual difference in body size known as sexual size dimorphism (SSD). SSD is common and often spectacular in animals (Shine 1989, Andersson 1994, Fairbairn 1997, Blanckenhorn 2005). Understanding the causes of this widespread phenomenon has been a central quest in evolutionary biology ever since Darwin’s first treatment of the topic (Darwin 1871).

At the ultimate level, the direction and intensity of SSD is explained by a balance among sexual selection, fecundity selection, and viability selection within the constraints imposed by the genetic correlation between the sexes (reviewed by Andersson 1994, Blanckenhorn 2000, Blanckenhorn 2005). Sexual selection refers to the competition for mating opportunities. Competition between males of the same species (i.e. intrasexual competition) is the most often invoked ultimate cause to explain large body size in males. When males fight to gain mating opportunities, larger males typically have greater mating success leading to a positive selection on body size (Andersson 1994). Fecundity selection refers to the selective advantage of producing large litters or larger offspring (Reiss 1989, Andersson 1994). Because larger females have more room to accommodate more or larger offspring, there is potential for a positive selection on body size. Sexual selection (via intrasexual competition) thus tends to favour large body size in males while fecundity selection tends to favour large body size in females (Blanckenhorn 2000, 2005). Viability selection refers to selection on traits such as parasite resistance, energetic efficiency, or age at first reproduction (Price 1984, Wikelski and Trillmich 1997, Blanckenhorn 2005). Viability selection tends to favour smaller body size and, thus, it exerts forces in opposition to those of sexual and fecundity selection (Price 1984, Wikelski and Trillmich 1997, Blanckenhorn 2005). Hence, overall SSD is seen as the result of a balance among different selective forces, but its extent is also constrained by the genetic correlation between the sexes (Blanckenhorn 2005). In addition, it should be noted that SSD may also exist solely because of phylogenetic inertia (Fairbairn 1990): past selective pressures that are no longer present.

With the exception of birds and mammals, females are typically larger than males in most animals (Fairbairn 1997). Thus, in the vast majority of animals females are larger. It is also in species where females are larger that the most spectacular cases of SSD are observed. Selection for fecundity appears to be the over-riding selective pressure in such species (Reiss 1989). In theory, based on the relationships between size and reproductive output, females would still gain reproductive advantages by being 1000 times larger than males. In contrast, males never gain reproductive benefits when being more than 8 times larger than females (Reiss 1989). The fecundity advantage, however, has been criticized on the grounds that larger body size comes at some costs, including delaying maturity and allocating resources to growth rather than to reproduction (Shine 1988).

At the proximate level, SSD typically emerges because of intersexual differences in growth rate and/or timing of maturation (i.e. bimaturation Gibbons et al. 1981, Shine 1990, Stamps 1993, Stamps and Krishnan 1997). The mechanisms leading to this divergence in growth and maturation patterns are starting to be understood (Duvall and Beaupre 1998, John-Alder and Cox 2004, Cox et al. 2005, Taylor and Denardo 2005, Bonduriansky 2007, John-Alder et al. 2007). For instance, steroid hormones have been shown to be a biregulator of growth and SSD: testosterone decreases growth rate in species where males are smaller and increases growth rate in species where males are larger (Cox and John-Alder 2005, John-Alder et al. 2007). Resource availability during development was also recently shown to affect the extent of SSD (Bonduriansky 2007).

The majority of these studies, focused on the ultimate or proximate causation of SSD. The consequences of SSD are far less studied. SSD is expected to have many ecological consequences (Shine and Wall 2004) because the relationship between a species and its environment is greatly mediated by its body size (Peters 1983, Stevenson 1985). The response of an animal to many abiotic (e.g., temperature, dissolved oxygen) and biotic (e.g., resource availability, predation) factors is greatly affected by its body size because most physiological processes scale allometrically with body size (Schmidt-Nielsen 1984). Thus, understanding the consequences of a certain body size is critical for understanding the factors affecting the maintenance of SSD. Few detailed field studies have been conducted to elucidate the ecological implications of SSD (for exeception see Wikelski 2005). This thesis examines some of the causes and consequences of SSD in an extremely dimorphic reptile, the northern map turtle (*Graptemys geographica* Le Sueur). I use behavioural, physiological, and ecological approaches to this end.

The northern map turtle is widespread in central and northeastern North America. This species is a member of the largest genus of turtles in North America, a genus that is composed of turtles highly specialized to live in large water bodies (Ernst et al. 1994). The genus *Graptemys* exhibits one of the most extreme female-biased SSD in tetrapods (Fitch

1981, Gibbons and Lovich 1990). Female *Graptemys* are usually 1.5 to 2.5 times the linear dimension of males (Fitch 1981, Gibbons and Lovich 1990). The females of several species of *Graptemys*, including the northern map turtle, are mollusc specialists (Vogt 1981, Lindeman 2000a, Lindeman and Sharkey 2001). The females of these species, in comparison to males, possess enlarged crushing surfaces on the upper and lower jaws (called alveolar surfaces) that they use to immobilize and crush molluscs. This type of dimorphism in feeding structures is interesting because it is tied to a trait that is not directly used in reproduction and may thus constitute a case of ecological dimorphism (Shine 1989). In theory, ecological dimorphism emerges to promote ecological divergence between males and females in response to intersexual competition (Slatkin 1984). Although theoretically possible (Slatkin 1984), unequivoqual cases of ecological dimorphism appear to be rare in nature (Temeles et al. 2000). Because of its extreme size dimorphism and intriguing dimorphism in trophic morphology, the northern map turtle is an interesting subject in which to study the causes and consequences of sexual dimorphism and test various hypotheses related to sexual dimorphism in both body size and in trophic morphology.

In chapter one, I tested a prediction of the reproductive role hypothesis in relation to trophic morphology dimorphism (TMD). Most sexually dimorphic traits can be directly linked to the reproductive role of each sex (Trivers 1972). Sexual dimorphism in trophic structures (e.g., beak, jaws, teeth), however, often lacks a direct link to reproduction. Trophic structures can be linked indirectly to reproductive allocation via energy acquisition. The reproductive role hypothesis (a.k.a. the dimorphic niche hypothesis) posits such an indirect link, but has heretofore received little direct empirical support.

In my second chapter, I investigated SSD and TMD from the angles of habitat use and diet. SSD and TMD are often concordant with patterns of habitat use and diet (Shine and

Wall 2004). Proximate factors leading to intersexual differences in habitat use, however, are challenging to unravel because these differences may stem from sexual dimorphism or may be caused by intersexual competition. I used radio-telemetry and dietary analysis to determine the factors contributing to intersexual differences in diet and habitat use. I also tested an alternative, yet non-exclusive, hypothesis for sexual dimorphism in trophic morphology: the intersexual competition hypothesis.

In chapter three, I investigated patterns of growth and maturation. Sexual bimaturation, an intersexual difference in age at maturity, is a consequence of SSD and it 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) which may be linked to the metabolic cost of growth.

In my final chapter, I used biologging technology and measured body temperature in free ranging map turtles over three entire active seasons to investigate the implications of extreme sexual size dimorphism for thermoregulation. Body size affects body temperature in many ways. Among other things, body size limits the daily range of body temperature an ectotherm can achieve (Stevenson 1985). In addition, reproductive activities can conflict with behavioural thermoregulation, which may in turn affect growth rate and the development of SSD. Thus, allocation in thermoregulation may act as a mechanism promoting the development of SSD.

CHAPTER ONE

Functional and reproductive significance of trophic morphology dimorphism in the northern map turtle (*Graptemys geographica*): a test of the reproductive role hypothesis.

This chapter formed the basis for the following publication:

Bulté, G. D.J. Irschick and G. Blouin-Demers. 2008 The reproductive role hypothesis explains trophic morphology dimorphism in the northern map turtle. Functional Ecology 22: 824-830.

Introduction

Sexual dimorphism is widespread and often spectacular within both vertebrates and invertebrates (Fairbairn 1997, Blanckenhorn 2005). The causes of sexual dimorphism are complex, but at a broad level morphological divergence between males and females is the result of differential selection acting on the same trait (Blanckenhorn 2005). One of the key features of sexual dimorphism is the link to reproduction, and the magnitude of sexual dimorphism can often be understood by looking at factors limiting the reproductive success of each sex. For instance, in many species male reproductive success is limited by the ability to obtain mates via intrasexual or intersexual competition (Trivers 1972). In such cases, sexual selection will bias the expression of traits associated with courtship or combat in males leading to sexual dimorphism in those traits (Andersson 1994). In contrast, female fitness is typically limited by the amount of resources that can be allocated to the production of gametes (Reiss 1989). Thus, in females natural selection tends to bias the expression of traits associated with fecundity, such as body size. This special case of natural selection is typically referred to as fecundity selection and accounts for most cases of female biased sexual dimorphism in body size (Andersson 1994). Traits other than body size, however, are also important for fecundity, but dimorphism in those traits is much less studied (but see Casselman and Schulte-Hostedde 2004). Of particular importance are traits associated with the acquisition and processing of energy. Slatkin (1984, p 623) demonstrated that sexual dimorphism can evolve if "there are intrinsic differences between males and females because of their different energetic needs to ensure successful reproduction". Female-biased sexual dimorphism in feeding structures (e.g., snakes: Shine 1991; turtles: Lindeman 2000; spiders: Walker & Rypstra 2002) is an example of sexual dimorphism that could have evolved as a consequence of the different reproductive roles of each sex (Fig. 1-1). For many animals, the most important reproductive role of females is the acquisition and allocation of energy and nutrients to fuel egg production (Trivers 1972). Thus, female-biased dimorphism is expected in any trait that facilitates energy or nutrient acquisition (e.g., organ size Casselman & Schulte-Hostedde 2004). If some features of the feeding apparatus (e.g., gape size, bite force) limit the size of ingestible prey, trophic morphology dimorphism (hereafter TMD) may arise to enhance energy intake in females by providing them with increased capacity to ingest large prey items (Shine 1989, 1991). This hypothesis is generally referred to as the reproductive role hypothesis (hereafter RRH) (Shine 1991, Walker and Rypstra 2002) or the dimorphic niche hypothesis (Slatkin 1984, Hedrick and Temeles 1989). The RRH falls under the umbrella of ecological dimorphism (Fig.1-1). When applied to TMD, the RRH predicts a closer relationship between the limiting aspects of trophic morphology and fitness in females compared to males. Using northern map turtles as an example, I tested this prediction and showed that TMD increases female feeding performance and fitness (body condition and offspring size), indicating that this dimorphism has arisen to enhance acquisition and allocation of resources to reproduction in females.

Northern map turtles (*Graptemys geographica* LeSueur) offer an excellent system to test the RRH. Females have proportionally larger heads and alveolar surfaces (crushing surface of the jaw) than males. This dimorphism reflects intersexual diet differences (Lindeman 2000a, 2006a). Adult females tend to specialize on molluscs, whereas males have a more diversified diet that typically includes both molluscs and insect larvae (Vogt 1981, Lindeman 2000a) although exclusive molluscivory can also occur in males (White and Moll 1992). In addition, northern map turtles exhibit the most extreme female-biased sexual size dimorphism in chelonians (Gibbons and Lovich 1990), with females averaging eight to ten times the mass of males and two to three times the length. Because northern map turtles feed on hard prey, the performance of their trophic apparatus (e.g., bite force and gape size) likely limits the size and hardness of potential prey (Wainwright 1987, 1988). In turtles, bite force increases with head dimensions (Herrel et al. 2002). Thus, selection for large head dimensions in female turtles may arise to partly overcome the limitation on maximum prey size, therefore potentially raising the upper size limit of ingestible prey (i.e., increasing niche breadth). Consequently, a larger head could increase energy intake, which could in turn increase energy allocation to reproduction as predicted by the RRH.

Materials and methods

Study species and study site

I studied northern map turtles between May 2004 and June 2007 in Lake Opinicon (44°34’N 76°19’W) at the Queen’s University Biological Station approximately 100 km south of Ottawa, Ontario, Canada. Turtles were captured with basking traps and by snorkelling. All captured turtles were brought to the laboratory where I measured maximum plastron length (PL) with a forestry calliper (± 0.5 mm) and head width (HW) with a digital calliper (± 0.01 mm). I marked turtles individually by drilling small holes in the marginal scutes.

Bite force analysis and prey hardness

Bite force was measured in 52 turtles using an isometric Kistler force transducer (type 9023, Kistler Inc., Wintherthur, Switzerland) connected to a Kistler charge amplifier (type 5058a, Kistler Inc.). I induced turtles to bite forcefully on the free ends of the bite force device (Herrel and O'Reilly 2006). I measured bite force five times for each turtle, with a short rest (30–40s) between successive bites. If the turtle did not bite effectively, it was allowed to rest for 30 min before retesting. The highest bite force obtained from each session was taken as the maximal bite force for that individual. The distance between the biting plates was adjusted according to the size of the animal to standardize the gape angle. Care was taken to ensure that each turtle bit the plates in the same orientation.

I determined the maximum hardness of ingested prey by reconstructing the size and hardness of consumed snails (*Viviparus georgianus* Lea) from the size of the opercula recovered in the feces of map turtles. *V. georgianus* is the most important prey item of male and female map turtles in Lake Opinicon and is also the hardest. I collected feces by keeping turtles individually overnight in plastic bins filled with lake water. Water containing feces was filtered and the solid phase was preserved in ethanol until examination using a dissecting scope. For each sample, I measured the largest operculum.

To reconstruct snail hardness, I first determined the relationship between the length of the operculum and the shell length (SL) of the snail based on 90 snails collected in Lake Opinicon. Operculum length (OL) was a highly significant of SL ($R^2 = 0.95$, $F_{(1.88)}$, $P < 0.0001$: $SL = - 0.878 + 1.906*OL$). I then used the reconstructed SL to predict hardness of the snails using the equation specific to *V. georgianus* provided by Osenberg and Mittlebach (1989) assuming no important geographical variation in snail hardness.

Each feces sample represents the prey ingested over a short period of time (a few days). Consequently, a given sample may not contain a snail operculum representing the maximum potential prey size for the individual from which the sample was obtained, and any relationships drawn from all the samples will underestimate the maximum capacity of the turtles. To circumvent this problem and to identify the maximum realized capacity for an individual of a given HW or plastron length (PL), I used cyclical regressions to partition the data (Thomson et al. 1996). This approach involves a series of linear regressions (in my case, prey hardness regressed on HW or PL) in which the data are successively divided according to the sign of the residuals. The first cycle thus includes all the data, the second cycle includes only the data falling above the line of best fit of the first cycle (i.e., with positive residuals), and the third cycle includes only data falling above the line of best fit of the second cycle.

Measures of fitness: body condition and reproductive output

To determine if trophic morphology is linked to fitness, I investigated the relationship between head size and two important measures of fitness: body condition and reproductive output. I measured body condition as the residuals of an ordinary least square regression with $\log_{10}$ PL as the independent variable and $\log_{10}$ mass as the dependent variable (Jakob et al. 1996). This index of condition is frequently used as an indirect measure of energetic status where individuals with higher residual values are viewed as having superior energetic status (Jakob et al. 1996, Schulte-Hostedde et al. 2005). Among animals, body condition is correlated with important reproductive traits, such as testis size (Schulte-Hostedde et al. 2005) and reproductive output (Brown and Shine 2005, Litzgus et al. 2008). I calculated body condition only for individuals captured within three weeks of emergence from hibernation (i.e., ~15 April to 7 May). Turtles captured during that period have empty stomachs, thereby eliminating the confounding effect of digestive status on mass.

As a second measure of fitness, I measured reproductive output in 61 females. I used mean hatchling size as my metric of maternal fitness because body size is an important trait for hatchling survival in turtles (Janzen et al. 2000). I captured females digging their nests and induced oviposition in the laboratory with an injection of oxytocin. Eggs were incubated in the laboratory at 29°C on moist vermiculite (1:1 ratio by mass of water and vermiculite) and hatchlings ($n = 514$) were measured and weighed.

Statistical analyses

Data were tested for normality and homoscedasticity prior to analysis. Bite force, prey hardness, HW, and PL were $\log_{10}$ transformed prior to analysis to achieve normality. I expressed relative HW as the residuals of a least-square regression between PL and HW. Reduced major axis regressions for scaling relationships were performed with Model II (Legendre 2001). Other analyses were performed with JMP 5.0.1 (SAS Institute Inc).

Results

Sexual dimorphism in body size and trophic morphology

Females ranged from 65 to 253 mm PL (mean = 179, $n = 351$), whereas males ranged from 62 to 125 mm PL (mean = 97, $n = 267$). Allometric scaling of HW to PL indicated that turtles were also very dimorphic in head size (Fig. 2, Table 1). I compared HW as a function of PL in males and females using ANCOVA. To avoid comparing largely non-overlapping PL ranges, I restricted the analysis to females with PL < 125 mm. The ANCOVA model was significant ($R^2 = 0.91$, $F_{(3,295)} = 1159.83$, $P < 0.0001$) and both sex ($R^2 = 0.43$, $F_{(1,295)} = 1433.91$, $P < 0.0001$) and PL ($R^2 = 0.36$, $F_{(1,295)} = 1195.24$, $P < 0.0001$) were significant predictors of HW (Fig. 2). The interaction between PL and sex was significant ($F_{(1,295)} = 27.92$, $P < 0.0001$), but explained less than 0.1% of the variation in HW ($R^2 = 0.008$).

Bite force analysis

Overall, bite force scaled positively with HW in males, but did not deviate from the expected slope of two (Meyers et al. 2002) in females (Fig. 3, Table 1). I compared bite force as a function of PL in males (n = 18) and females (n = 11) using ANCOVA. The model was significant ($R^2 = 0.72$, $F_{(3,25)} = 21.49$, $P < 0.0001$). PL and sex were both significant predictors of bite force (PL: $R^2 = 0.27$, $F_{(1,25)} = 23.99$, $P < 0.0001$; sex: $R^2 = 0.23$, $F_{(1,25)} = 20.70$, $P < 0.0001$). However the slopes were the same ($R^2 = 0.02$, $F_{(1,25)} = 1.82$, $P = 0.19$) for both sexes, suggesting that the difference in absolute bite force between the sexes over the same range of body size is due to differences in HW not PL.

Prey hardness

I examined the feces of 121 individuals (77 females, 44 males) ranging from 48 to 242 mm PL. The number of snail opercula found in each sample ranged from 1 to > 800. For each sex, I used two regression cycles to determine the relationship between maximum prey hardness and HW or PL. For females, this resulted in using 21 (for PL) and 24 (for HW) data points out of the original 77. For males, I used 11 (for PL) and 12 (for HW) data points out of 44. In both sexes, I found strong relationships between maximum hardness of ingested snails and both HW and PL (Fig. 4, Table 1). By expressing the hardness of ingested prey as a percentage of the maximum crushing capacity of the turtles (measured with the bite force analysis), I found that females consumed snails that were significantly closer to their maximum bite force capacity (60 ± 4.22%) compared to males (28 ± 1.43%, t-test: $t_{(1,31)} = 5.52$. $P < 0.001$).

Body condition and reproductive output

Body condition increased with relative HW in males ($R^2 = 0.12$, $F_{(1,123)} = 17.10$, $P < 0.0001$) and in females ($R^2 = 0.28$, $F_{(1,52)} = 20.71$, $P < 0.0001$) (Fig. 1-5). Relative HW, however, explained about twice as much variation in body condition in females compared to males. Mean mass of hatchlings increased with PL ($R^2 = 0.23$, $F_{(1,60)} = 17.89$, $P < 0.0001$), but clutch size did not ($R^2 = 0.03$, $F_{(1,61)} = 1.83$, $P = 0.18$). The mean coefficient of variation of hatchling mass within clutches was 6.2% (S.D.= 3.29%), indicating that the within clutch variance in hatchling mass is small. I tested for the effect of PL and for the effect of HW controlling for PL on mean hatchling mass using multiple regression. The full model was significant ($R^2 = 0.33$, $F_{(3,57)} = 9.45$, $P < 0.0001$) and both PL ($R^2 = 0.21$, $F_{(1,57)} = 11.81$, $P < 0.0001$) and relative HW ($R^2 = 0.09$, $F_{(1,57)} = 4.98$, $P = 0.007$) were significant predictors of mean hatchling mass (Fig. 6). There was no significant interaction between relative HW and PL ($R^2 = 0.03$, $F_{(1,57)} = 1.77$, $P = 0.104$).

Discussion

Sexual dimorphism has received substantial attention from evolutionary ecologists (Hedrick and Temeles 1989, Fairbairn 1997, Blanckenhorn 2005). In the absence of sexual selection, sexual dimorphism can theoretically evolve to accommodate the reproductive roles of each sex (Slatkin 1984), but few empirical data exist to support this hypothesis. My findings offer clear support for the RRH of TMD, which states that ecological dimorphisms have arisen as a consequence of different energetic requirements between the sexes.

If trophic morphology limits energy intake, the RRH predicts a relationship between relative head width and fitness in durophageous turtles. The relationships between my measures of fitness and relative head width support this prediction. Body condition is an important determinant of fitness in both male (Schulte-Hostedde et al. 2005) and female (Litzgus et al. 2008) vertebrates. I found that relative HW explains more than twice the variation in body condition in females than in males, indicating that relative head size is more tightly linked to fitness in females than in males. Furthermore, I demonstrated that females with relatively larger heads were able to produce larger offspring. I assume here that head size has a strong genetic basis, a reasonable assumption in this group of turtles (Lindeman 2000b), although phenotypic plasticity may also contribute to variation in head dimensions.

The morphological (head size), functional (bite force), and ecological (prey size) divergence between males and females has likely arisen as a consequence of the feeding mode (durophagy) of map turtles, which imposes a mechanistic limitation on energy intake. Prior studies of molluscivorous fish (Wainwright 1987, 1988) have shown that durophagy requires important morphological specialization, but this mode of feeding can allow consumers to exploit resources for which there is little competition (Wainwright 1987, 1988). For durophageous species, the performance of the trophic apparatus limits the size and hardness of prey that can be ingested; (Wainwright 1987, 1988, Aguirre et al. 2003), thereby resulting in strong associations between morphology and prey use. My findings are largely concordant with this prior work because head size in northern map turtles is a strong predictor of both bite force and maximum consumed prey size or hardness, indicating that the size of prey consumed by map turtles is also apparently limited by bite force.

In animals lacking parental care, the reproductive role of females is restricted largely to the allocation of energy and nutrient to eggs. Increasing body size is one mechanism by which females can produce more or larger offspring, especially in animals with indeterminate growth. To realize the potential benefits of a larger body size, however, females must allocate more energy to at least three compartments: 1) growth for achieving a larger body size (Shine 1988); 2) maintenance, because metabolic rate increases with body size (Andrews and Pough 1985); and 3) egg production because more, or larger, eggs are more energetically costly (Nagle et al. 1998). Thus, selection on energy intake and fecundity may be inextricably linked: without a concomitant increase in energy intake, females cannot realize the fecundity potential of a larger body size. In males, on the other hand, the connection between energy intake and fitness may be weaker. In non-territorial species with scramble competition for mates, such as northern map turtles, male fitness is expected to be more limited by mate encounter rates than by energy supplies (Trivers 1972). Thus, in such species selection on energy acquisition is expected to be stronger in females than in males. My results suggest that larger heads in females have evolved in response to selection on energy intake. Indeed, bite force performance and head shape may be highly important to fitness in female turtles but less critical for male fitness. This interpretation is concordant with a comparative analysis of HW and alveolar width in *Graptemys* (Lindeman and Sharkey 2001) which suggests that modifications of the trophic morphology occurred in females only in response to durophagy.

Although my results are concordant with the RRH, Slatkin (1984) suggested two other hypotheses for the evolution of sexual dimorphism in the absence of sexual selection: the bimodal niche and the competitive displacement hypotheses (Fig 1.). A bimodal niche is unlikely to lead to sexual dimorphism because it requires very low genetic correlation (Slatkin 1984). On the other hand, competitive displacement could lead to sexual dimorphism, including TMD. Contemporary intersexual competition for prey, however, does not appear to be important in my study population. I conducted detailed dietary analyses

(Bulté and Blouin-Demers 2008, Bulté et al. 2008a) and found nearly complete diet overlap between the sexes. In addition, in species exhibiting extreme dimorphism in body size, such as map turtles, intersexual competition between adults is unlikely to lead to TMD because trophic morphology would differ markedly in absolute size due the effect of body size alone (Shine 1991). Intersexual competition is expected to be most intense when males and females overlap in body size. Yet, males and small females of turtles exhibiting TMD have overlapping diets (Tucker et al. 1995, Lindeman 2006a).

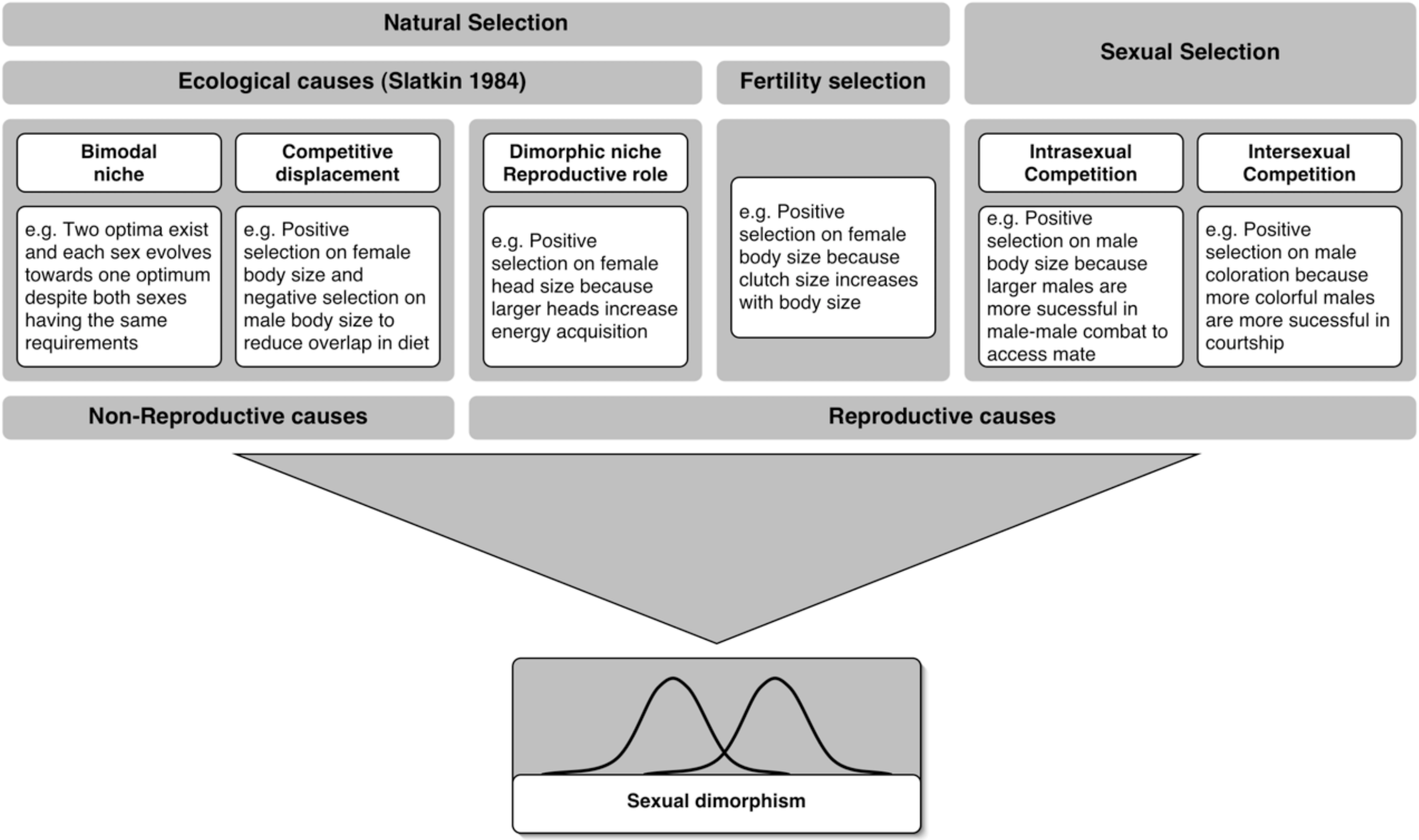
The results presented in this chapter indicate the functional significance of HW and bite force, and that a positive selection on HW and bite force is likely responsible for the maintenance of TMD. I cannot formally exclude the possibility, however, that negative selection or other proximate factors contribute to TMD by constraining HW in males. Males can ingest large quantities of snails (White and Moll 1992, Bulté et al. 2008a) and the positive relationship between relative HW and body condition indicates that HW and bite force are also important for energy intake in males. Male *Graptemys* mature very early compared to females (Bulté et al. 2009) and head growth may be constrained by the inhibitory effect of testosterone (Shine and Crews 1988). Interestingly, I found that males have higher allometric coefficients of bite force compared to females (Table 1), meaning that bite force increases faster with HW in males than in females. Greater relative bite force in males may have evolved to compensate the inhibitory effect of testosterone on head growth. However, males are unable to match the absolute bite force of similar sized females because their heads are much smaller. This explanation, coupled with my results on the effect of HW on fitness in females, could also explain the general pattern of TMD in *Graptemys*. All species of *Graptemys* exhibit TMD, even non-molluscivorous species (Lindeman 2000b). However, TMD is more pronounced in molluscivorous species (Lindeman 2000b). This pattern within the genus supports the idea that some constraint (e.g., testosterone) affects negatively head growth in males, but that molluscivory creates an even greater divergence in TMD between the sexes by favoring large heads in females (see also Lindeman and Sharkey 2001).

The data presented in this chapter provide empirical evidence that ecology and reproductive allocation are linked by the performance of the trophic apparatus (i.e., bite force), which mediates resource use and, thus, energy acquisition. My data also underscore the notion that the evolution of morphology (head shape), body size, energetics, and fecundity may be inextricably linked.

Table 1-1: Scaling relationships of head width, bite force, and prey hardness as a function of body size and head size. Data are $\log_{10}$ transformed. Slopes and intercepts are estimated with reduced major axis regressions. Significance tests are from least-square regressions. In all cases, $P < 0.001$.

Predictor	**Dependent variable**	**Sex**	**n**	**Slope (95% C.I.)**	**Intercept (95% C.I.)**	**R^2**
Plastron length	Head width	Female	351	0.85 (0.83 – 0.87)	-0.37 (-0.43 – -0.36)	0.97
		Male	267	0.52 (0.49 – 0.55)	0.19 (0.13 – 0.24)	0.78
Plastron length	Bite Force	Female	26	1.93 (1.59 – 2.35)	-2.19(-3.06 – -1.47)	0.79
		Male	26	1.96 (1.54 – 2.49)	-2.38 (-3.43 – -1.56)	0.67
Head width	Bite force	Female	26	2.09 (1.95 – 2.25)	-1.04 (-1.26 – -0.83)	0.97
		Male	26	3.62 (2.91 – 4.49)	-2.93 (-4.01 – -2.07)	0.73
Plastron length	Maximum prey hardness	Female	24	2.64 (2.38 – 2.94)	-4.07 (-4.73 – -3.48)	0.94
		Male	11	1.91 (1.25 – 2.94)	-2.85 (-4.88 – -1.52)	0.66
Head width	Maximum prey hardness	Female	21	2.99 (2.48 – 3.61)	-2.65 (-3.59 – -1.88)	0.84
		Male	12	4.13 (2.83 – 6.04)	-4.14 (-6.49 – -2.53)	0.7

Figure 1-1: Ultimate causes of sexual dimorphism with examples.



e.g. Two optima exist and each sex evolves towards one optimum despite both sexes having the same requirements

e.g. Positive selection on female body size and negative selection on male body size to reduce overlap in diet

e.g. Positive selection on female head size because larger heads increase energy acquisition

e.g. Positive selection on female body size because clutch size increases with body size

e.g. Positive selection on male body size because larger males are more sucessful in male-male combat to access mate

e.g. Positive selection on male coloration because more colorful males are more sucessful in courtship

Figure 1-2:Head size increases with body size in female and male northern map turtles from lake Opinicon, Ontario, but females have wider heads for their body size than males. Inset picture shows a male (left) and a female (right) of equal body size.

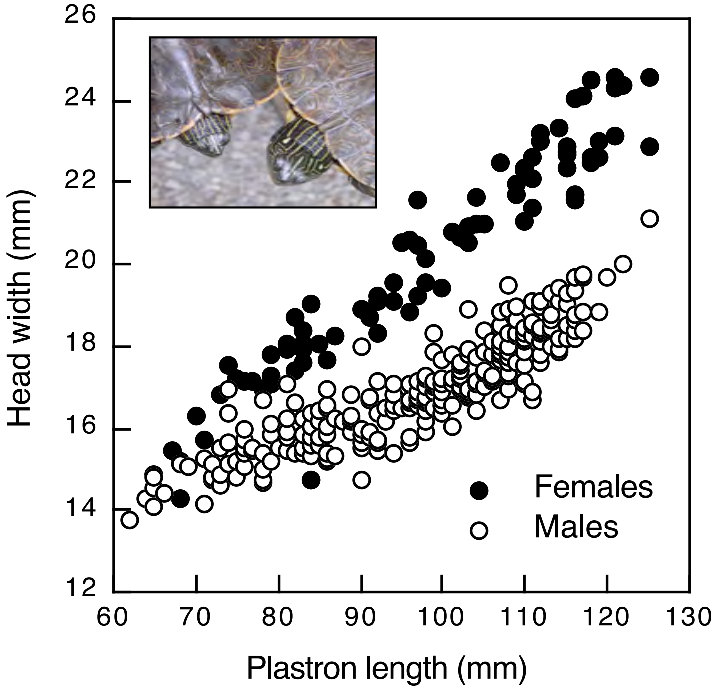


Figure 1-3: Bite force increases allometrically with head width in northern map turtles from lake Opinicon, Ontario. Squares indicate females overlapping in body size with males.

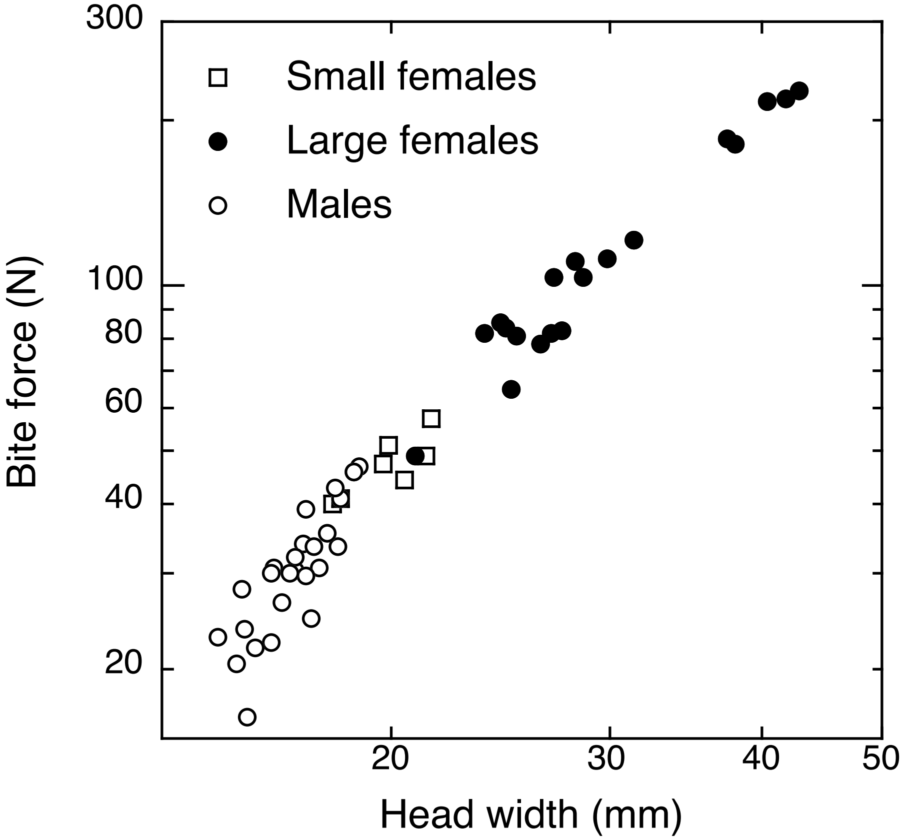


Figure 1-4: Female (top) northern map turtles in lake Opinicon, Ontario, ingest snails closer to their maximum biting capacity than males (bottom). Open symbols denote snail hardness and filled symbols denote bite force.

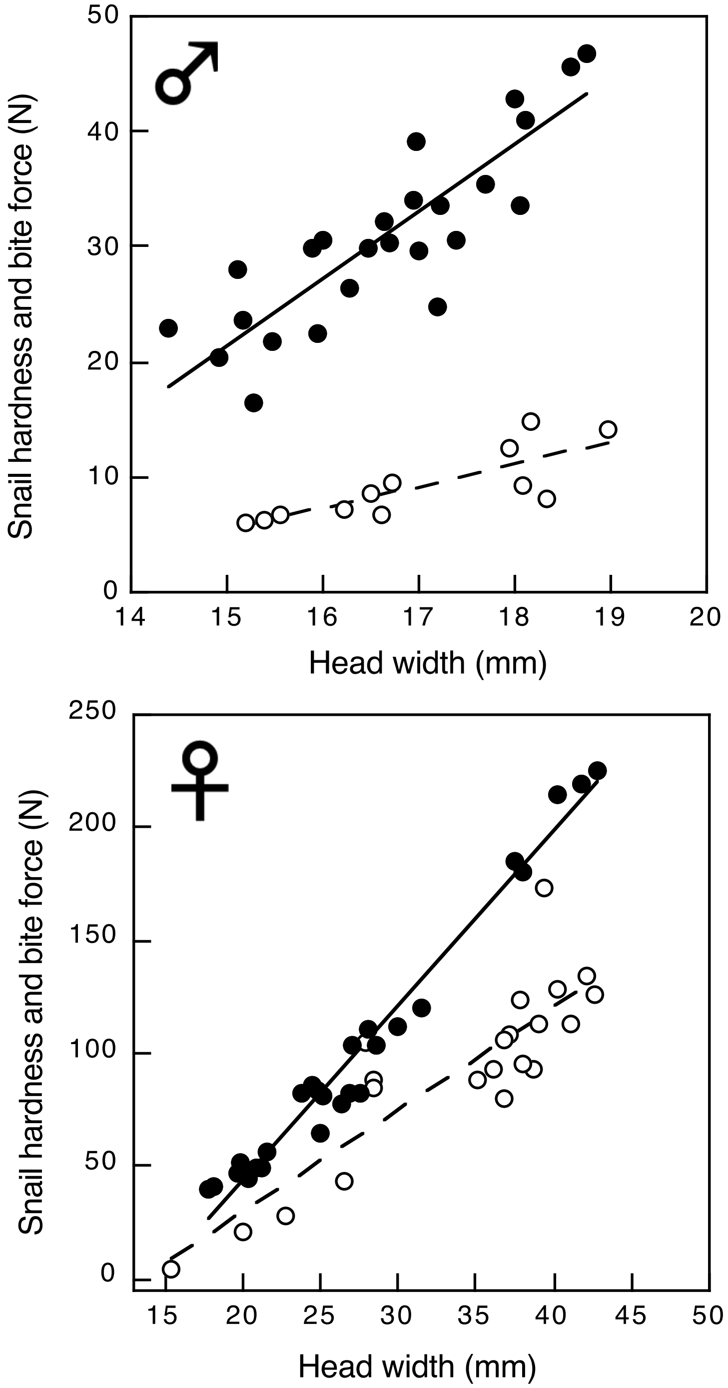


Figure 1-5. Body condition increases with relative head width in male (top) and in female (bottom) northern map turtles from Lake Opinicon, Ontario.

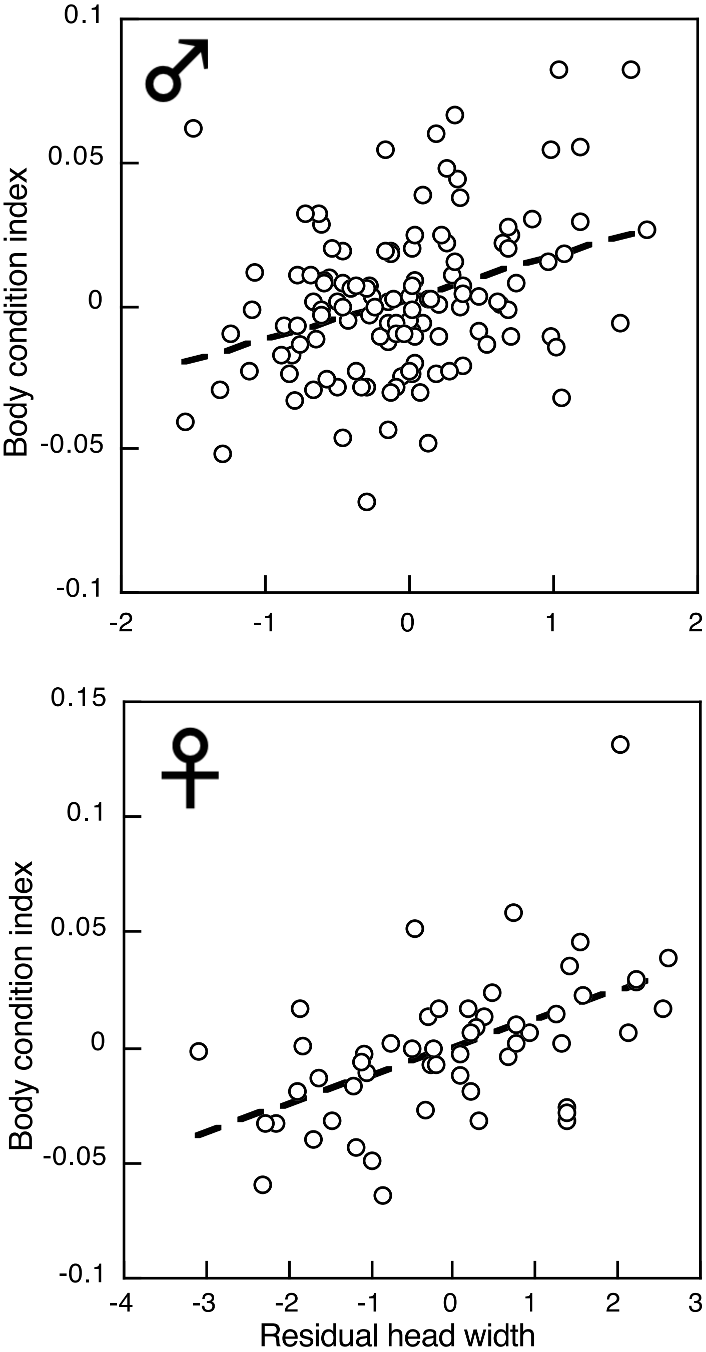
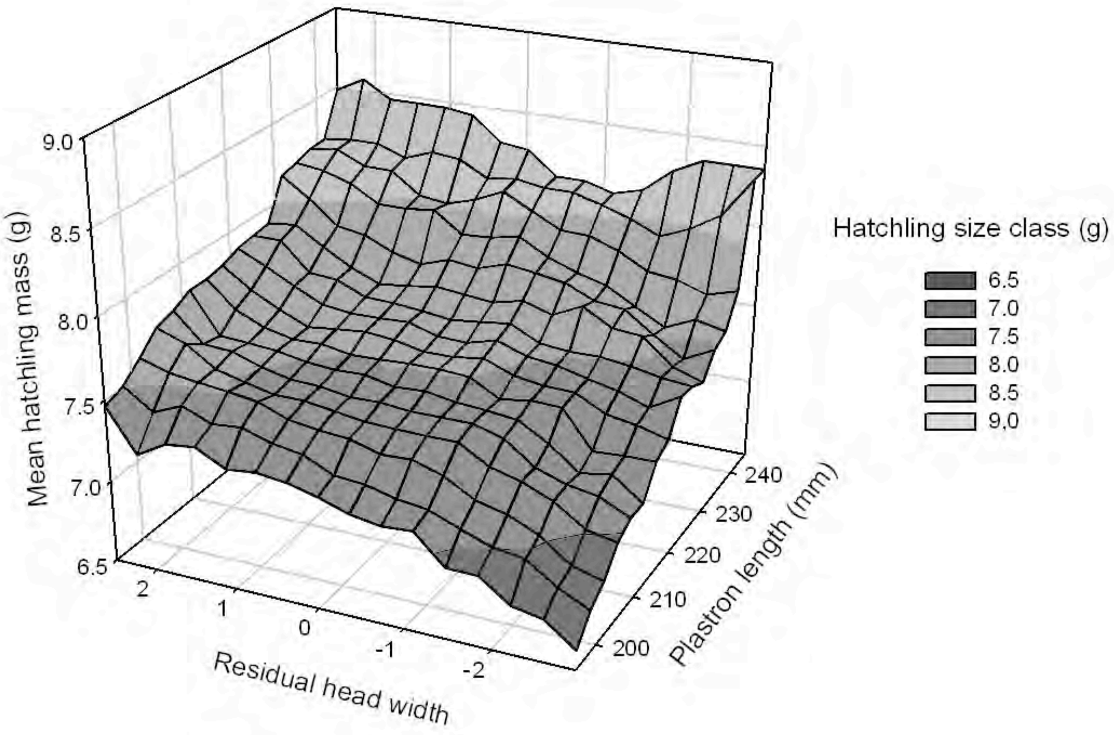


Figure 1-6: Mean offspring mass increases with both body size (plastron length) and relative head width in northern map turtles from lake Opinicon, Ontario



CHAPTER TWO

Intersexual niche divergence in northern map turtles (*Graptemys geographica*): the roles of diet and habitat

This chapter formed the basis for the following publication:
Bulté, G. M.-A. Gravel and G. Blouin-Demers. 2008. Intersexual niche divergence in northern map turtles (*Graptemys geographica*): the roles of diet and habitat. Canadian Journal of Zoology 86: 1235-1243.

Introduction

Sexual dimorphism is widespread in animals and is often accompanied by ecological niche divergence between the sexes (Shine 1989). Sexual size dimorphism (SSD) is among the most conspicuous forms of dimorphism in animals (Fairbairn 1997). In most animals, females are larger than males (Fairbairn 1997) and selection for fecundity is typically held responsible for the evolution and maintenance of such dimorphism (Andersson 1994). In addition to its critical role for reproduction, body size is also one of the most important determinants of the ecology of animals (Peters 1983). Indeed, body size dictates critical ecological processes such as prey and habitat use (Mittelbach 1981, Osenberg and Mittlebach 1989). Moreover, most physiological processes scale allometrically with body size (Schmidt-Nielsen 1984) and, thus, the relationship between an animal and its physical environment (e.g., temperature, dissolved oxygen, water velocity) largely depends on its body size (Stevenson 1985, Robb and Abrahams 2003). Therefore, ecological niche divergence (e.g., in diet and habitat use) between the sexes is expected when extreme differences in body size are found (Shine 1991).

Ecological niche divergence may also be linked to sexual dimorphism in traits other than body size. For instance, sexual dimorphism in feeding structures (trophic morphology dimorphism, hereafter TMD) and, consequently, in diet is common in animals (reviewed by Shine 1989). Two leading hypotheses to explain the evolution of TMD are the competition hypothesis and the reproductive role hypothesis (Slatkin 1984, Hedrick and Temeles 1989). The competition hypothesis suggests that TMD has evolved to reduce intersexual competition for food. On the other hand, the reproductive role hypothesis suggests that TMD reflects the different reproductive roles of males and females. Because the fitness of females is usually more directly limited by energy supplies than the fitness of males (Trivers 1972), any trait linked to energy acquisition (e.g., gape size for gape-limited predators) should be over expressed in females relative to males as long as sexual selection is not also acting on the same trait in males. Whether TMD has evolved via intersexual competition or to accommodate the reproductive roles of each sex, both hypotheses predict intersexual differences in the size or type of prey consumed.

Ecological niche divergence between males and females has received substantial attention by ecologists (Hedrick and Temeles 1989, Shine 1991, Temeles et al. 2000, Shine et al. 2002, Radford and Du Plessis 2003, Thom et al. 2004, Lailvaux and Vincent 2007) but the proximate factors responsible for ecological divergence are often challenging to identify. For instance, at the ultimate level dietary divergence can be driven by the different energy requirements of males and females (Bulté et al. 2008b), but prey distribution may be a proximate cause of habitat use divergence if the preferred prey of each sex occur in different habitats (Shine 1986). In contrast, if body size limits the use of certain habitats (e.g. Robb and Abrahams 2003), intersexual differences in habitat use may be a passive consequence of SSD and be unrelated to foraging. Thus, unravelling the factors responsible for ecological niche divergence necessitates the measurement of several variables for each sex: habitat use, diet composition, prey size, and prey distribution.

In this chapter, I identify the factors responsible for intersexual differences in habitat use and diet in a population of northern map turtles (*Graptemys geographica* LeSueur 1817). Northern map turtles exhibit extreme female-biased SSD with females being sometimes more than twice the length of males (Gibbons and Lovich 1990). Northern map turtles are also sexually dimorphic in trophic morphology with females having wider heads, larger alveolar surfaces (crushing surface of the jaws) (Lindeman 2000a), and greater bite force

(Bulté et al. 2008b). The sexual dimorphism in body size and trophic morphology is accompanied by intersexual differences in diet (Vogt 1981, Lindeman 2006a) and habitat use (Pluto and Bellis 1988, Carrière 2007). Pluto and Bellis (1986) found that female northern map turtles use habitats with higher current velocity, with deeper water, and that are further from shore than males. Other lotic turtles exhibiting SSD comparable to that found in northern map turtles also show similar intersexual habitat use differences (Jones 1996, Bodie and Semlitsch 2000, Lindeman 2003). Intersexual differences in habitat use could be a passive consequence of SSD because swimming capacity increases with body size (Pluto and Bellis 1986). Consequently, in a lotic environment, more habitats are available to females than to males. Because dietary differences exist between the sexes, prey distribution may also explain intersexual habitat use differences (Lindeman 2003). Most studies of intersexual differences in diet or habitat use in turtles have focused on adults (Vogt 1981, Pluto and Bellis 1986, Jones 1996, Bodie and Semlitsch 2000) in which the effects of sex and of size are confounded. As indicated by Lindeman (2003), juvenile females overlapping in body size with males, but with a trophic morphology intermediate between that of adult males and that of adult females, allow us to isolate the effects of sex and size on diet and habitat use.

I quantified habitat use, diet composition, and prey size for adult males, juvenile females overlapping in size with males, and adult female northern map turtles. My first objective was to determine if habitat use differences previously reported in this species were a consequence of the greater swimming capacity of females (itself dependant on body size; Pluto and Bellis 1986) or if these differences were the result of prey distribution. While northern map turtles typically inhabit rivers and large lakes (Ernst et al. 1994), some populations live in smaller lakes, which provides the opportunity to control for the effect of current velocity on habitat use. I radio-tracked northern map turtles in a small lake and predicted that, if current velocity constrains the movements of smaller individuals (i.e., males and small females) in lotic environments, no difference in habitat use should be detected in a small lake. Alternatively, if habitat use differences are a consequence of dietary differences, these differences should be present in a lentic environment as long as the preferred prey of each sex occurs in different habitats.

Adult female northern map turtles eat mostly molluscs, while males have a more diversified diet that includes more aquatic insect larvae and juvenile females have a diet intermediate between that of adult males and that of adult females (Lindeman 2006a). My second objective was to determine the presence of intersexual dietary niche partionning in northern map turtles. I emphasised life stages during which males and females overlap in body size because it is during these stages that intersexual competition for resources is most likely (Shine 1991). I compared the size of molluscan prey consumed with fecal analysis and diet composition with stable isotopes analysis. I predicted that, if the competition hypothesis applies, there should be little overlap in diet (composition, prey size, or both) between males and females of similar body size.

Materials and methods

Study site

I studied northern map turtles between May 2004 and September 2007 in Lake Opinicon (44°34’N, 76°19’W) at the Queen’s University Biological Station, approximately 100 km south of Ottawa, Ontario, Canada. Lake Opinicon is a small (788 ha) and shallow (mean depth 4.9 m) mesotrophic lake part of the Rideau Canal waterway linking the cities of

Ottawa and Kingston. I captured northern map turtles with basking traps and by hand while snorkelling.

Radio-telemetry and habitat use

I tracked 53 northern map turtles with radio-telemetry. Turtles equipped with radio-transmitters were selected to fit in one of the following categories: adult females (plastron length = 201-234 mm; n = 17), juvenile females overlapping in size with males (plastron length = 114-135 mm, n = 18, hereafter small females), and adult males (plastron length = 111-125 mm, n = 18). I attached the radio-transmitters (model SI-2FT and SB-2T, Holohil Systems, Carp, Ontario) to the rear marginal scutes of the carapace with stainless steel bolts and nuts. The edges of the transmitters were smoothed with non-toxic aquarium silicone to prevent snagging on aquatic vegetation. Individual turtles were followed for one to three active seasons. I located each individual every two to three days from late April to early September and once a week from mid-September to mid-October. Each individual location was plotted in the field on a detailed map of the lake and UTM coordinates (NAD1983) were later obtained from the electronic version of the same map with the software ArcGIS 9.0 (ESRI 2000).

I used water depth and distance to shore as my metrics of habitat use. Depth was obtained from a bathymetric chart of the lake. I am aware that intersexual differences can exist in other habitat variables, or that ontogenetic changes can be apparent on habitat variables measured at a finer scale. Depth and distance to shore, however, are regularly associated with extreme SSD in aquatic reptiles (Pluto and Bellis 1986, Shine 1986, Bodie and Semlitsch 2000, Lindeman 2003, Carrière 2007). In addition, important biotic (e.g., macrophyte cover, prey distribution) and abiotic variables (e.g., temperature, dissolved oxygen) in lakes are dictated by either depth or distance to shore. Thus, these two habitats variables should integrate most habitat variables likely to vary between sexes or ontogenetically. I broke down the depth of the lake in three classes: 0-2 m, 2-4 m, and > 4 m and calculated the proportion of observations in each depth class for each group (males, small females, and large females). Because the proportions of each depth class used by an individual are compositional data (i.e., they always sum to one), they are not independent from each other and thus must be transformed (Aebischer et al. 1993). The linear independence of each x_i component (i.e., the depth classes) can be achieved with the following transformation: $y_i = \ln(x_i/x_j)$, where x_j is one of the components and y_i is the transformed variable (Aitchison 1986). This transformation requires the exclusion of one component from the analysis (i.e., x_j). I used the class > 4 m as x_j because this class comprised less than 2% of the turtle observations. I excluded from the depth analysis all the observations for which the turtles were basking out of the water (692 / 2963 observations).

Prey distribution

To estimate the relative abundance and the size distribution of available prey in the lake, I counted and measured prey items in sites selected at random in the lake. I divided the lake in two zones for sampling. The first zone was within 5 m of the shoreline and is referred to as the near shore habitat. The second zone was the rest of the lake (i.e., everything > 5 m from the shoreline) and is referred to as open water habitat. Distance to shore of the random points in this zone ranged from 20 to 224 m. Ten locations were sampled in the near shore habitat and 12 in the open water habitat. All the locations sampled in the near shore habitat were in < 1.5 m of water, while the points in the open water habitat ranged in depth from 1 to 6 m. I restricted my sampling to three prey items: trap-door snails (*Viviparus georgianus* Lea, 1834), zebra mussels (*Dreissena polymorpha* Pallas, 1771), and caddisfly larvae (Trichoptera: Leptoceridae). Collectively, these three prey items make up the vast majority of the diet of northern map turtles at my study site (see Results). At each sampling location, I collected and measured all prey items present in a 0.25m^2 quadrat. Caddisfly larvae were not abundant enough to be detected with my sampling effort and, consequently, the analysis of prey distribution was restricted to zebra mussels and trap-door snails.

Prey size

I reconstructed prey size from mollusc structures found in the feces of turtles (Hamilton 1992, Tucker et al. 1995). I collected feces samples by keeping turtles individually overnight in plastic bins filled with 5 cm of lake water. Water containing feces was then filtered and the solid phase was preserved in ethanol until examination under a dissecting scope. For each sample, I counted the number of trap-door snail opercula and zebra mussel septa and I measured the smallest and the largest structure (operculum and septum). To reconstruct the size of ingested molluscs, I determined the relationship between opercula length (for snails) or septum length (for zebra mussels) and shell length for 90 snails and 120 zebra mussels collected in lake Opinicon. I then predicted the size of the ingested molluscs from the size of the structures (opercula or septa) present in the feces. Opercula length ($R^2 = 0.95$, $P < 0.0001$, SL = - 0.878 + 1.906*operculum length) and septa length ($R^2 = 0.90$, $P < 0.0001$ SL = 1.07 + 8.172*mean septa length) were both strong predictors of shell length. Only a few fecal samples from males (6 / 41) contained zebra mussel septa. Thus, the analyses related to prey size were restricted to snails for males. For each individual, I calculated the prey size spectrum of each prey by subtracting the length of the smallest ingested prey from the length of the largest.

I used cyclical regression to determine the relationship between body size and maximum prey size (Thomson et al. 1996, King 2002). Each fecal sample represents only the prey ingested over a short period of time (a few days) and thus may not contain the maximum possible prey size for the individual from which the sample was collected. Cyclical regressions allow estimating the maximum relationship between body size and prey size. This approach involves a series of linear regressions (in my case PL versus prey size) in which the data are successively divided according to the sign of the residuals. The first cycle includes all the data, the second cycle includes only the data falling above the line of best fit (i.e., with positive residuals), and the third cycle includes only data falling above the line of best fit of the second cycle. To estimate the proportion of ingestible prey at any given plastron length in each habitat, I used the predicted maximum prey size obtained from the cyclical regressions and compared it to the prey size distribution sampled in each habitat.

Stable isotopes analysis, diet composition, and niche overlap

To determine the diet composition of northern map turtles, I used stable isotopes analysis. In temperate lakes, $\delta^{13}C$ can be used to discriminate pelagic consumers (e.g., mussels) from benthic consumers (e.g., trichoptera and snails) (Post 2002). In addition, $\delta^{15}N$ can be used to differentiate consumers based on their trophic level (Post 2002). The diet of northern map turtles at my study site is composed almost exclusively of three prey items (trichoptera, zebra mussels, and trap-door snails).

For the turtles, I measured stable isotope ratios in whole blood. In freshwater turtles, blood has a complete turnover rate for nitrogen of 5-7 months (Seminoff et al. 2007), thus reflecting diet over one or two active seasons. I collected blood (0.5 ml) from the caudal vein (Bulté et al. 2006) of males ($n = 23$) and females ($n = 38$). I sampled prey items at three sites

in the lake to account for spatial variation in the isotopic ratio (Post 2002). In addition, to control for the potential effect of size on the isotope ratio of molluscs, I divided molluscan prey into size classes. For each prey type, I measured the isotopic ratios on composite samples of 10 to 26 individuals for each size class and site. For the analysis of prey, I used the soft tissues only excluding the digestive tract. Tissue samples from turtles and prey were freeze-dried and isotope ratios were measured on a mass spectrophotometer at the Hatch Isotopes Laboratory at the University of Ottawa. Stable isotope values are reported in the δ notation where for carbon $\delta^{13}C = ([^{13}C/^{12}C \text{ sample}/^{13}C/^{12}C\text{standard}]-1)*1000$.
Mean standard deviations for replicates were 0.19‰ for $\delta^{13}C$ and 0.25‰ for $\delta^{15}N$.

I estimated the relative contribution of each prey type to the diet with a three-end member linear mixing model (Phillips and Gregg 2001). The model was computed with the spreadsheet Isoerror 1.04 (Phillips and Gregg 2001). To account for trophic fractionation of nitrogen isotopes between trophic levels, I used the discrimination factor of +2.2‰ (Seminoff et al. 2007). Isotopic fractionation of carbon in whole blood is unknown in freshwater turtles. To account for the isotopic fractionation of carbon, I used a value of +0.23 which was experimentally measured in claws of the freshwater turtle *Trachemys scripta* (Aresco and James 2005).

To test for niche overlap among males, small females, and large females, I calculated Pianka's niche overlap index (Pianka 1973) using the proportions obtained with the mixing model. Pianka's overlap index varies from 0 to 1, with 1 being complete overlap. I then compared my measured overlap to a null model that represents the expected distribution of overlap indices given the absence of competition. I used the software ECOSIM (Gotelli and Entsminger 2007) to for this analysis. This software calculates the distribution of the null model by randomizing the data matrix and calculating an overlap index at each iteration. The null model is based on 1000 simulations. The niche overlap is considered significantly different from the null model if 95% of the simulated indices are larger or smaller than the measured index. If competition affects diet composition, the measured overlap index is expected to be smaller then that of the null model.

Results

Habitat use

Mean distance to shoreline differed among groups of individuals (ANOVA: $F_{(2,50)} = 3{,}48$, $p = 0.038$). A Tukey-Kramer HSD pairwise comparison revealed that small females stayed closer to shore than large females, but males did not differ from either small or large females (Fig. 2-1). Overall, the percentages of observations in each depth class were very similar between groups, with over 90% of the observations falling in the 0-2 m class (Fig. 2-2). Nevertheless, a one-way MANOVA indicated that the three turtle groups used the water depth classes (log-ratio transformed) differently (Wilk's Lambda = 0.73, $F_{(4,104)} = 4.31$, $p < 0.003$). One-way ANOVAs revealed no effect of turtle group in the 0-2 m zone ($F_{(2,53)} = 2.81$, $p < 0.07$), but a significant effect of turtle group in the 2-4 m zone ($F_{(2,53)} = 8.54$, $p < 0.0006$). A Tukey-Kramer HSD test revealed that small females used the 2-4 m zone less than males and large females.

Prey distribution

The mean density of zebra mussels did not differ between the near shore habitat and the open water habitat (t-test: $t_{(1,20)} = 0.07$, $p = 0.95$) and averaged 2592 individuals / m^2 (range 0 –

18144, $n = 22$). The mean density of *Viviparus* snails also did not differ between the near shore habitat and the open water habitat (t-test: $t_{(1,20)} = 0.61$, $p = 0.55$) and averaged 35 individuals / m^2 (range = 0 – 128, $n = 22$). However for both prey, mean shell length was longer in the near shore habitat compared to the open water habitat (zebra mussels: t-test: $t_{(1,17)} = 3.48$, $P = 0.003$ snails: t-test: $t_{(1,16)} = 3.05$, $p = 0.007$). Using the predicted maximum prey size (from the cyclical regressions), I estimated that, for males, the open water habitat contained between 7 and 11% more ingestible snails than the near shore habitat (Fig. 2-3). Similarly, for small females the open water habitat contained 7% to 22% more ingestible snails and 36% to 70 % more ingestible zebra mussels (Fig. 2-3).

Prey size

I examined the feces of 126 individuals ranging from 48 to 242 mm PL. Trap-door snails, zebra mussels, and trichoptera larvae made up > 99% of all identifiable prey items found in the feces. In both males and females, maximum prey size increased with body size (Table 2-1). Over the same range of body sizes (PL < 135mm), the maximum size of ingested snails did not differ between males and females (ANCOVA with PL as covariate, $R^2 = 0.02$, $F_{(3,62)} = 0.514$, $p = 0.95$; Fig. 2-4). The range of prey size ingested increased with body size in both sexes (Table 2-1).

Diet composition and niche overlap

Because both types of mollusc prey are represented by a large size spectrum, I divided mollusc prey in three size classes and tested if mollusc size class affected isotopic ratio. Kruskal-Wallis tests showed that isotope ratios were not affected by size class in zebra mussels (δ^{15}N: $\chi^2 = 2.59$, $P = 0.46$; δ^{13}C: $\chi^2 = 1.25$, $P = 0.74$) or in snails (δ^{15}N: $\chi^2 = 3.71$, p

= 0.16; δ^{13}C: $\chi^2 = 3.71$, $P = 0.16$). Consequently, I pooled all the size classes for the mixing model. The three prey items did not overlap in isotope ratio (Fig. 2-5). Zebra mussels had a very negative δ^{13}C relative to snails and trichoptera, and trap-door snails had a more positive δ^{15}N relative to trichoptera (Fig. 2-5). One-way ANOVAs showed that large females, small females, and males had different δ^{13}C ($F_{(2,58)} = 10.23$, $P = 0.0002$), but similar δ^{15}N ($F_{(2,58)} = 2.18$, $P = 0.12$). A Tukey-Kramer HSD test showed that large females had a more negative δ^{13}C than males, but that small females were not different from males or large females. The three-end members mixing model showed considerable overlap in diet composition between the three groups (Fig. 2-6). However, large females ate more zebra mussels than males and small females (Fig. 2-6).

To test for dietary niche overlap, I compared the observed niche overlap index to a null model. The measured overlap index was 0.91 while the mean of the simulated indices (i.e., the null model) was 0.72. The simulated indices were greater than the observed index 90 % of the time and smaller 10% of the time. Thus, the measured diet overlap index was not significantly different from the null model indicating low intersexual competition.

Discussion

My goal was to elucidate the factors contributing to ecological niche divergence in diet and habitat use in a turtle exhibiting extreme female-biased SSD and TMD. In a lentic environment, I found that northern map turtles exhibit little intersexual divergence in habitat use. Although some intersexual dietary differences were apparent, I could not detect any evidence of intersexual competition for food.

My findings on habitat use contrast with previous studies of sexually dimorphic turtles living in rivers (Pluto and Bellis 1986, Bodie and Semlitsch 2000, Lindeman 2003, Carrière 2007). Those studies found intersexual differences in habitat use with females using deeper and faster moving water. I found that small females (overlapping in body size with males) tended to stay in shallow water and close to shore compared to large females, but that habitat use by males did not differ from that of small or large females. Small females also used the 2-4 m zone less than males and adult females. Because > 90% of the observations for each group were made in the 0-2 m zone, however, the difference I found in the use of the 2-4 m zone is may not bear much biological significance. Thus, overall, I did not find large habitat use differences between the groups. Nevertheless, although depth and distance to shore integrate most biotic and abiotic variables in lakes, I concede that my design may have failed to detect differentiation in other fine-scale habitat variables such as the type of substrate or the percentage of macrophyte cover.

Although both types of mollusc prey were equally abundant in the near shore habitat compared to the open water habitat, the open water habitat harboured more molluscs ingestible by small turtles (i.e., males and small females). Prey size and hardness limit prey use in northern map turtles and crushing capacity increases with head size and body size in this species (Bulté et al. 2008b). Consequently, the diet of males and of small females is restricted to smaller molluscs. If prey distribution dictates patterns of habitat use, males and small females should use habitats containing the greatest density of small molluscs (the open water habitat in this case). For a fully-grown male, for instance, the open water habitat contains nine times (9% compared to 1%) more ingestible *Viviparus* snails than the near shore habitat (Fig. 3). The lack of habitat use differences in my lentic population, despite marked differences in ingestible food distribution, suggests that current velocity, rather than prey distribution, is responsible for intersexual habitat use differences observed in lotic populations of map turtles (e.g. Pluto and Bellis 1986, Carrière 2007). In Lac des Deux Montagnes, Québec, Flaherty and Bider (1984) found that food resources were actually less abundant in bays occupied by northern map turtles than in unoccupied bays and concluded that food distribution was not an important predictor of habitat use. In other sexually size dimorphic reptiles, however, differences in prey use was shown to lead to habitat use differences (Shine 1986, Lindeman 2003). Intersexual differences in habitat use are likely to be site specific. Factors leading to habitat use differences include the extent of intersexual dietary divergence, the distribution of prey in the environment, and the capacity of each sex to use available habitats, which is largely dictated by body size (Mittelbach 1981). In addition, differences in prey distribution may not lead to habitat use differences if resources are abundant enough in all habitats to support each sex. Lake Opinicon is a shallow (mean depth 4.9 m) and thus highly productive lake. Therefore, turtles may not have to adjust their habitat use according to prey availability.

My second objective was to test for intersexual dietary niche partitioning and thus evaluate the importance of intersexual competition. Although I identified differences in diet composition between the groups (e.g., large females consumed more zebra mussels and fewer caddisfly larvae), dietary niche overlap was not smaller than expected in the absence of competition (i.e., the null model). One of the most important dietary differences I found was the consumption of larger snails by large females compared to males and small females. This ability reflects the larger head and stronger bite of large females (Bulté et al. 2008b). As females grow, however, they do not specialize on large prey, but instead enlarge the size spectrum of prey they ingest. Males also exhibit an ontogenetic broadening of their niche, but to a lesser extent than females. This pattern of prey use was described as an "ontogenic telescope" (Arnold 1993) and contrasts with an ontogenetic shift that would be expected under strong intersexual competition. Indeed, if intersexual competition were responsible for dietary differences, males should specialize on small molluscs and females on large molluscs. In addition, intersexual competition is expected to be most intense when males and females overlap in body size (Shine 1991). The diets of male and female map turtles of the same body size overlap completely in both prey composition and prey size. Given the high availability of food in lake Opinicon and of turtle habitats in general (Congdon 1989, Tucker et al. 1995), I interpret high dietary overlap as indicative of low intersexual competition. On the other hand, high dietary overlap could also be interpreted as an indication of intense competition if resources are scarce (Gotelli and Graves 1996). Although the extremely high food abundance in my study suggests low competition, I could not formally reject the alternative interpretation that high dietary overlap is indicative of high competition. Indeed, measuring niche overlap is an indirect measure of the intensity of competition. Experimental manipulation of sex ratio and of density would be necessary to assess fully the extent of intersexual competition in northern map turtles.

Intersexual competition has been shown to be a potential driver for the evolution of sexual dimorphism (Slatkin 1984) such as trophic morphology dimorphism (TMD). The apparent lack of competition for food in northern map turtles does not support the competition hypothesis for the evolution of TMD. Although theoretically possible (Slatkin 1984), the competition hypothesis was argued to be of minor importance for the evolution of sexual dimorphism (Shine 1991, Fairbairn 1997, Blanckenhorn 2005). In contrast, the important niche broadening observed in females supports the reproductive role hypothesis which proposes that females have evolved larger heads and stronger bites to increase their energy intake and reproductive allocation (Bulté et al. 2008b). Indeed, the capacity to ingest a wide spectrum of prey size likely contributes to increased energy intake by increasing foraging efficiency.

In contrast to previous studies that relied on stomach content and fecal analyses to estimate diet composition in turtles, I used stable isotopes analysis. Stable isotope analysis is a cruder dietary analysis compared to traditional approaches (i.e., stomach content and fecal analyses) and may not have the resolution required to capture subtle, yet meaningful, differences. Nonetheless, this approach has several advantages over traditional techniques that also make it a very powerful tool (Vander Zanden and Vadeboncoeur 2002). In molluscivorous turtles, fecal analysis and stomach content analysis can lead to conflicting results regarding diet composition (Lindeman 2003). In addition, stomach flushing (Legler 1977) is highly invasive and can be detrimental to turtles (Lindeman 2006a). Stomach content and fecal analyses are likely to overestimate prey items with hard structures, such as molluscs, and underestimate prey with soft, easily digestible tissue, such as insect larvae. In addition, these two techniques provide only a “snapshot” of diet composition (e.g., a few days), which may not be representative of the diet composition over longer time periods (e.g., a season). Stable isotopes analysis has the advantage of providing a measure of assimilated food, as opposed to ingested or egested food, and thus is not biased towards certain prey types. In addition, stable isotopes provide an estimate of diet composition over longer time periods (depending on the turnover rate of the tissue analyzed). Northern map turtles are a good species in which to use simple isotopic mixing models because they have a specialized diet composed of few prey (Vogt 1981, White and Moll 1992, Lindeman 2006b). Isotopic analysis is a powerful approach to investigate intersexual niche partitioning and ontogenetic shifts (Post 2003, Newsome et al. 2007). Its application to consumers exhibiting sex-specific diet would help improve our understanding of the factors leading to sexual dietary divergence.

Table 2-1:Results of linear regressions of maximum prey size and prey size spectrum as a function of body size in northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada.

Sex	Prey species	*n*	Dependant variables	*P*	R^2
Females	Zebra mussels	22 / 41	Maximum length*	< 0.0001	0.58
		43	Size spectrum	< 0.0001	0.21
Females	*Viviparus georgianus*	26 / 77	Maximum length*	< 0.0001	0.91
		85	Size spectrum	< 0.0001	0.37
Males	*Viviparus georgianus*	11 / 41	Maximum length*	0.004	0.62
		41	Size spectrum	0.018	0.13

*Note: Maximum prey size was obtained from cyclical regressions.

Figure 2-1: Mean distance from shore for radio-tracked northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada. Stars indicate statistically significant differences.

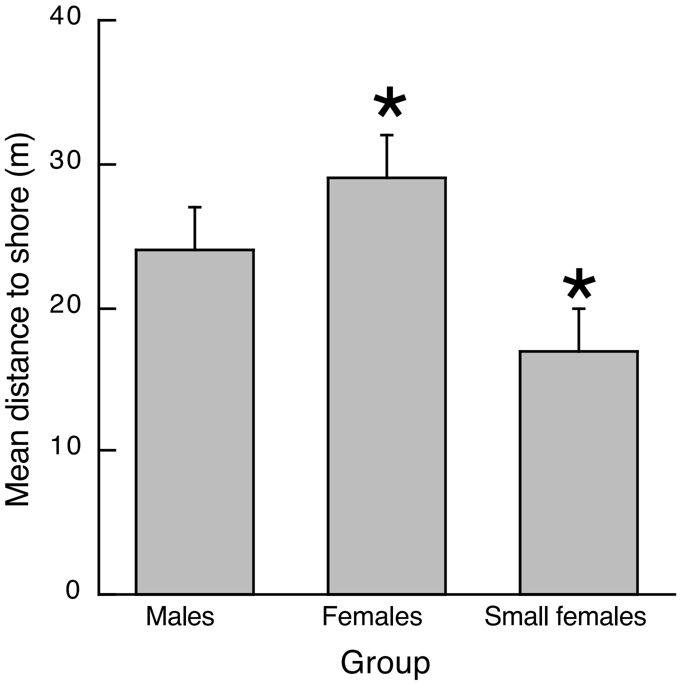


Figure 2-2: Percentage of observations of radio-tracked northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada in three water depth classes. Error bars indicate one standard deviation.

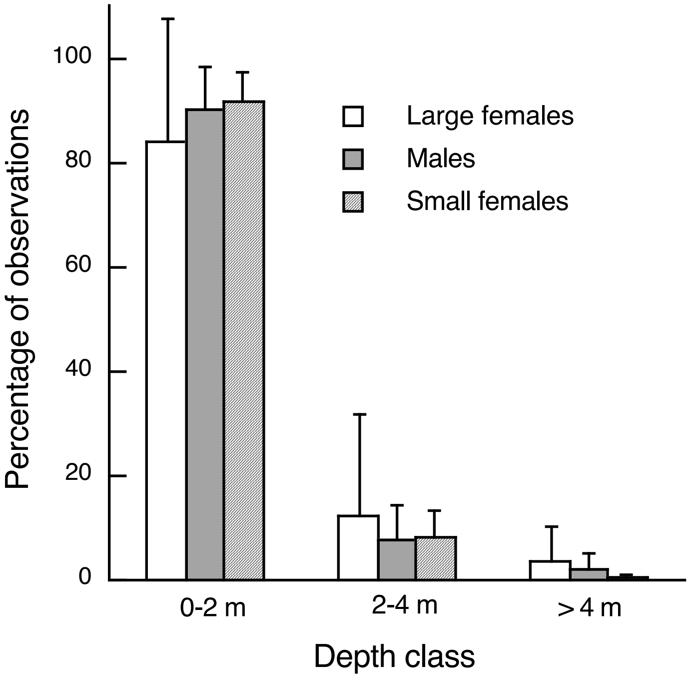


Figure 2-3: Predicted proportions of ingestible molluscs as a function of body size for females (A) and males (B) northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada. Black lines indicate snails (*Viviparus georgianus*) and grey lines indicate zebra mussels (*Dreissena polymorpha*). Solid lines indicate the open water habitat and dashed lines indicate the near shore habitat.

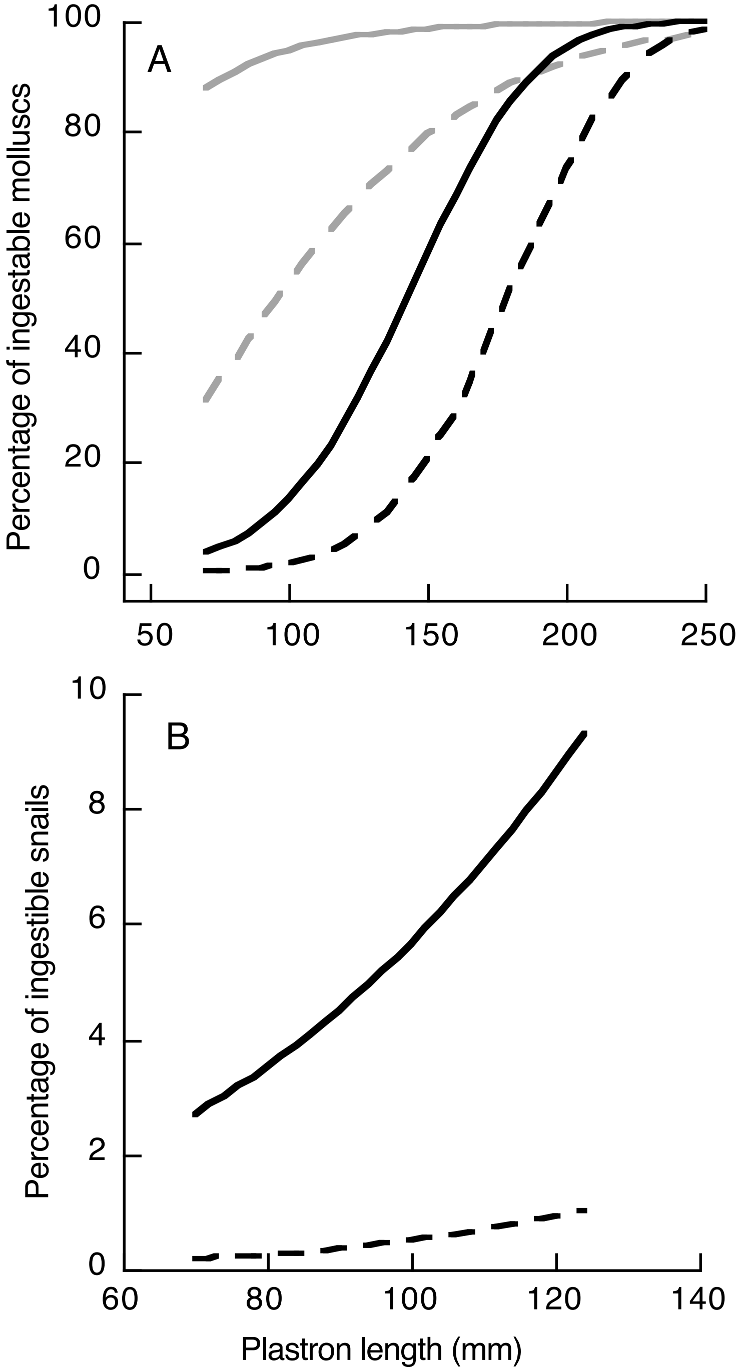


Figure 2-4: Maximum and minimum prey size as a function of body size in female (A) and male (B) northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada. The grey box indicates the prey size spectrum of males.

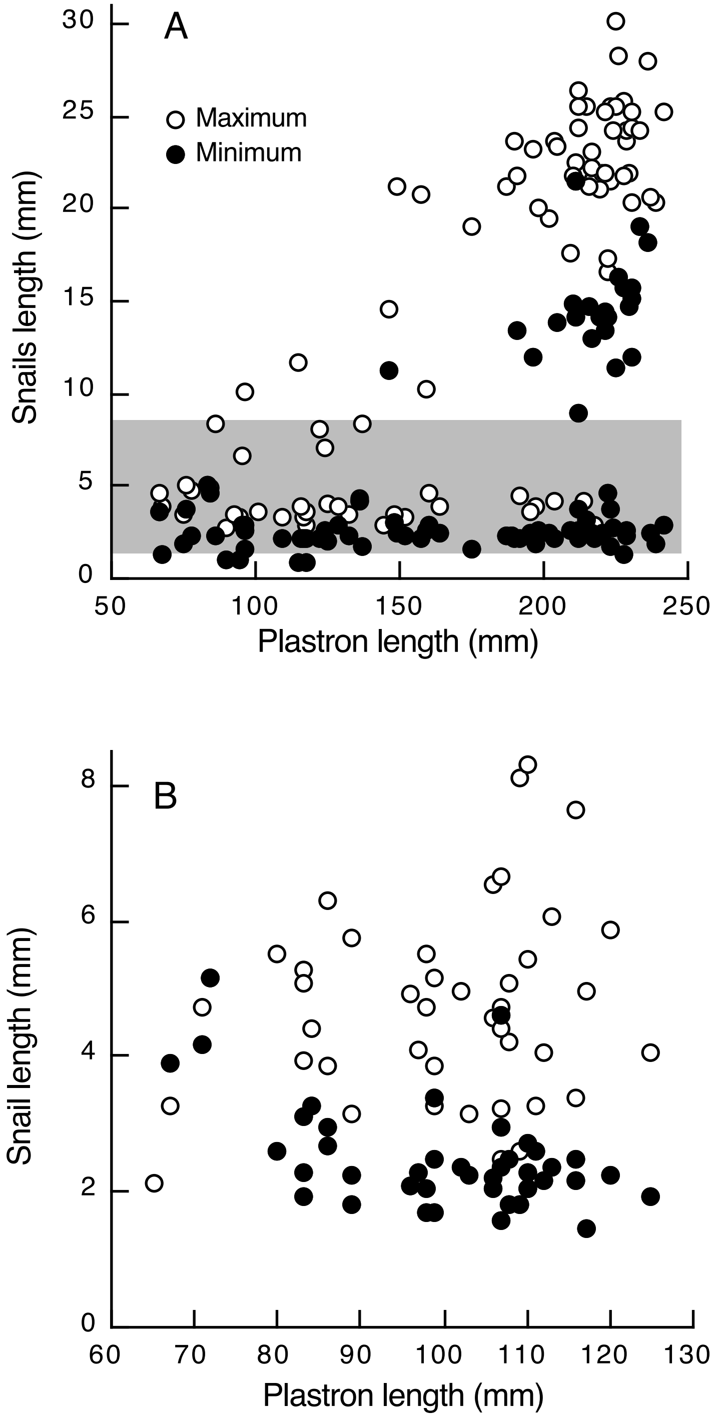


Figure 2-5:δ^{13}C and δ^{15}N values for northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada and their prey.

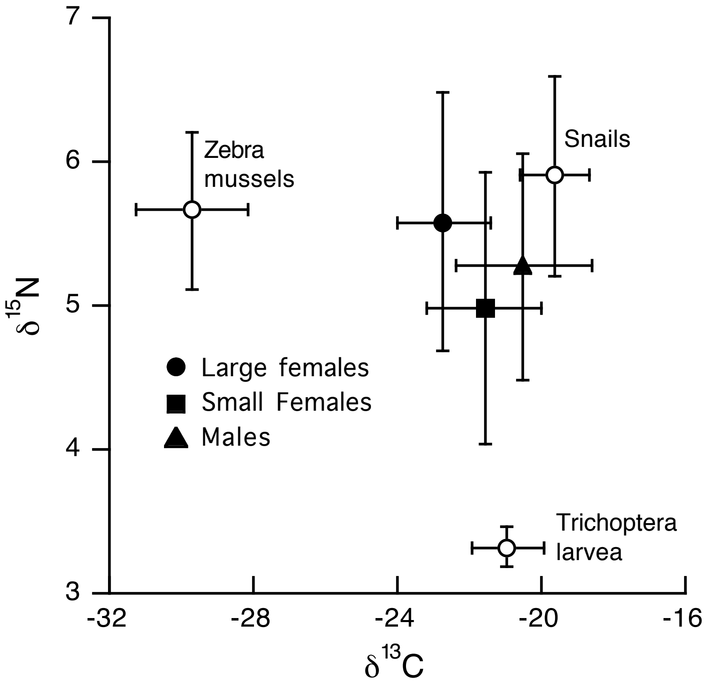
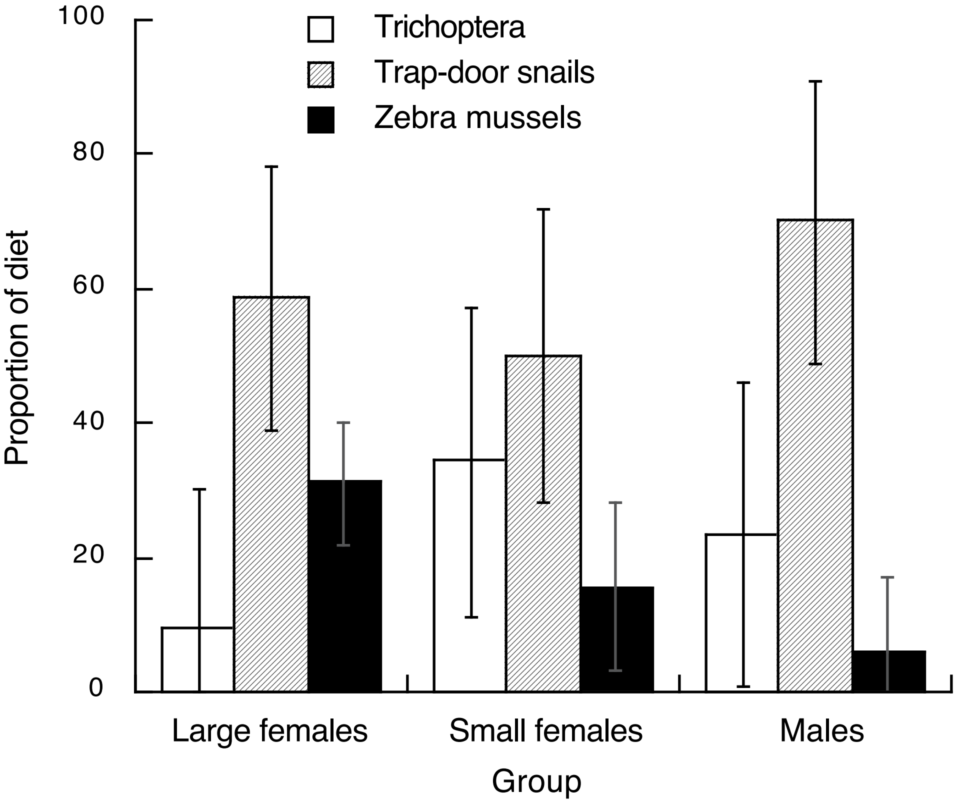


Figure 2-6: Percentages of the three main prey items in the diet of northern map turtles (*Graptemys geographica*) from lake Opinicon, Ontario, Canada, estimated with a three-source isotopic mixing model. Error bars indicate the 95% confidence limits.



CHAPTER THREE

Does sexual bimaturation affect the metabolic cost of growth and the operational sex ratio in the northern map turtle?

This chapter formed the basis for the following publication:

Bulté, G. and G. Blouin-Demers (2009). Does sexual bimaturation affect the metabolic cost of growth and on the operational sex ratio in a reptile extremely dimorphic in body size. Écoscience, 16: 175-182.

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 and Krishnan 1997). In size dimorphic animals, the larger sex virtually always matures later (Stamps and Krishnan 1997). Among tetrapods, SSD reaches an extreme in emydid turtles in which females can be twice the size of males (Fitch 1981, Gibbons and Lovich 1990). Large body size in female turtles confers a reproductive advantage because reproductive output typically increases with body size (Iverson 1992). 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 and 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 and Gibbons 1990, Jones and 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 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 and Gibbons 1990). Sexual bimaturation also seemingly affects the energetics of size dimorphic animals. In many dimorphic reptiles, the larger sex maintains higher absolute growth rates than the smaller sex (Roosenburg and Kelley 1996, Brown and 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 et al. 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, however, there is little empirical evidence that fast growth is costly (Peterson et al. 1999, Nagy 2000), but few studies have attempted to measure the metabolic cost of growth in reptiles (Nagy 2000). Moreover, to my knowledge, no study has investigated the metabolic cost of growth in the context of sexual bimaturation. Interestingly, despite the larger sex 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).

I studied growth in a population of northern map turtles (*Graptemys geographica;* LeSueur, 1817) from Ontario. I 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. I then examined whether sexual bimaturation biases the sex ratio towards males as predicted by Lovich and Gibbons (1990). Finally, I used respirometry to test if fast-growing juvenile females incur a metabolic cost compared to non-growing adult males of similar body size.

Materials and methods

Study site

I conducted this study from 2003 to 2007 at the Queen's University Biological Station (44°34'N, 76°19'W) approximately 100 km south of Ottawa, Ontario, Canada. I captured northern map turtles in Lake Opinicon with basking traps, by snorkelling, and by surveying nesting areas. I brought back every captured turtle to the laboratory where I measured maximum plastron length using a forestry calliper (± 0.5mm). I 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 hours. I determined sex based on external sexual characteristics. Males have long tails and their cloacal openings are past the posterior margin of the carapace. In contrast, females have short tails and their cloacal openings are at the margin the carapace. In addition, females have relatively wider heads than males (Bulté et al. 2008b).

Growth rates and growth model.

To compare growth rates between males and females, I 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), I subtracted the number of days spent hibernating in the calculation of $t_r - t_{c.}$. I determined the hibernation period in Lake Opinicon from radio-telemetry data on 53 individuals (Bulté et al. 2008a). For the model, I assumed that turtles in my focal population hibernate from 1 October to 1 April (212 days per year).

I estimated growth parameters of males and females by fitting my mark-recapture data to the von Bertalanffy growth equation (Fabens 1965, Frazer et al. 1990),

$$PL = a\ (1 - b\mathrm{e}^{-kt}),$$

[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 (75 to 130 mm), the difference in the predicted mass of males and females does not exceed 1.5 % (Bulté unpublished data). Compared to other growth curves (e.g., logistic, Gompertz), the von Bertalanffy curve fits growth data of emydid turtles best (Lindeman 1997, Litzgus and Brooks 1998), including

Graptemys (Jones and Hartfield 1995, Lindeman 1999). The von Bertalanffy equation requires knowing the age (i.e., t) of each individual, however, which is seldom possible with wild animals. To circumvent this limitation, I used the growth interval model derived from the von Bertalanffy equation by Fabens (1965),

$$PL_r = a - (a - PL_c)\,e^{-kd}\,, \tag{3}$$

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

$$1 - (PL_h\,/a), \tag{4}$$

where PL_h is the size at hatching (Schoener and Schoener 1978). I set PL_h to the mean PL (28.4 mm) of 514 hatchlings from my focal population (Bulté et al. 2008b). The Fabens model was shown to provide reliable estimates of growth parameters in turtles of unknown ages (Frazer et al. 1990).

I 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). I calculated 95% support-plane confidence intervals (Schoener and Schoener 1978) around estimates of a and k to compare parameter estimates between males and females. I calculated d as the number of days (then converted to years) spent growing between captures. I estimated d from the number of activity days. In my study population, map turtles are active from 1 May to 1 October (d = 153 days). To satisfy the assumption of independence, I included only the first and the last capture of each individual in the growth model (i.e., a single growth interval per individual). I 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.

I estimated age at maturity (t_m) from size at maturity,

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

where a, b, and k are as in equation 1, and PL_m is plastron length at maturity. In females, I estimated PL_m from the smallest gravid female captured in my focal population. For males, I estimated PL_m from the smallest male exhibiting an enlarged and elongated tail, a secondary sexual character in map turtles. I 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 my estimates of age at maturity, I conducted a Monte Carlo simulation. Using equation 5, I 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 my 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 only had 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 my estimate of age at maturity.

Sex ratio and survival.

I 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 in the program MARK (White and Burham 1999). I used a sampling interval of one year in the model. For each sex, I first evaluated the goodness of fit of the global model (i.e., the model with the most parameters) by examining the variance inflation factor (c-hat). In both sexes, the value of c-hat was close to one (males = 0.5, females = 1.51). I then fitted simpler models and compared their fit with bias-corrected Akaike's Information Criteria (AIC_c) to select the best model to estimate population size. With five years of data, I generated three estimates of population size for each sex. I tested wether 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, I estimated annual survival (ϕ) and recapture rate (p) with the Cormack-Jolly-Seber model (Lebreton et al. 1992) also with the program MARK. I fitted a set of candidate models and compared their fit with AIC_c. I confirmed that the global model fitted the data well with a bootstrap goodness of fit test of 1000 iterations (Cooch and White 1998). To test whether survival differed between the sexes, I 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_c) than models without sex-specific survival. I corrected for the lack of fit by adjusting the c-hat to its estimated value (1.34). I 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). I predicted that this cost would be higher in juvenile females with high growth rates relative to non-growing adult males of equal body size. I estimated SMR by measuring oxygen consumption (VO_2) on resting, post-absorptive turtles with open-flow respirometry. I measured VO_2 at 26°C in six males (mean mass = 177 g, S.E. = 18) and eight females (mean mass = 188 g, S.E. = 11). Mean mass did not differ between males and females (t-test: $t_{12} = 0.552$, $P = 0.59$). I compared juvenile females and males to control for the effect of mass on SMR. To allow gut clearance, I fasted turtles in outdoor basins for at least two days prior to measurements. I 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. I left the turtles undisturbed in the respirometry chamber for at least two hours before beginning the measurements. During VO_2 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, NV). The concentration of O_2 in the chamber was measured every 20 seconds for 220 minutes and baseline measurements were taken at the beginning and at the end of each trial to correct for instrument drift. All VO_2 measurements were made between 18:00 and 24:00 hours, a period during which these diurnal turtles are normally resting. To eliminate bouts of activity from my estimates of SMR, I 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 and Hopkins 2003, Hopkins et al. 2004). I calculated SMR from VO_2 using the software Datacan (Sable Systems Datacan V, Henderson NV) following Withers (1977).

Results

I marked 981 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 (S.E.= 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 126 mm (Fig. 3-1). The mean PL of all the mature males was 99 mm (S.E. = 0.61).

Growth rates

I was able to obtain two 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 (Fig. 3-2). There was evidence, especially in males, that the relationship between PL and GR slightly deviated from linearity. I thus tested if 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 that adding curvature to the line did 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. I used ANCOVA to compare GR between males and females, but because the relationship between PL and GR was non-linear in males (Fig. 3-2), I restricted my analysis to smaller turtles (PL < 95 mm, 113 individuals: 39 females and 74 males; Fig. 3-3) 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 3-1 and the fitted model in Fig. 3-4. Asymptotic plastron length (*a*) was 228 mm for females and 111 mm for males and, not surprisingly, the 95% SPCI did not overlap (Table 3-1). In contrast, the 95% SPCI of the rate of approach of *a* (*k*) overlapped slightly (by 0.007; Table 3-1).

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

Adult sex ratio and survival

Between 2003 and 2007, I 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. I thus used only this model to estimate population size. In males, however, the top two models fitted the data equally well (52 and 48 % of the support). I consequently averaged the estimates of population size of these two models. The estimated adult male population size was 335 (95% C.I. = 281 –391) compared to 317 (95% C.I. = 243 –391) for adult females. The operational sex ratio (male:female) was 1:0.94 and was not significantly different from 1:1 (Pearson's $\chi^2 = 0.44$, $P = 0.50$). For the survival analysis, the top model received 80% of the support and the four top candidate models (receiving collectively 100% of the support) included sex specific survival (Table 3-2). Mean annual survival rate was 87.3% in females compared to 82.6% in males (Table 3-3).

Cost of growth

The mean SMR of juvenile females was 23% higher than that of males (0.098 ml O_2 hr^{-1} gr^{-1} compared to 0.075 ml O_2 $hr^{-1}gr^{-1}$), but this difference was not statistically significant (t-test: $t_{12} = 0.85$, $P = 0.41$). My modest sample size provided me with low statistical power, so I conducted *a posteriori* power analyses to determine the minimum detectable difference with my sample size and the necessary sample size to detect a significant difference given my effect size. The analyses indicated that I had sufficient power to detect a difference of 0.06 ml O_2 $hr^{-1}gr^{-1}$in SMR (80%) and that I 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, I found marked differences in growth and maturation parameters that are concordant with those reported for other size dimorphic reptiles (Brown and Weatherhead 1999, Lindeman 1999). In particular, I found that females need more than twice as long as males to reach sexual maturity (11.7 vs. 4.5 years).

Based on the early maturation of males, I expected a male-biased adult sex ratio (Lovich and Gibbons 1990). I found that the sex ratio in my 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 and Gibbons 1990). I have no reason to think that my 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 et al. 1994). Thus, it is plausible that females are overproduced in my focal population via selection of warmer nesting sites by nesting females. I 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 et al. 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 and Ouellet 2007, Bulté et al. 2009). The smaller body size of males may also make them more vulnerable to a wider range of predators. Alternatively, 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 temperature-dependent 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 than the smaller sex (Brown and Weatherhead 1999, Lindeman 1999). These patterns were also apparent in northern map turtles. In females, my estimate of *k* was similar to those reported for other species of *Graptemys* (Jones and Hartfield 1995, Lindeman 1999). In contrast, in males, my estimate of *k* was smaller than those for three species of *Graptemys* reported by Lindeman (1999), but was similar to the *k* reported for male *G. oculifera* (Jones and Hartfield 1995). A lower value of *k* in the larger sex appears to reflect a constraint on energy acquisition (Stamps and Krishnan 1997). Thus, the relatively smaller *k* in male *G. geographica* (this study) and *G. oculifera* (Jones and 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, I estimated that females grow on average 2.1 times faster than males before sexual maturity. I 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 the low statistical power prevented the detection of a significant difference. Yet, the power of my analyses indicate that a sample size much larger (n = 77) than what is 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 et al. 2005), suggesting that such a cost may be difficult to detect in animals with intrinsically low metabolic rates such as turtles. Therefore, I cannot conclude that the metabolic cost of growth accounts for the lower value of *k* typically found in the larger sex. My 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 dimorphism in *k* found in most sexually dimorphic animals with indeterminate growth (Stamps 1993).

Studies investigating the 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.

Table 3-1:Mean parameters (95% CI) of the von Bertalanffy growth model 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	***n***	***a* (mm)**	***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 3-2: 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 AICc and higher AICc weights fit the data better.

ϕ	***p***	**AIC$_c$**	**Δ AIC$_c$**	**AIC$_c$ weight**	**Number of parameters**
sex	*t* x *sex*	1545.84	0.00	0.80	10
t x *sex*	*t*	1550.20	4.36	0.09	11
t x *sex*	*Sex*	1550.37	4.53	0.08	10
t x *sex*	*t* x *sex*	1552.91	7.07	0.02	14

Table 3-3: 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)

Figure 3-1: Size distributions of male and female northern map turtles from Lake Opinicon, Ontario, Canada (n = 551 females, 400 males) sampled in 2003 to 2007. Arrows indicate the estimated sizes at maturity.

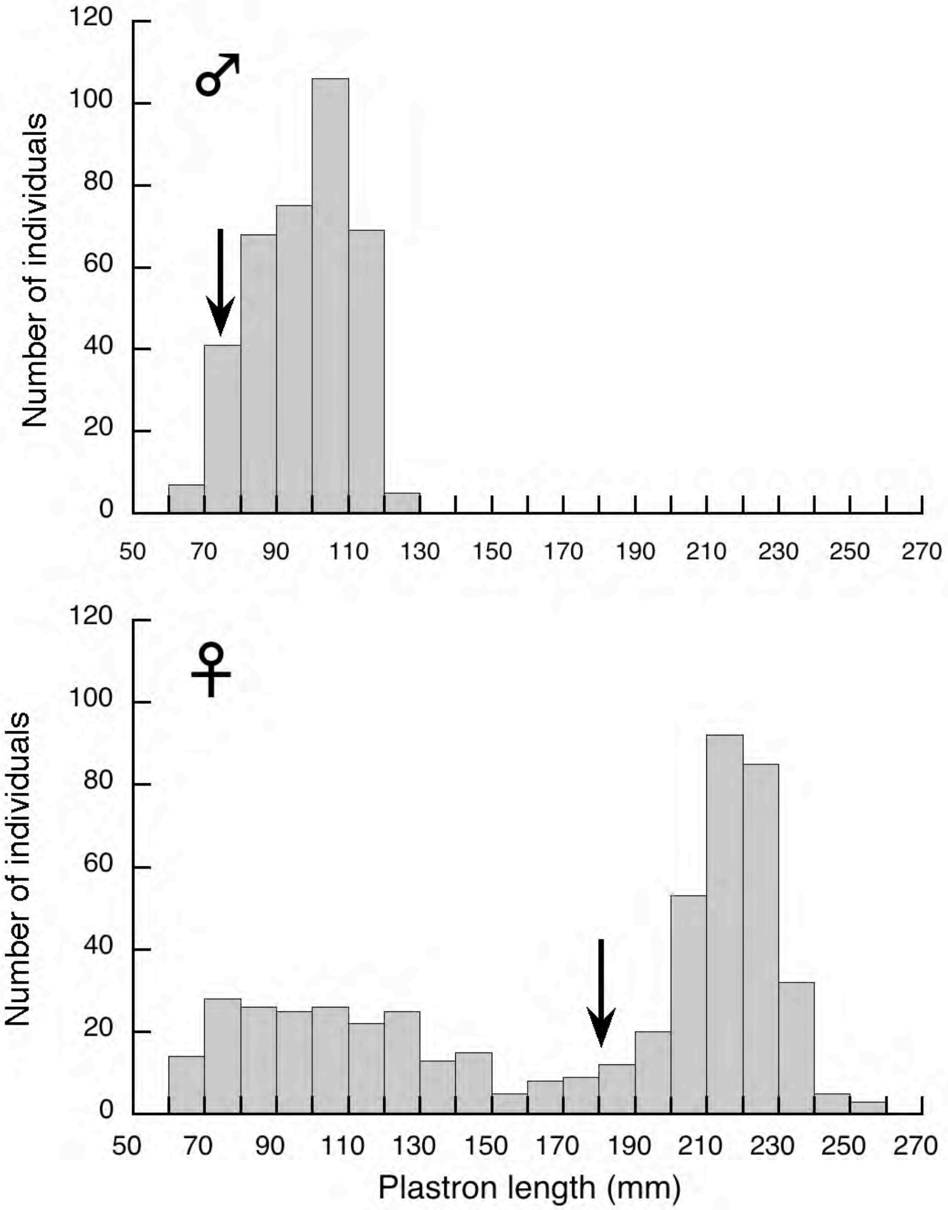


Figure 3-2:Growth rates as a function of initial plastron length in male and female northern map turtles from Lake Opinicon, Ontario, Canada.

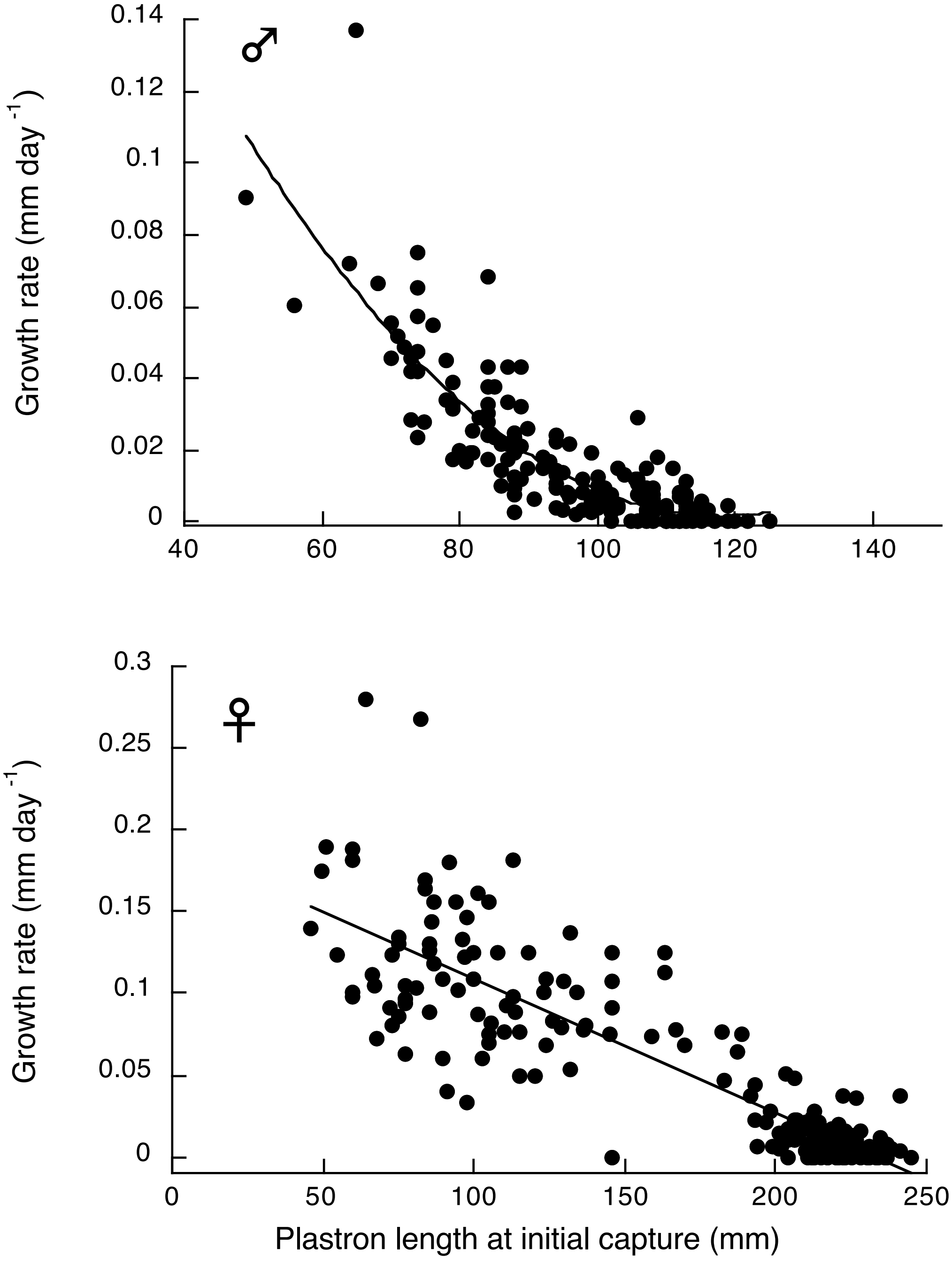


Figure 3-3: Female northern map turtles from Lake Opinicon, Ontario, Canada, maintain higher growth rates than males at overlapping body sizes.

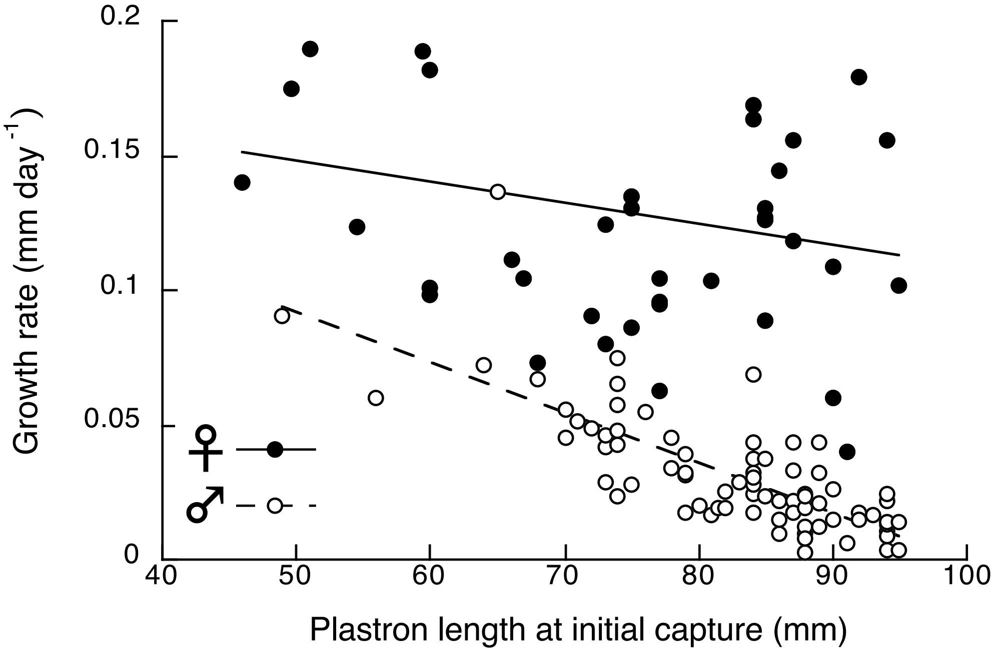
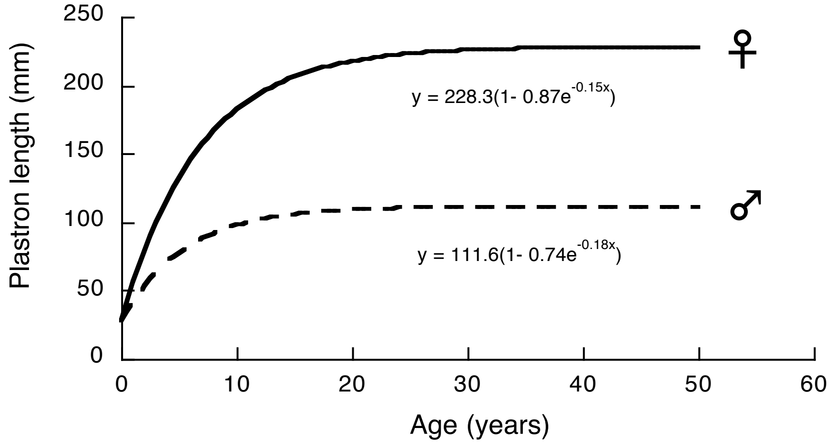


Figure 3-4: Fitted von Bertalanffy growth models for northern map turtles from Lake Opinicon, Ontario, Canada.



CHAPTER FOUR

Implications of extreme sexual size dimorphism for thermoregulation.

This chapter formed the basis for the following publication:

Bulté, G. and G. Blouin-Demers. Implications of extreme sexual size dimorphism for thermoregulation in a freshwater turtle. Oecologia, *in press*.

Introduction

Body size is often the most conspicuous trait differing between males and females. Understanding the causes and consequences of this widespread phenomenon has thus been an important quest in evolutionary biology. The most extreme cases of sexual size dimorphism (hereafter SSD) are found in ectothermic animals. In reptiles, for instance, females can be one order of magnitude heavier than males (Fitch 1981, Cox et al. 2007). Ectotherms, by definition, have limited capacity for metabolic heat production and must rely on behavioural thermoregulation to buffer the ubiquitous effects of T_b on physiological performance (Huey and Kingsolver 1989). Because body size and body temperature (T_b) interact in many ways (Fig. 4-1), extreme SSD is expected to have important consequences for thermoregulation in reptiles.

T_b of an ectotherm is the result of interactions between abiotic factors (e.g., ambient temperature, solar radiation) and the ability of the animal to use behavioural and physiological processes to control the fluctuations in T_b. Body size affects both behavioural and physiological thermoregulation. Larger animals heat and cool more slowly (Grigg et al. 1979), leading to more stable body temperatures (Stevenson 1985). Thus, body size should have an important influence on thermoregulatory decisions, such as the frequency of shuttling required to maintain a stable T_b. Moreover, larger ectotherms are better able to exploit physiological processes to maintain their T_b within a desired range (Dzialowski and O'Connor 2004). Hence, intersexual differences in field T_b or in thermoregulatory behaviour are expected in ectotherms with pronounced SSD. On the other hand, intersexual differences in T_b or in behavioural thermoregulation may also act as a mechanism promoting the development of SSD.

SSD develops because each sex follows a different growth trajectory, leading to intersexual differences in growth rates and in age and size at maturity (Shine 1990, Stamps 1993, Stamps and Krishnan 1997). In ectotherms, growth rate is largely temperature dependant (Avery 1994, Steyermark and Spotila 2001). Thus, if intersexual differences in thermoregulatory behaviour are present, intersexual differences in growth are expected so long as food is not limited. In reptiles where males are smaller, energetically expensive behavioural and physiological processes tied to male reproductive effort are triggered by an increase in plasma testosterone at the onset of sexual maturity (Cox et al. 2005, John-Alder et al. 2007). These processes appear to take away most of the energy available for growth in males, thus leading to a steep decrease in growth rates after the attainment of sexual maturity (Cox et al. 2005, John-Alder et al. 2007). Therefore, the onset of reproductive activities in males could create a conflict between reproduction and behavioural thermoregulation. Such a conflict may have important effects on growth and on the development of SSD because reptiles, especially in temperate areas, rely on behavioural adjustments to regulate their body temperature (T_b) within their preferred range (Huey et al. 1989, Blouin-Demers and Weatherhead 2001, Quirt et al. 2006, Row and Blouin-Demers 2006), a process that is presumed to maximize energy acquisition (Huey and Slatkin 1976).

To understand better the interactions between thermoregulation, body size, and SSD, I investigated patterns of thermoregulation in an extremely size dimorphic reptile: the northern map turtle (*Graptemys geographica*). In this species, the largest females are 10 times the mass of the largest males (Fig. 4-2). I compared patterns of thermoregulation between adult males, immature females overlapping in size with males, and adult females to test predictions regarding the effect of SSD on thermoregulation. I first predicted that, because of their smaller size, males and immature females would be able to raise their T_b higher than adult females. In addition, I predicted that large adult females would experience a narrower range of daily T_b than males and small females because of their larger thermal inertia. I also investigated whether the conflict between reproduction and thermoregulation in males could be the proximate cause for the decrease in male growth rates following maturity and, thus, a mechanism underlying the development of SSD. A potential conflict between thermoregulation and reproduction should be most apparent when comparing mature, non-growing males to immature fast-growing females because these groups correspond to life stages at which the difference in allocation to growth versus reproduction is the most extreme and where the confounding effect of body size on T_b is absent.

Most aquatic emydid turtles regularly and conspicuously bask outside of the water. Basking behaviour is often presumed to function in thermoregulation (Boyer 1965, Crawford et al. 1983). There are very few measurements of internal T_b in free ranging turtles (Manning and Grigg 1997, Edwards and Blouin-Demers 2007), however, and the thermal significance of the frequent basking bouts remains largely unknown. The only study I am aware of that addressed this question found that basking had no thermoregulatory function in the Australian turtle *Emydura signata* (Manning and Grigg 1997). Therefore, my second objective was to investigate the thermal significance of basking behaviour in northern map turtles. I wanted to quantify the thermoregulation benefits accrued through basking in a temperate emydid living in a thermally challenging environment.

Materials and Methods

Study species and study site

The northern map turtle is a widely distributed freshwater turtle in Eastern and Central North America. It is characterized by an extreme SSD with females being more than twice the length of males and no overlap in size at maturity (Bulté and Blouin-Demers 2009). I conducted this study between 2004 and 2006 in Lake Opinicon, a small mesotrophic lake at the Queen's University Biological Station, 150 km south of Ottawa, Ontario, Canada.

Biologging and radio-telemetry

In late April and early May, I captured map turtles while snorkeling at a communal hibernation site. I surgically implanted temperature loggers (Thermochron ibutton DS 2422 and DS1921; Dallas Semiconductor, Sunnyvale, CA, USA) in the abdominal cavity of 14 juvenile females (average carapace length 140 mm; range = 130 to 151 mm), 19 adult males (average carapace length = 136 mm; range = 127 to 148), and 18 adults females (average carapace length = 238 mm; range = 217 to 260). Details of the anesthetic and surgical procedures for the logger implantation can be found in Edwards and Blouin-Demers (2007). The loggers could hold 2048 (DS 1921) or 8192 (DS 2422) temperature readings. Some adult females were implanted with two loggers (model DS 1921). Using these loggers, I obtained T_b readings every 110 minutes (single DS 1921), 55 minutes (two DS 1921), or 25 minutes (single DS 2422) between May and September. Each turtle implanted with a logger was also equipped with a radio-transmitter (SI-2FT and SB-2FT; Holohil Systems, Carp, ON, Canada) bolted to the outside edge of the carapace. I located each individual every 2 to 3 days. When tracking turtles, I applied special care not to disrupt normal basking behaviour. I recaptured the turtles to remove the transmitters and the loggers the fall or spring following implantation.

Preferred body temperature (T_{set}) and accuracy of body temperature (d_b)

A widely used index to quantify the accuracy of thermoregulation is the deviation of field T_b from preferred T_b (T_{set}). T_{set} is the T_b selected in an environment without any costs associated with temperature selection, such as a laboratory thermal gradient (Hertz et al. 1993). It was recently demonstrated that the upper voluntary maximum (UVM) T_b selected in a thermal gradient matches the optimal temperature for energy assimilation in a freshwater turtle (Dubois et al. 2008). Therefore, UVM offers a measure of T_{set} with an important functional significance for growth. I thus used UVM to determine T_{set} because I was mostly interested in testing wether a conflict between thermoregulation and reproduction could affect growth rates.

I used a basking arena (Ben-Ezra et al. 2008) to measure UVM because aquatic or dry thermal gradients would be artificial environments for a species with pronounced aerial basking behaviour such as the northern map turtle. In the basking arena, turtles displayed typical basking behaviour, suggesting they were thermoregulating normally. The arena was composed of a basin with circulating cold water (10-14°C) and a basking platform heated with a heat lamp. To insure that turtles could reach their UVM, I adjusted the heat lamp so that turtles would eventually overheat by staying under the lamp (reach 50°C) and would thus be forced to return to the water to cool. I placed turtles individually in the basking arena and recorded their cloacal temperature every minute for 48 hours using a 36-gauge copper-constantan thermocouple attached to a temperature logger (HOBO H12- 003, Onset Computer Inc, Pocasset, MA, USA).

Because energy assimilation is likely optimized within a narrow range of T_b rather than at a single T_b, I used the interval between the upper 75th and 95th quantiles of selected T_b in the basking arena as my measure of T_{set}. I verified that my measure of T_{set} approximated a range of T_b that is functionally important for growth by comparing it to the optimal temperature for food consumption in a closely related species, the red-ear slider (*Trachemys scripta*) (Parmenter 1980). The 75^{th}-95^{th} quantile range corresponds to T_b where food consumption is ≥95% of the maximum. I then measured the accuracy of T_b (d_b) as the deviation of the field T_b from $T_{set.,}$ in absolute value (Hertz et al. 1993). I also calculated the proportion of time T_b was within T_{set} as an alternate measure of the accuracy of thermoregulation (Christian and Weavers 1996).

Basking behaviour and thermal gain

To investigate the thermal significance of basking behaviour, I calculated the percentage of time spent basking as the percentage of time when T_b exceeded the maximum surface water temperature of the lake (S_{max}). Using temperature loggers (Thermochron ibutton DL 1922; Dallas Semiconductor, Sunnyvale, CA, USA), I measured surface water temperatures at four locations in the lake. I calculated hourly S_{max} as the maximum surface temperature of the four locations. I determined if a turtle was basking by calculating the difference between T_b and S_{max} for each hour of the day. Positive values indicated that the turtle was basking and negative values indicated that the turtle was submerged. It is reasonable to assume that when T_b is below S_{max}, the turtle is submerged because turtles rapidly equilibrate with water temperature once submerged due to the high specific heat of water (Grigg et al. 1979). I then used the difference between T_b and S_{max} to calculate the thermal gain of basking (T_{gain}). For every positive difference between T_b and S_{max}, I calculated the difference between T_b and the mean surface temperature (S_{mean}) of the lake. This index provides a measure, in °C, of the thermal gain realized during basking in air as opposed to remaining at the water surface.

Statistical analyses

To test for the effect of size on maximum daily body temperature (T_{max}) and the daily body temperature range (T_{range}), I calculated the daily maximum T_b and the daily range of T_b for each individual. I then calculated an overall mean T_{max} and mean T_{range} for each individual and tested for group (adult male, adult female, juvenile female) effects using one-way ANOVAs. When the ANOVA was significant, I used *a posteriori* Tukey-HSD pairwise comparisons to determine between which groups the difference lay.

I tested the effects of group (male, female, juvenile female) and month (May to September) on the mean T_b, d_b, T_{gain}, and the percentage of time spent basking with repeated measures ANOVAs. Because I was mostly interested in intergroup differences, when a significant group effect was found I conducted individual one-way ANOVAs for each month followed, when significant, by *a posteriori* Tukey-HSD pairwise comparisons. I calculated mean hourly T_b for each individual and used these hourly means to calculate individual mean monthly T_b values that I used in the repeated measures ANOVAs. I arcsin transformed the percentage of time spent basking and I log-transformed d_b to normalize the distributions. All tests were considered significant at a $\alpha = 0.05$. Statistical analyses were conducted with JMP 5.01.

Results

Preferred body temperature

I measured T_{set} in 13 adult females, 11 juvenile females, and 12 adult males. There were no difference in the 75th quantile (ANOVA: $F_{(2,33)} = 2.00$, $P = 0.15$) and the 95th quantile

(ANOVA: $F_{(2,33)} = 0.79$, $P = 0.46$) among the three groups. The overall mean 75th quantile was 28.7°C (s.e. = 0.77) and the overall mean 95th quantile was 32.5°C (s.e. = 0.4).

Body temperature and accuracy of thermoregulation

I obtained 156 646 mean hourly T_b measurements between May and September from the 51 turtles (18 adult females, 14 juvenile females and 19 adult males) I implanted with temperature loggers. Overall, monthly mean T_b closely matched the monthly average S_{max}, but was always higher than S_{mean} (Fig. 4-3A). Mean hourly T_b across the entire season was lower than S_{max}, but higher than S_{mean} between 1700h and 0700h (Fig. 4-3B). Between 0800h and 1600h, turtles maintained T_b above S_{max} (Fig. 4-3B). Season had a strong and significant effect on T_b, but group had a marginally non-significant effect (Table 4-1).

Month of the year had a strong and significant effect on d_b (Table 4-1). d_b was highest in July and lowest in May (Fig. 4-4A). The effect of group was also marginally non-significant (Table 4-1). Overall, 9% of the T_b measured fell within T_{set}. During the day (0700h to 1800h), however, 15.8% of T_b measured fell within T_{set}. The percentage of observations when T_b was within T_{set} was significantly affected by month, but also by group, and there was a nearly significant month by group interaction (Table 4-1). I found a significant group effect in July ($F_{(2,48)} = 3.34$, $P = 0.043$), August ($F_{(2,48)} = 5.33$, $P = 0.008$), and September ($F_{(2,47)} = 5.57$, $P = 0.007$). Juvenile females kept their T_b more often within T_{set} than adults of both sexes (Fig. 4-4B). In July and September, the percentage of $T_b = T_{set}$ observations was higher in juvenile females than in adult females, and males did not differ from either female group. In August, the percentage of $T_b = T_{set}$ observations was higher in juvenile females compared to both adult groups.

Daily maximum body temperature (T_{max}) and daily range of body temperature (T_{range})

Across all five months, males and juvenile females had higher T_{max} than adult females ($F_{(2,48)} = 8.75$, $P = 0.0006$; Fig 4-5A). Adult females had a narrower T_{range} than males and juvenile females ($F_{(2,48)} = 5.32$, $P = 0.008$; Fig 4-5B).

Basking behaviour and thermal gain

Across the entire season, the average percentage of T_b observations above S_{max} varied between 13 and 54% and month explained most of this variation (Table 4-2). Group also had a significant effect, however, and a significant month by group interaction was present (Table 4-2). Group differences in the percentage of T_b observations above S_{max} were found in May ($F_{(2,42)} = 6.28$, $P = 0.004$) and in August ($F_{(2,48)} = 5.8$, $P = 0.005$). In May, the T_b of adult females were more frequently above S_{max} than the T_b of juvenile females and adult males while in August the T_b of adult males were more frequently below S_{max} than the T_b of adult and juvenile females (Fig. 4-6A).

The monthly average T_{gain} across the entire season ranged from 0.3 to 2°C and was highest in May and lowest in September (Fig. 4-6B). In addition to the significant effect of month, the effect of group was also significant along with a nearly significant month by group interaction (Table 4-2). Individual one-way ANOVAs for each month indicated a significant effect of group in August only ($F_{(2,48)} = 7.99$, $P = 0.001$; Fig. 4-6B). In August, T_{gain} was on average 0.3°C higher in juvenile females compared to both adult groups and *a posteriori* Tukey-HSD pairwise comparison indicated that this difference was statistically significant.

On a daily basis, T_{gain} varied considerably with the lowest values between 2000h and 0800h and the highest values between 1100h and 1400h (Fig. 4-7A). In May between these hours, mean T_{gain} could reach 6°C (Fig 4-7A). Mean monthly maximum T_{gain}, however, could be substantially higher. For instance, mean maximum T_{gain} in May across all groups was 17°C and around 10°C in the remaining months (Fig. 4-7B).

Discussion

Thermal preference

The upper voluntary maximum (UVM) temperature I measured on map turtles in a shuttle arena was similar to the value of approximately 30°C reported for other temperate reptiles (Dubois et al. 2008). UVM was demonstrated to match the optimal temperature for energy assimilation in emydid turtles (Dubois et al. 2008). This measure is thus particularly appropriate to investigate the interplay among thermoregulation, growth, and SSD.

General patterns in body temperature and the accuracy of thermoregulation

I found important seasonal variation in T_b, d_b, and the percentage of time T_b is within T_{set}. These seasonal patterns were concordant with those of other reptiles from the same latitudes (Blouin-Demers and Weatherhead 2001, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007). This seasonal effect reflects the seasonal variation in environmental temperature as well as in the thermal quality of the environment. The highest air and water temperatures are in June and July. Thus, it is not surprising that it is during these months that the highest T_b are achieved. In addition, it is also in June and July that the thermal quality of the environment is the highest in my study area (Blouin-Demers and Weatherhead 2001, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007). Thermal quality is usually measured by the deviation of the environmental temperature from T_{set} (Hertz et al.

1993). When thermal quality is high, d_b is typically low and the percentage of time T_b is within T_{set} is high (Blouin-Demers and Weatherhead 2001) indicating a high accuracy for thermoregulation.

Thermal consequences of sexual size dimorphism

Because thermal inertia increases with body size, larger ectotherms have a more restricted range of possible daily T_b (Stevenson 1985). Thus, I expected smaller turtles (adult males and juvenile females) to be able to achieve higher T_{max} and to experience wider T_{range} than larger turtles (i.e. adult females). Small turtles did indeed achieve higher T_{max} than the large adult females. T_{range} was also wider in smaller turtles than in large females. Overall these results show that body size does restrict the possible range of daily T_b and that pronounced SSD does have implications for the thermal ecology of reptiles. Despite smaller turtles being able to achieve higher T_{max} and experience wider T_{range}, however, the overall mean T_b was the same between small and large turtles. The daily window of time turtles have to reach T_{max} was limited to 2-3 h per day and the difference in average T_{max} between large adult females and small turtles was only 1°C. Thus, the leverage of T_{max} was insufficient to affect the mean values.

Although larger reptiles experience restricted T_{range} compared to their smaller counterparts, being larger also permits a more stable T_b to be maintained (Grigg et al. 1979, Pearson et al. 2003). In addition, larger size appears to facilitate the effectiveness of physiological processes to regulate T_b (Dzialowski and O'Connor 2004). Thus, large turtles could be predicted to thermoregulate more accurately than small turtles. I did not find appreciable differences in d_b, but I did find that, contrary to my prediction, T_b of adult females was less often within T_{set}. These results are surprising because it should be easier for adult females to maintain a stable T_b. In addition, reproductive females are expected to thermoregulate more accurately than males and non-reproductive females (Blouin-Demers and Weatherhead 2001) and in my study population females lay eggs every year (Bulté pers. obs.). The lower accuracy of thermoregulation in adult females may reflect the cost-benefit balance of thermoregulation. If adult females experience higher costs than males and juvenile females when thermoregulating, they should thermoregulate less accurately (Huey and Slatkin 1976). I have, however, no reason to think that the costs of thermoregulation are higher in adult females than in males or juvenile females. On the contrary, accurate thermoregulation should have high reproductive benefits in adult females, such as speeding follicular development (Sarkar et al. 1996) which may be critical at northern latitudes where the active season is short (Rollinson and Brooks 2007). I found that adult females actually spend more time basking than males and juvenile females prior to and during the nesting season (May and June). Sex bias in basking behaviour was also observed in painted turtles (Carrière et al. 2008). Despite more time spent basking, large adult females were not able to thermoregulate as accurately as small turtles. These findings strongly suggest that body size limits the ability to thermoregulate accurately in large females rather than facilitating it. Larger turtles take longer to warm up than smaller turtles (Grigg et al. 1979) and given the short window of time available daily to reach T_{set}, large adult females may be less capable of reaching T_{set} than smaller turtles.

Thermoregulation – reproductive conflict and the expression of SSD

T_b is a central determinant of growth rate in reptiles and SSD is realized by intersexual differences in growth rate and maturation (Shine 1990). Thus, intersexual differences in thermoregulation may affect the expression of SSD. Reproductive activities including mate searching, courtship, and mating occur in water in northern map turtles. Thus, reproductive behaviours may impede thermoregulatory behaviours, especially aerial basking. This impediment may be especially pronounced in males since they invest more in courtship and mate searching than females. Thus, this impediment could contribute to the steep decrease in growth rate observed in males at the onset of sexual maturity (Bulté and Blouin-Demers 2009). I found that juvenile females kept T_b within T_{set} more than males and adult females in June, July, and August, but not in May and September. The lower accuracy of thermoregulation of males during the months of June, July and August is unlikely to stem from a conflict between thermoregulation and growth because northern map turtles, as most temperate emydid, mate in spring (April and May) and in autumn (September and October)(Ernst et al. 1994). The difference in the accuracy of thermoregulation between males and juvenile females can be explained from a life-history perspective. Immature females are expected to maximize growth to reach maturity early to decrease the probability of death before maturity (Congdon et al. 1993). Maintaining T_b within the range that optimizes energy assimilation (i.e. T_{set}) should promote faster growth. In contrast, mature males are not growing and, during summer, are not mating. Thus, the benefit of thermoregulation may not be as important in males during the summer. Contrary to my findings, I expected to find the most important discrepancy in the accuracy of thermoregulation between mature males and immature females during the mating season. Spermatogenesis occurs in fall in temperate turtles (Gist et al. 2002, Meylan et al. 2002) and accurate thermoregulation during that period may accelerate spermatogenesis. Thus, the benefit of thermoregulation in terms of spermatogenesis may be higher than the potential cost in terms of lost mating opportunities.

Overall my results do not support the notion that male reproductive activities involve an important thermoregulatory cost contributing to the development of SSD. My study is among the first to investigate the links between thermoregulation and SSD (but see also Brown and Weatherhead, 1999). Although comparing different sexes and age groups provided good insights into these links, an experimental approach such as manipulating steroid hormones levels via castration (e.g. Cox and John-Alder 2005) would provide a more direct test of the effect of reproductive behaviour on thermoregulation. Unfortunately, such manipulation is challenging on turtles with a hard carapace.

Thermal significance of basking

Aerial basking is a very conspicuous behaviour in many aquatic turtles (Boyer 1965) and is assumed to play an important thermoregulatory role. Very few studies, however, have investigated the thermoregulatory benefit of basking by directly measuring internal T_b in free ranging freshwater turtles (Manning and Grigg 1997). The thermoregulatory role of basking is thus unclear. Manning and Grigg (1997) found that *Emydura signata*, a turtle exhibiting aerial basking behaviour, rarely raised its T_b above water temperature. Manning and Grigg (1997) thus concluded that basking behaviour has no thermoregulatory function in this species and argued that this may be the case in most small aquatic turtles. My results contrast with these findings. Northern map turtles raise their T_b above S_{max} on a daily basis. For instance, in May map turtles kept their T_b on average 4 to 6°C above S_{max} for six to seven hours per day. The daily maximum T_{gain} during that period was on average 17°C and even during the warmest month the maximum daily T_{gain} were high (~10°C). Aerial basking is actually necessary for map turtles to reach their optimal temperature for energy assimilation (i.e. T_{set}) because water temperature is always cooler than the optimal range for assimilation. Although I cannot say with confidence that the primary goal of basking is thermoregulatory, northern map turtles certainly derive a thermal benefit from this conspicuous behaviour. Interestingly, however, their overall T_b closely match S_{max}. Nonetheless, it would be erroneous to conclude that map turtles are thermoconformers because at night map turtle T_b were below S_{max} while during the day they were above S_{max}. Without aerial basking, the mean T_b of map turtles would be below S_{max}. My findings support the idea that basking plays an important thermoregulatory role in northern map turtles, but more studies are necessary to confirm the generality of this phenomenon. Basking likely serves other purposes as well, such as enhancing vitamin metabolism (Ferguson et al. 2003), desiccating leeches (Ernst 1971), and creating fevers to fight infection (Monagas and Gatten 1983).

Table 4-1: Summary of repeated measures ANOVAs testing for the effects of group and month on body temperature (T_b) and the accuracy of T_b (d_b) for adult male, juvenile female, and adult female northern map turtles from Lake Opinicon, Ontario, Canada.

Response variables	**Factors**	**DF**	***F***	***P***	***R*²**
Body temperature (T_b)	Full model	62,185	28.98	<0.0001	0.88
	Group	2,185	3.05	0.056	
	Month	4,185	431.47	<0.0001	
	Group*Month	8,185	1.23	0.28	
Accuracy of T_b (d_b)	Full model	62,185	31.08	<0.0001	0.89
	Group	2,185	2.63	0.082	
	Month	4, 185	465.14	<0.0001	
	Group*Month	8, 185	1.2	0.3	

Table 4-2: Summary of repeated measures ANOVAs testing for the effects of sex and month on the thermal gain of basking, the percentage of time body temperature is within the preferred range (% $T_b = T_{set}$), and the percentage of time spent basking (% $T_b > S_{max}$) for adult male, juvenile female, and adult female northern map turtles from Lake Opinicon, Ontario, Canada.

Response variables	**Factors**	**DF**	***F***	***P***	***R*²**
Thermal gain of basking	Full model	62,185	4.5	<0.0001	0.54
(log-transformed)	Group	2,185	4.64	0.014	
	Month	4,185	58.45	<0.0001	
	Group*Month	8,185	1.93	0.057	
% $T_b = T_{set}$	Full model	62,185	7.95	<0.0001	0.68
(arcsin transformed)	Group	2,185	4.65	0.0142	
	Month	4,185	98.38	<0.0001	
	Group*Month	8,185	1.96	0.054	
% $T_b > S_{max}$	Full model	62,185	3.36	<0.0001	0.47
(arcsin transformed)	Group	2,185	3.58	0.03	
	Month	4, 185	18.51	<0.0001	
	Group*Month	8, 185	2.99	0.003	

Figure 4-1 Conceptual diagram illustrating possible interactions between body size and body temperature.

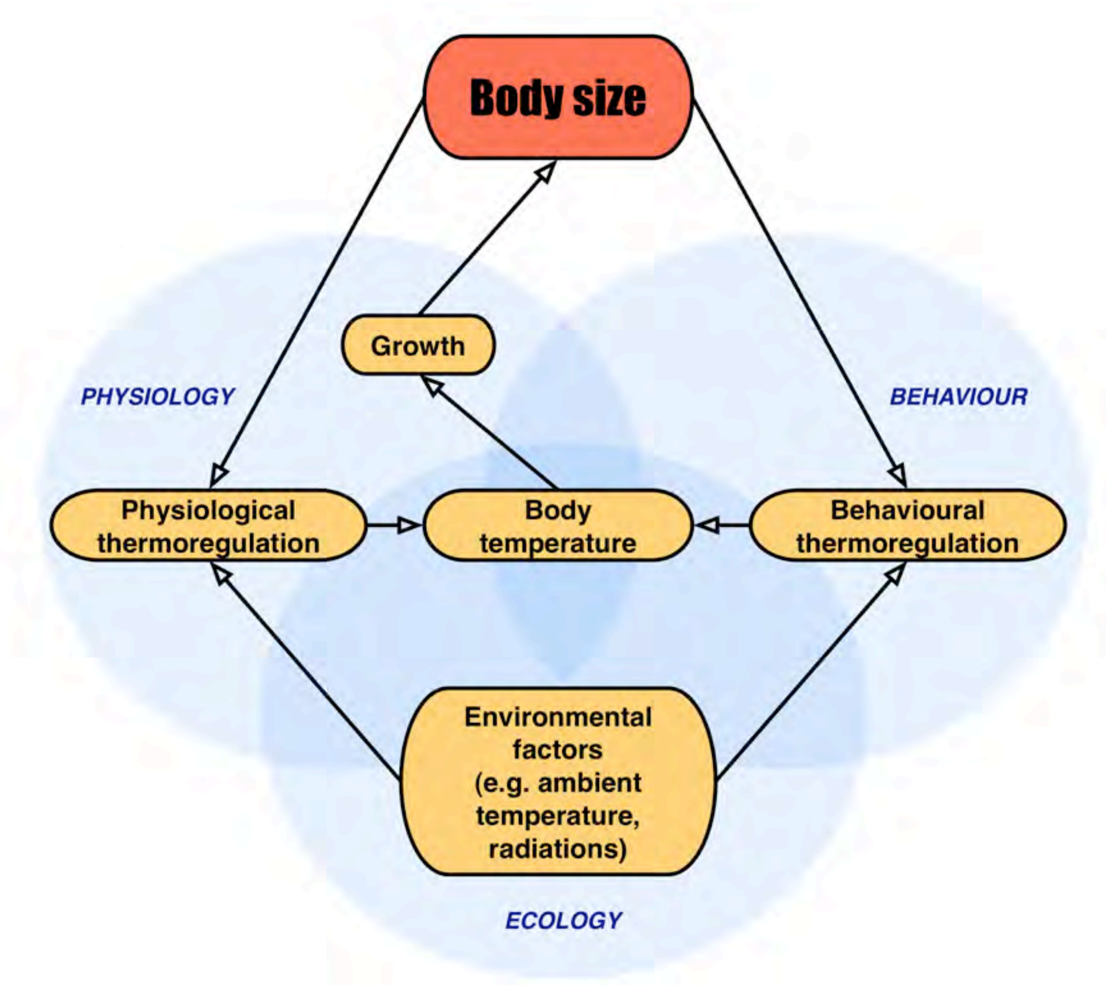


Figure 4-2**:** Adult male (left) and adult female (right) northern map turtles displaying typical aerial basking behaviour in Lake Opinicon, Ontario, Canada. Note the extreme sexual size dimorphism.

Figure 4-3**:** A) Monthly average body temperatures of northern map turtles from Lake Opinicon, Ontario, Canada compared to maximum and mean surface water temperatures. B) Hourly average body temperatures of northern map turtles from May to September compared to hourly maximum and mean water surface temperatures for the same period.

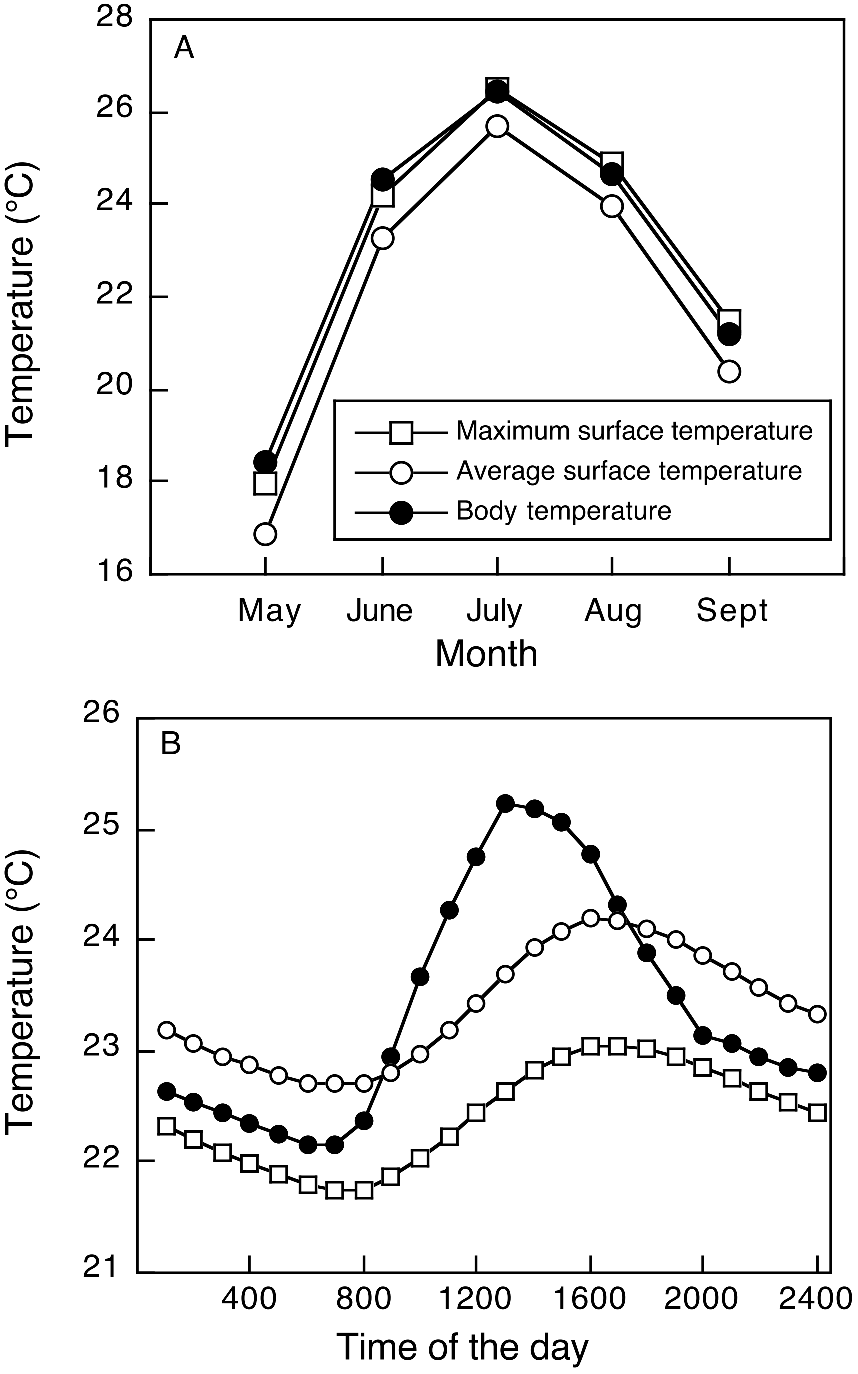


Figure 4-3**:** Monthly average accuracy of thermoregulation (d_b; panel A) and the percentage of time when body temperature is within the preferred range ($T_b = T_{set}$; panel B) for adult female, immature female, and adult male northern map turtles from Lake Opinicon, Ontario, Canada. Error bars indicate one standard error. Group labelled with different letter within each month letter are statistically different.

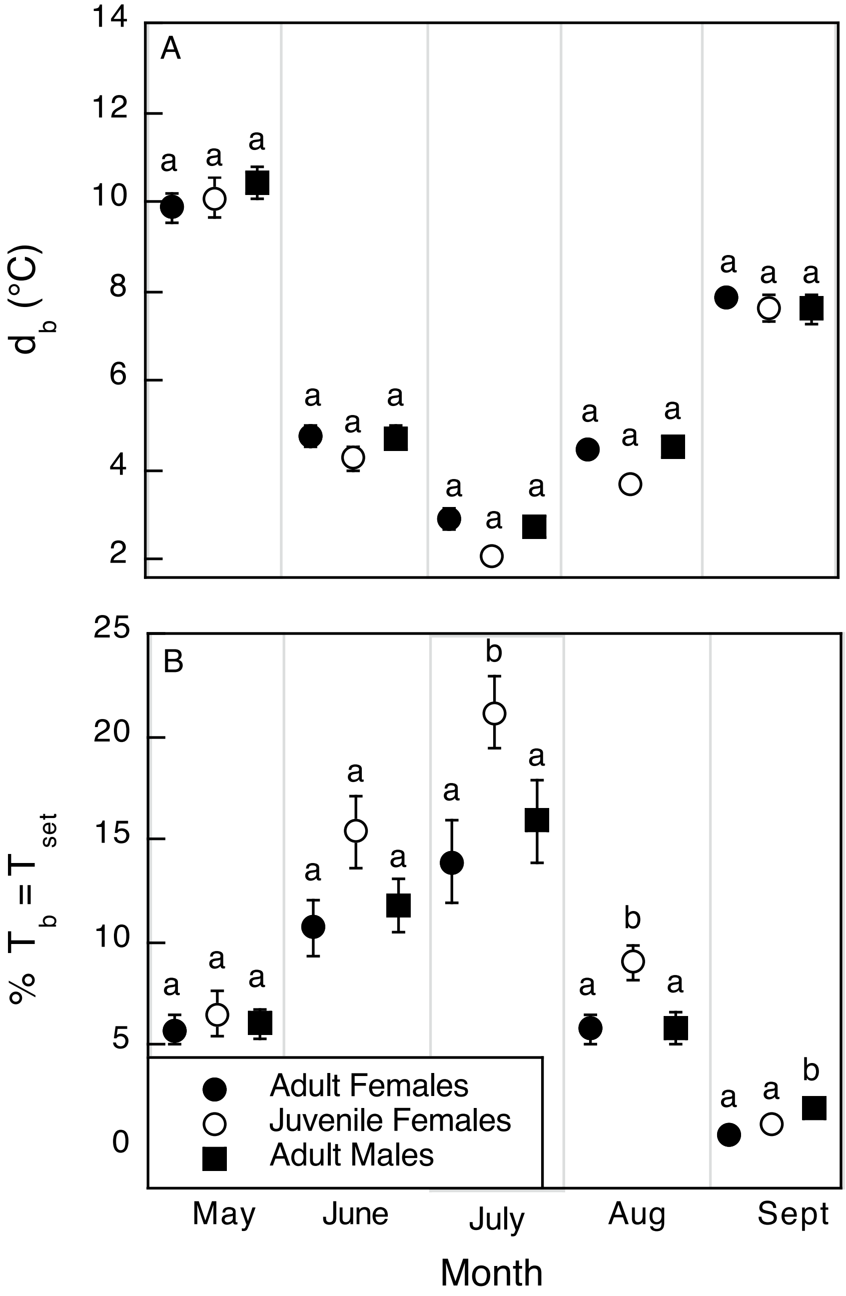


Figure 4-4: Average daily maximum body temperature (panel A) and daily range of body temperatures (panel B) between May and September in northern map turtles from Lake Opinicon, Ontario, Canada. Error bars indicate one standard deviation. Group labelled with different letter are statistically different.

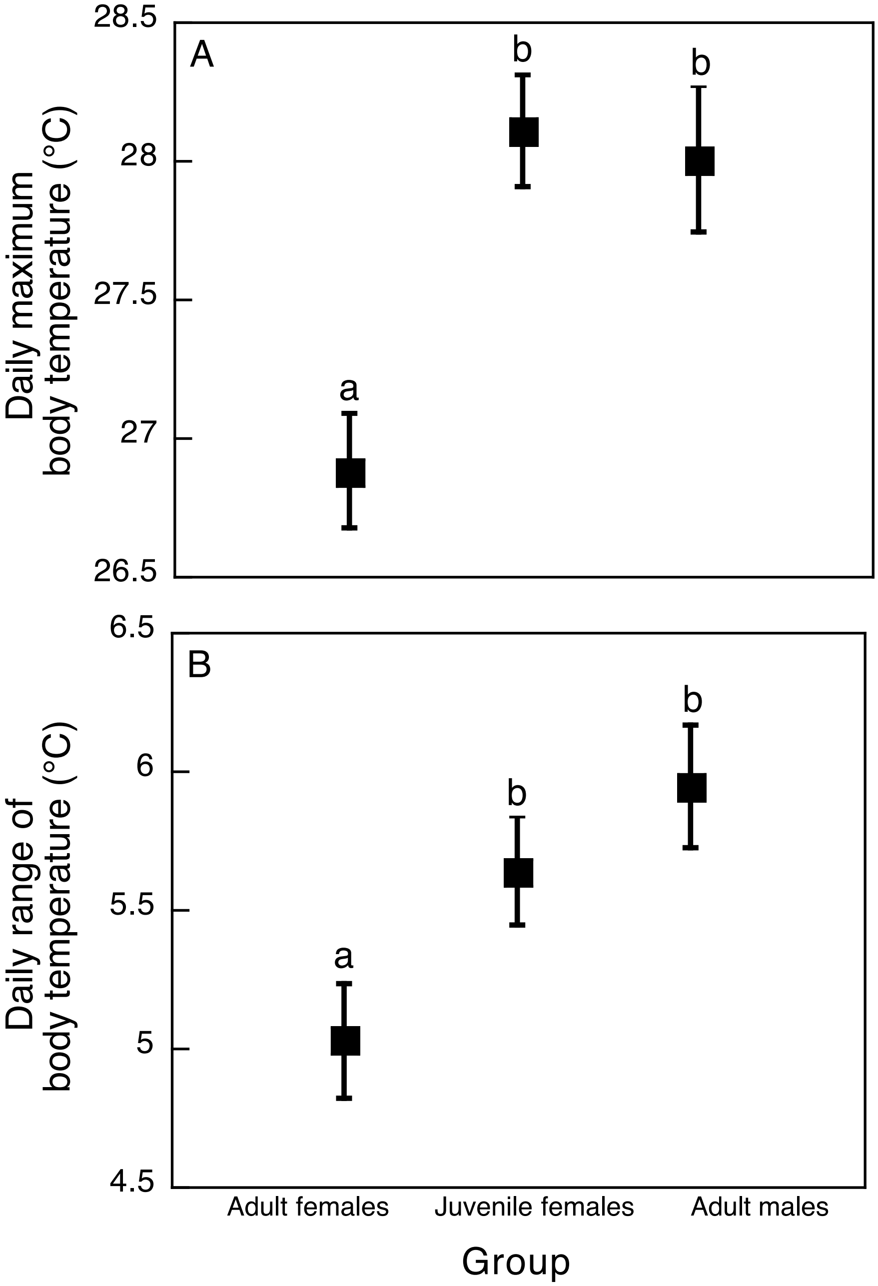


Figure 4-5**:** Monthly average percentage of time spent basking (%$T_b > S_{max}$; panel A) and thermal gain of basking (T_{gain}; panel B) in adult female, immature female, and adult male northern map turtles from Lake Opinicon, Ontario, Canada. Error bars indicate one standard error. Group labelled with different letter within each month letter are statistically different.

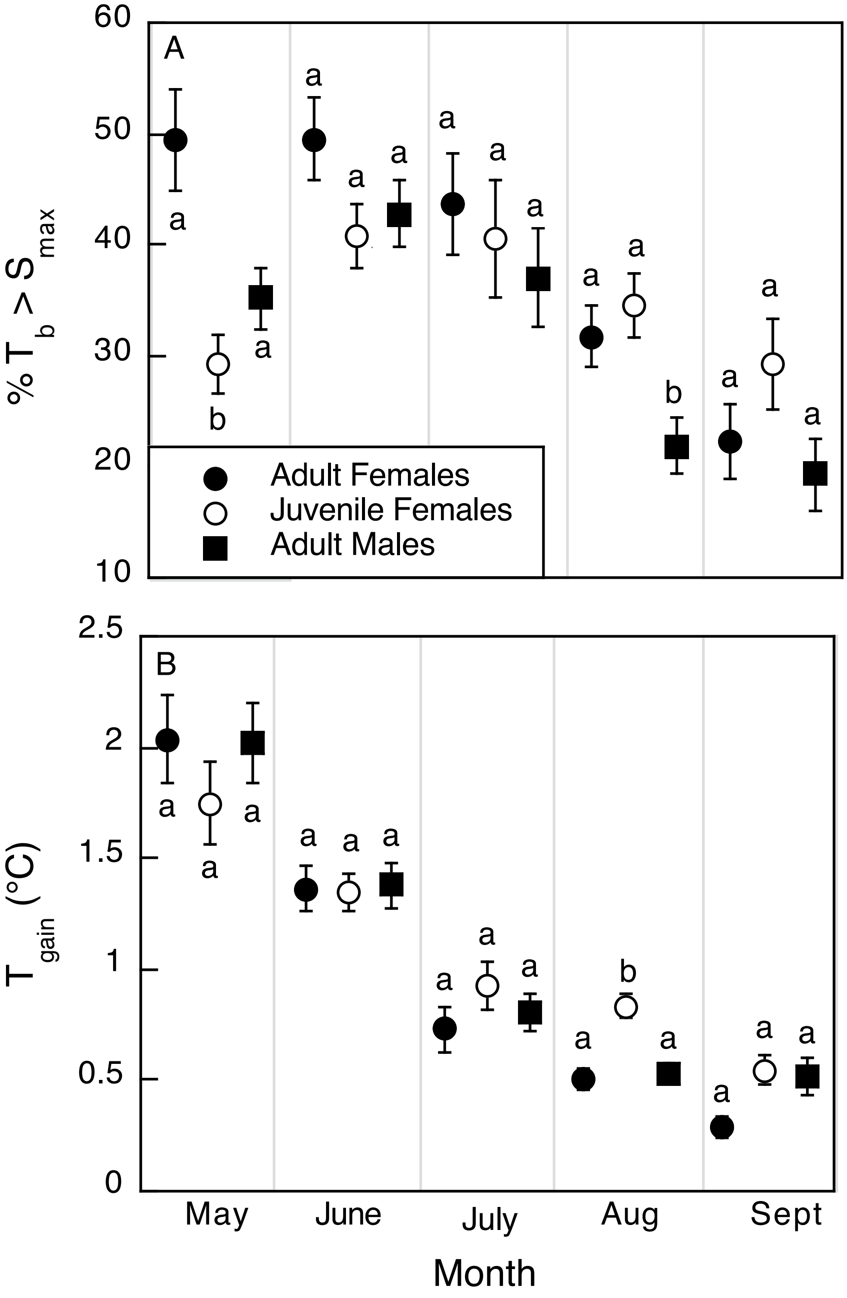
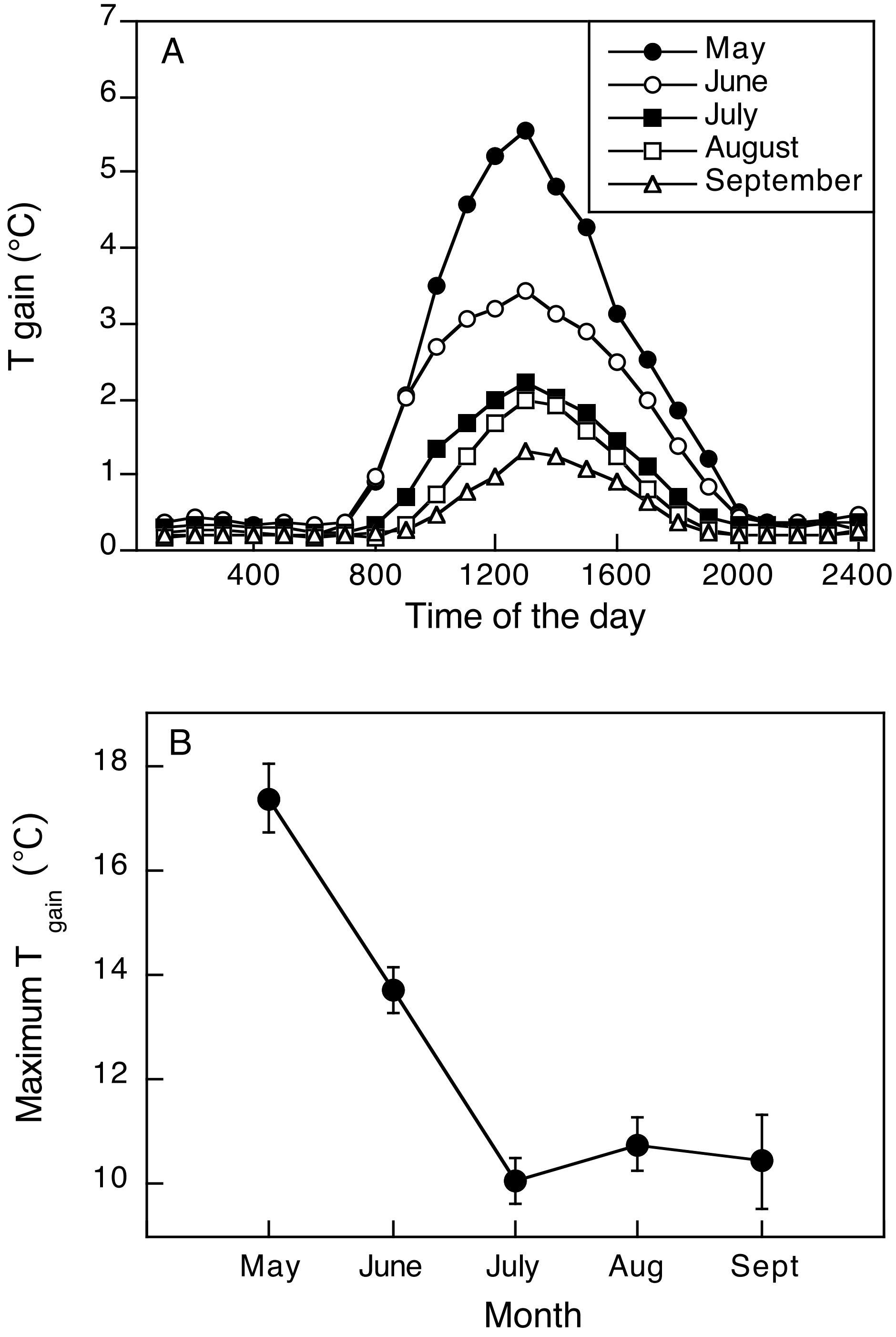


Figure 4-6**:** A) Daily average thermal gain of basking (T_{gain}) for every month of the active season in northern map turtles from Lake Opinicon, Ontario, Canada. B) Average daily maximum T_{gain} for every month of the active season.



CONCLUSION

Sexual size dimorphism is a very common yet complex phenomenon. Evolutionary ecologists have been interested in SSD for many decades and the number of published studies on SSD has been steadily increasing (Blanckenhorn 2005). Studies on SSD are conducted at all levels of biological organisation: from sex specific expression of size related genes (Badyaev 2002) to broad scale patterns of interspecific variation in SSD (Fairbairn 1997, Szekely et al. 2004). The purpose of my thesis was to investigate the ecological causes and consequences of sexual dimorphism in a population of northern map turtles. I used a variety of approaches to test hypotheses about SSD as well as sexual dimorphism in trophic morphology.

Collectively, my thesis provides novel ideas on the ecophyiological consequences of SSD, particularly regarding the interaction among size, growth, and thermoregulation (Chapter 4) as well as the consequences of bimaturation on the metabolic cost of growth (Chapter 3). In addition, chapter 2 offers compelling evidence for the indirect link between trophic morphology dimorphism (TMD), reproductive roles, and SSD. These studies can now serve as a basis for manipulative experiments such as castration studies conducted on lizards (e.g.Cox and John-Alder 2005, Cox et al. 2006, John-Alder et al. 2007). For instance, combining castration and bio-logging would permit a direct test of the hypothesis that a conflict between reproduction and thermoregulation is affecting growth and the expression of SSD. Castration experiments would also permit the inhibitory effect of testosterone on head size development in males to be awnsered. Such experiments would greatly improve our understanding of the physiological mechanisms regulating the expression of SSD and TMD. In chapter 2, I suggested that the lower intrinsic rate of approach of the asymptotic size typically found in the larger sex (Stamps 1993) could be a consequence of the metabolic cost of growth. My data did not support this suggestion, but our study system was not ideal and logistical constraints limited our statistical power. This hypothesis is, however, worth revisiting with a more powerful study design and with a species better suited for respirometry studies (e.g., lizards born in captivity).

APPENDIX ONE

Abstracts of other publications directly resulting from this thesis.

Bulté, G. and G. Blouin-Demers (2006). Cautionary notes on the descriptive analysis of performance curve in reptiles. Journal of Thermal Biology. 31: 287-291.

Abstract

Organismal performance curves are important functions for the study of reptilian ecology and evolution, but their interpretation can be affected strongly by the choice of analytical approach. We first use an example from the literature to demonstrate that excluding biologically meaningful data alters the description of performance and leads to nonsensical inferences. We then use fictional data to show that linear models (ANOVA) commonly used in the descriptive analysis of performance curves can also be biologically misleading or can lack biological relevance. Our examples demonstrate that fitting non-linear curves to performance data is more meaningful and avoids erroneous representation and interpretation of these important biological functions.

Ben-Erza E, G. Bulté and G. Blouin-Demers (2008). Are preferred basking temperature and locomotor performances coadapted in northern map turtles (*Graptemys geographica*)? Journal of Herpetology, 42: 322-331

Abstract

We tested a common prediction of the thermal coadaptation hypothesis in the northern map turtle (*Graptemys geographica*), an aquatic emydid with pronounced aerial basking. We measured the effect of body temperature on two locomotor performances (swimming and righting) to determine optimal temperature of performance (T_o) for each trait. According to the thermal coadaptation hypothesis, the preferred body temperature range (T_{set}) of ectotherms should match T_o of thermally sensitive traits that influence fitness. However, we predicted that preferred basking temperature and locomotor performance of map turtles would not be coadapted, given that the former occurs on land and the latter in water. We also tested for an ontogenetic shift in performance curves. We found that adult map turtles have a wide T_{set} ($19^oC – 30^oC$), both hatchlings and adults can achieve near-maximum performance over a wide range of temperatures, and an ontogenetic shift is present for swimming but not for righting. While T_o for the two locomotor performances of adult turtles were within T_{set}, the large range of T_{set} coupled with the wide breadth in locomotor performance makes falsifying or supporting the coadaptation hypothesis difficult for these traits in map turtles. Other metabolic and physiological processes need to be considered to understand more fully thermal coadaptation in aquatic emydids.

Bulté, G. and G. Blouin-Demers (2008). Northern map turtles (*Graptemys geographica*) derive energy from the pelagic pathway through predation on zebra mussels (*Dreissena polymorpha*). Freshwater Biology 53: 497-508

Summary

1. Zebra mussels (*Dreissena polymorpha*) derive their energy from the pelagic energy pathway by filtering plankton**.** Because zebra mussels occur in high densities in littoral habitats, they potentially constitute an important trophic link between littoral consumers and pelagic energy sources. Northern map turtles (*Graptemys geographica*) are widespread in North America and consume zebra mussels.
2. We used stable isotopes analyses to quantify the flow of energy from the pelagic pathway to northern map turtles and to infer the contribution of zebra mussels to map turtle biomass. We then built a bioenergetic model to estimate the annual intake of zebra mussels by northern map turtles in Lake Opinicon, Ontario, Canada.
3. Stable isotopes analyses indicated that zebra mussels constitute between 0 and 14% of the diet of males and between 4 and 36% of the diet of females. Assuming that zebra mussels account for all of the pelagic contribution, we estimated that map turtles consume 3200 kg of zebra mussels annually. Because female map turtles are much larger than males and consume more zebra mussels, they are responsible for 95% of the zebra mussel biomass ingested annually.
4. The pelagic pathway supports an important part of the standing crop biomass of map turtles in Lake Opinicon. We highlight the importance of freshwater turtles in lake ecosystems. Unravelling the trophic interactions mediated by freshwater turtles will lead to a more integrated picture of lake ecosystems.

Carrière, M.A., G. Bulté and G. Blouin-Demers (2008). Spatial ecology of Northern Map Turtles (*Graptemys geographica*) in lotic and lentic habitats. Journal of Herpetology, *in press*.

Abstract

Lentic (i.e., lake) and lotic (i.e., river) environments differ in several biotic and abiotic variables such as water velocity, productivity, thermal regimes, and depth. These variables can interact with important factors such as sex, body size, and life-history stage to shape the spatial ecology of aquatic animals such as freshwater turtles. We used radio-telemetry to study seasonal movement patterns and home range size of juvenile and adult Northern Map Turtles (*Graptemys geographica*) both in a small lake and in a large river in eastern Ontario, Canada. Adult females in the lotic environment moved longer distances and had larger home ranges than conspecifics from the lentic environment. Males and juvenile females at each site had similar patterns of space use. A seasonal effect on movement was only apparent for adult females in the lotic environment in which adult females moved longer distances during the nesting season. Differences in swimming abilities due to a larger body size, in natal homing, or in nest site availability are potential factors explaining the site difference in the spatial ecology of adult females. Our findings illustrate the complexity of interactions shaping patterns of space use by aquatic reptiles.

Bulté, G, M.-A. Carrière et G. Blouin-Demers. 2009. Impacts of recreational powerboating on the northern map turtle (*Graptemys geographica*). Aquatic Conservation: Marine and Freshwater Ecosystems. *In press*

Abstract

1. Recreational boating is growing in popularity in North America. This activity is known to have lethal and sub-lethal effects on aquatic wildlife and freshwater turtles may be particularly sensitive to this activity.
2. In this study, we report on patterns of traumatic injuries inflicted by powerboat propellers to northern map turtles (*Graptemys geographica*) from two sites differing in boat traffic intensity in Ontario, Canada.
3. We assessed the relative vulnerability of turtles as a function of age and sex, in light of seasonal patterns in boat traffic as well as detailed sex and age specific movement patterns, habitat use, and basking behaviour obtained by radio-telemetry. We also conducted population viability analyses (PVA) to evaluate the potential demographic consequences of mortality induced by powerboats.
4. The prevalence of propeller injuries was much higher in adult females than in adult males and juvenile females. Patterns of movement, habitat use, and aquatic basking indicated that adult females are more exposed to collision with boats. PVA showed that boat induced mortality in adult females could lead to rapid population extinction if the risk of mortality when hit by a boat is >10%.
5. Collectively, our results showed that recreational powerboating is a serious threat to northern map turtles, even under moderate boat traffic. We stress the need to adopt measures restricting boat traffic in areas important to turtles.

APPENDIX TWO

Abstracts of publications arising from graduate courses

Bulté, G., A. C. Plummer, A. Thibaudeau and G. Blouin-Demers (2009). Infection of yarrow spiny lizards (*Sceloporus jarrovii*) by chigger mites and malaria in the Chiricahua mountains (AZ). Southwestern Naturalist. 54: 204-207.

Abstract

We measured prevalence of malaria infection and prevalence and intensity of chigger infection in Yarrow's spiny lizards (*Sceloporus jarrovii*) from three sites in the Chiricahua Mountains of southeastern Arizona. Our primary objective was to compare parasite load among sites, sexes, and reproductive classes. We also compared our findings to those of previous studies on malaria and chiggers in *S. jarrovii* from the same area. Of lizards examined, 85 and 93% were infected by malaria and chiggers, respectively. Prevalence of malaria was two times higher than previously reported for the same area, while prevalence of chiggers was similar to previous findings. Intensity of chigger infection was variable among sites, but not among reproductive classes. The site with the highest intensity of chigger infection also had the most vegetative cover, suggesting that this habitat was more favorable for non-parasitic adult chiggers.

Cooke S.J., C.D. Suski, S. E. Danylchuk, A.J. Danylchuk, M.R. Donaldson, C. Pullen, G. Bulté**, A. O'Toole, K.J. Murchie, T.L. Goldberg, and A.J. Adams. (2008). Effects of capture techniques on the physiological condition of bonefish *Albula vulpes* (Linnaeus, 1758) evaluated using field diagnostic tools. Journal of Fish Biology. Journal of Fish Biology 73:1351–1375.**

A study was conducted on bonefish *Albula vulpes* in The Bahamas to assess the utility of portable physiological diagnostic tools (i-STAT analyser with E3+ ion and haematology cartridge, ACCU-CHEK glucose meter and Lactate Pro lactate meter) for field physiology applications in remote locations. Physiological values derived from portable diagnostic tools were significantly related to values obtained from standard laboratory techniques [glucose (r^2 = 0.96), packed cell volume (PCV; r^2 = 0.33), Na+ (r^2 = 0.28), K+ (r^2 = 0.71) and Cl- (r^2 = 0.15)]. Actual values (i.e. intercepts), however, tended to deviate slightly between the two techniques. Nonetheless, these tools showed promise for documenting relative differences among fishes experimentally exposed to treatments inducing different levels of 'stress'. These tools were then used to characterize the effects of different capture techniques on the stress response of *A. vulpes*. *Albula vulpes* captured in seines and then temporarily held in pens were physiologically sampled between 1 and 45 min postcapture to evaluate postcapture stress dynamics. Blood glucose and lactate as well as PCV and haemoglobin (Hb) increased rapidly after capture but stabilized at maximal values by c. 20 min postcapture. When angled, larger *A. vulpes* took longer to exhaust and land than did smaller individuals. In addition, there was a positive relationship between the magnitude of increase in lactate and the duration of the angling event, implying that anglers can reduce stress by minimizing the duration of the fight. Fish sampled before and after a simulated angling treatment displayed clear increases in blood lactate, K+, PCV and Hb, providing some of the first data on how individual *A. vulpes* respond to angling stress. In summary, this study revealed that techniques are now available for conducting field physiological studies on *A. vulpes* and possibly other species in remote locales, and that haematological and biochemical indicators of physiological disturbance vary with the intensity of the angling event.

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