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

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Abstract: Sexual dimorphism in body size and in trophic morphology are common in animals and are often concordant with patterns of habitat use and diet. 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. Intersexual differences in diet and habitat use are common in size dimorphic reptiles. In this study, we investigated factors contributing to intersexual differences in diet and habitat use are common in size dimorphic reptiles. In this study, we investigated factors contributing to intersexual differences in diet and habitat use in a population of northern map turtles (*Graptemys geographica* (Le Sueur, 1817)) from Ontario, Canada. Using radiotelemetry, we showed that in a lake map turtles do not exhibit intersexual differences in habitat use, in contrast to river populations. Patterns of habitat use were also inconsistent with prey distribution. The lack of intersexual habitat use differences in our lake population, despite marked differences in prey distribution, also indicated that intersexual habitat use differences documented in river populations are a consequence of sexual dimorphism in swimming capacity. Using stable isotope analysis and fecal analysis, we found a large dietary overlap between males and females, indicating no intersexual competition for food. Patterns of prey selection in females, however, were concordant with the reproductive role hypothesis.

Résumé : Le dimorphisme sexuel de la taille corporelle et de la morphologie trophique est commun chez les animaux et s'accorde souvent avec les patrons d'utilisation de l'habitat et de régime alimentaire. Les facteurs proximaux qui expliquent ces différences intersexuelles d'utilisation de l'habitat sont, cependant, difficiles à démêler parce que ces différences peuvent provenir du dimorphisme sexuel ou être causées par la compétition entre les sexes. Les différences intersexuelles de régime alimentaire et d'utilisation de l'habitat sont communes chez les reptiles qui ont un dimorphisme de taille. Nous examinons, dans notre recherche, les facteurs qui contribuent aux différences intersexuelles de régime alimentaire et d'utilisation de l'habitat dans une population de tortues géographiques (*Graptemys geographica* (Le Sueur, 1817)) de l'Ontario, Canada. Par radiotélémétrie, nous montrons que les tortues géographiques d'un lac n'ont pas de différences sexuelles d'utilisation de l'habitat, contrairement aux populations de rivières. Les patrons d'utilisation de l'habitat dans la population lacustre, malgé des différences marquées dans la répartition des proies, indique aussi que les différences intersexuelles d'utilisation de l'habitat observées chez les populations de rivières sont une conséquence du dimorphisme sexuel de la capacité de nage. Une analyse des isotopes stables et une analyse des fèces révèlent un important chevauchement alimentaire entre les mâles et les femelles, ce qui indique une absence de compétition intersexuelle pour la nourriture. Les patrons de sélection des proies des femelles s'accordent cependant avec l'hypothèse du rôle reproducteur.

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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 fertility is typically held responsible for the evolution and maintenance of such

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¹Corresponding author (e-mail: gbult087@uottawa.ca). ²Present address: Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada. 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 Mittelbach 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 and Wall 2004).

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

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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 (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 (e.g., Bulté et al. 2008), but prey distribution may be a proximate cause of habitat use divergence if the preferred prey of each sex occur in different habitats (e.g., 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 may 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 study, we identify the factors responsible for intersexual differences in habitat use and diet in a population of northern map turtles (Graptemys geographica (Le Sueur, 1817); also known as common map turtles). 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 2000), and greater bite force (Bulté et al. 2008). The sexual dimorphism in body size and trophic morphology is accompanied by intersexual differences in diet (Vogt 1981; Lindeman 2006b) and habitat use (Pluto and Bellis 1986; Carrière 2007). Pluto and Bellis (1986) found that female northern map turtles use habitats with higher current velocity, deeper water, and farther from shore than males. Other lotic turtles exhibiting SSD comparable with 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.

We quantified habitat use, diet composition, and prey size for adult males, juvenile females overlapping in size with males, and adult female northern map turtles. Our 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. We 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, then no difference in habitat use should be detected in a small lake. Alternatively, if habitat use differences are a consequence of dietary differences, then 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; juvenile females have a diet intermediate between that of adult males and that of adult females (Lindeman 2006b). Our second objective was to determine the presence of intersexual dietary niche partitioning in northern map turtles. We 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). We compared the size of molluscan prey consumed with fecal analysis and diet composition with stable isotope analysis. We predicted that if the competition hypothesis applies, then 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

We studied northern map turtles between May 2004 and September 2007 in Lake Opinicon $(44^{\circ}34'N, 76^{\circ}19'W)$ 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 that is part of the Rideau Canal waterway linking the cities of Ottawa and Kingston. We captured northern map turtles with basking traps and by hand while snorkelling.

Radiotelemetry and habitat use

We tracked 53 northern map turtles with radiotelemetry. 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). We 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 nontoxic aquarium silicone to prevent snagging on aquatic vegetation. Individual turtles were followed for one to three active seasons. We located each individual every 2-3 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 version 9.0 (Environmental Systems Research Institute, Inc. 2000).

We used water depth and distance to shore as our metrics of habitat use. Depth was obtained from a bathymetric chart of the lake. We are aware that males and females can differ on 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, most biotic (e.g., macrophyte cover, prey distribution) and abiotic (e.g., temperature, dissolved oxygen) variables in lakes are dictated by either depth or distance to shore. Thus, our two habitat variables should integrate most habitat variables likely to vary between sexes or ontogenetically. We broke down the depth of the lake into three classes (0-2, 2-4, 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: $y_i = \ln(x_i/x_i)$, where x_i 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_i). We used the class >4 m as x_i because this class comprised <2% of the turtle observations. We excluded from the depth analysis all the observations for which the turtles were basking out of the water (692 of 2963 observations).

Prey distribution

To estimate the relative abundance and the size distribution of available prey in the lake, we counted and measured prey items in sites selected at random in the lake. We divided the lake in two zones for sampling. The first zone was within 5 m of the shoreline and is referred to as the nearshore 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 nearshore habitat and 12 in the openwater habitat. All the locations sampled in the nearshore habitat were in <1.5 m of water, while the points in the open-water habitat ranged in depth from 1 to 6 m. We restricted our sampling to three prey items: trap-door snails (*Viviparus georgianus* (I. Lea, 1834)), zebra mussels (*Dreissena polymorpha* (Pallas, 1771)), and Trichoptera (Leptoceridae). Collectively, these three prey items make up the vast majority of the diet of northern map turtles at our study site (see Results). At each sampling location, we collected and measured all prey items present in a 0.25 m² quadrat. Trichoptera larvae were not abundant enough to be detected with our sampling effort and, consequently, our analysis of prey distribution is restricted to zebra mussels and trap-door snails.

Prey size

We reconstructed prey size from mollusc structures found in the feces of turtles (Hamilton 1992; Tucker et al. 1995). We collected fecal 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, we counted the number of trapdoor snail opercula and zebra mussel septa and we measured the smallest and the largest structure (operculum and septum). To reconstruct the size of ingested molluscs, we determined the relationship between operculum length (for snails) or septum length (for zebra mussels) and shell length for 90 snails and 120 zebra mussels collected at our study site. We then predicted the size of the ingested molluscs from the size of the structures (opercula or septa) present in the feces. Operculum length ($R^2 = 0.95$, p < 0.0001, SL = -0.878 + 1.906 \times operculum length) and septum length ($R^2 = 0.90$, p < 0.0001, SL = 1.07 + 8.172 × septum length) were both strong predictors of shell length. Only a few fecal samples from males (6 of 41) contained zebra mussel septa. Thus, the analyses related to prey size were restricted to snails for males. For each individual, we calculated the prey size spectrum of each prey by subtracting the length of the smallest ingested prey from the length of the largest.

We 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 our case plastron length 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, we used the predicted maximum prey size obtained from the cyclical regressions and compared it with the prey size distribution sampled in each habitat.

Stable isotope analysis, diet composition, and niche overlap

To determine the diet composition of northern map tur-

tles, we used stable isotope analysis. In temperate lakes, δ^{13} C can be used to discriminate pelagic consumers (e.g., mussels) from benthic consumers (e.g., Trichoptera and snails) (Post 2002). In addition, δ^{15} N can be used to differentiate consumers based on their trophic level (Post 2002). The diet of northern map turtles at our study site is composed almost exclusively of three prey items (Trichoptera, zebra mussels, and trap-door snails).

For the turtles, we measured stable isotope ratios in whole blood. In common sliders (Trachemys scripta (Schoepff, 1792)), 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. We collected blood (0.5 mL) from the caudal vein (Bulté et al. 2006) of males (n = 23) and females (n = 38). We 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, we divided molluscan prey into size classes. For each prey type, we measured the isotopic ratios on composite samples of 10-26 individuals for each size class and site. For the analysis of prey, we 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 $\delta^{13}C$ = $[({}^{13}C/{}^{12}C_{sample})/({}^{13}C/{}^{12}C_{standard}) - 1] \times 1000$. Mean standard deviations for replicates were 0.19‰ for $\delta^{13}C$ and 0.25‰ for $\delta^{15}N$.

We 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 version 1.04 (Phillips and Gregg 2001). To account for trophic fractionation of nitrogen isotopes between trophic levels, we 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, we used a value of +0.23% that was experimentally measured in claws of the common slider (Aresco and James 2005).

To test for niche overlap between males, small females, and large females, we calculated Pianka's niche overlap index (Pianka 1973) with the proportions obtained with the mixing model. Pianka's overlap index varies from 0 to 1, with 1 being complete overlap. We then compared our measured overlap to a null model that represents the expected distribution of overlap indices given the absence of competition. We used the software EcoSim version 7 (Gotelli and Entsminger 2007) to perform 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, then our measured overlap index is expected to be smaller than the null model. For the simulation, we used the algorithm RA3 (Lawlor 1980), which maintains the niche breadth of each group.

Results

Habitat use

Mean distance to shoreline differed between groups (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 that males did not differ from either small or large females (Fig. 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). Nevertheless, a oneway MANOVA indicated that the three turtle groups used the water depth classes (log-ratio-transformed) differently (Wilks' $\lambda = 0.73$, $F_{[4,104]} = 4.31$, p < 0.003). One-way AN-OVAs 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 nearshore habitat and the open-water habitat (Student's t test: $t_{[1,20]} = 0.07$, p = 0.95) and averaged 2592 individuals/m² (range = 0 - 18144, n = 22). The mean density of trap-door snails also did not differ between the nearshore habitat and the open-water habitat (Student's t test: $t_{[1,20]} = 0.61$, p = 0.55) and averaged 35 individuals/m² (range = 0-128, n = 22). For both prey, mean shell length was longer in the nearshore habitat compared with the open-water habitat (zebra mussels: Student's t test: $t_{[1,17]} = 3.48$, p = 0.003; snails: Student's t test: $t_{[1,16]} = 3.05, p = 0.007$). Using the predicted maximum prey size (from the cyclical regressions), we estimated that for males the open-water habitat contained between 7% and 11% more ingestible snails than the near-shore habitat (Fig. 3B). Similarly, for small females the open-water habitat contained between 7% and 22% more ingestible snails and between 36% and 70% more ingestible zebra mussels (Fig. 3A).

Prey size

We examined the feces of 126 individuals ranging from 48 to 242 mm plastron length. 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 1). Over the same range of body sizes (plastron length <135 mm), the maximum size of ingested snails did not differ between males and females (ANCOVA with plastron length as covariate: $R^2 = 0.02$, $F_{[3,62]} = 0.514$, p = 0.95; Fig. 4). The spectrum of prey size ingested increased with body size in both sexes (Table 1).

Diet composition and niche overlap

Because both types of mollusc prey are represented by a large size spectrum, we 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: $\chi^2 =$

Fig. 1. Mean distance to shore for radio-tracked northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada. Letters indicate statistically significant differences.



Fig. 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.



3.71, p = 0.16; δ^{13} C: $\chi^2 = 3.71$, p = 0.16). Consequently, we pooled all the size classes for the mixing model. The three prey items did not overlap in isotope ratio (Fig. 5). Zebra mussels had a very negative δ^{13} C relative to snails and Trichoptera larvae, and trap-door snails had a more positive δ^{15} N relative to Trichoptera larvae (Fig. 5). One-way AN-OVAs 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. 6). However, large females ate more zebra mussels than males and small females (Fig. 6).

To test for dietary niche overlap, we 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

Fig. 3. Predicted proportions of ingestible molluscs as a function of body size for (A) female and (B) male northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada. Black lines indicate trap-door snails (*Viviparus georgianus*) and gray lines indicate zebra mussels (*Dreissena polymorpha*). Solid lines indicate the open-water habitat and broken lines indicate the nearshore habitat.



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

Our 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, we found that northern map turtles exhibit little intersexual divergence in habitat use. Although some intersexual dietary differences were apparent, we could not detect any evidence of intersexual competition for food.

Our 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 showed intersexual differences in habitat use with females using deeper and faster moving water. We found that small females (overlapping in body size with males) tended to stay in shallow water and close to shore compared with 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

Prey species	Dependant variables	n	р	R^2
Female zebra mussels (Dreissena polymorpha)	Maximum length*	22 of 41	< 0.0001	0.58
	Size spectrum	43	< 0.0001	0.21
Female trap-door snails (Viviparus georgianus)	Maximum length*	26 of 77	< 0.0001	0.91
	Size spectrum	85	< 0.0001	0.37
Male trap-door snails	Maximum length*	11 of 41	0.004	0.62
	Size spectrum	41	0.018	0.13

Table 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.

*Maximum prey size was obtained from cyclical regressions.

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



adult females. Because >90% of the observations for each group were made in the 0-2 m zone, however, the difference we found in the use of the 2-4 m zone is unlikely to bear much biological significance. Thus, overall we did not find large habitat use differences between the groups. Nevertheless, we concede that although depth and distance to shore integrate most biotic and abiotic variables in lakes, our design may have failed to detect differentiation in other fine-scale habitat variables.

Although both types of mollusc prey were equally abundant in the nearshore habitat compared with 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





Fig. 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.



this species (Bulté et al. 2008). 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 with 1%) more ingestible trap-door snails than the nearshore habitat (Fig. 3B). The lack of habitat use differences in our 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, Quebec, 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.

Our second objective was to test for intersexual dietary niche partitioning and thus evaluate the importance of intersexual competition. Although we identified differences in diet composition between the groups (e.g., large females consumed more zebra mussels and fewer Trichoptera 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 we found was the consumption of larger snails by large females compared with males and small females. This ability reflects the larger head and stronger bite of large females (Bulté et al. 2008). As females grow, however, they do not specialize on large prey, but instead enlarge the size spectrum of prey that 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 in turtle habitats in general (Congdon 1989; Tucker et al. 1995), we 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 our study suggests low competition, our data do not permit formal rejection of 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 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). On the contrary, 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. 2008). 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, we used stable isotope analysis. Stable isotope analysis is a cruder dietary analysis compared with 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 isotope 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 (e.g., 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.

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