

# The reproductive role hypothesis explains trophic morphology dimorphism in the northern map turtle

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## Summary

1. Sexually dimorphic traits often reflect factors limiting the reproductive success of animals. Thus, most sexually dimorphic traits can be directly linked to the reproductive role of each sex. Sexual dimorphism in trophic structures (e.g. beak, jaws, teeth), however, often lacks a direct link to reproduction.

2. Trophic structures can be linked indirectly to reproductive allocation via energy acquisition. The reproductive role hypothesis (also known as the dimorphic niche hypothesis) posits such an indirect link, but has received heretofore little direct empirical support. We tested this hypothesis in a molluscivorous turtle exhibiting marked female-biased trophic morphology dimorphism.

3. Bite force analysis showed that females have stronger jaws than males and dietary analysis revealed that females ingest snails closer to their maximum biting capacity than males. Body condition of both sexes and reproductive output of females increased with relative head width, indicating that fitness is tightly linked to head size and bite force.

4. Our study provides strong evidence that reproductive role contributes to sexual dimorphism in trophic morphology. Our findings should apply to any animal in which energy intake is limited by trophic morphology.

**Key-words:** bite force, body condition, performance, reproductive output, reproductive role

## 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 they can allocate to the production of gametes (Reiss 1989). Thus, in females natural selection tends to bias the expression of traits associated

with fertility, 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 & 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). 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

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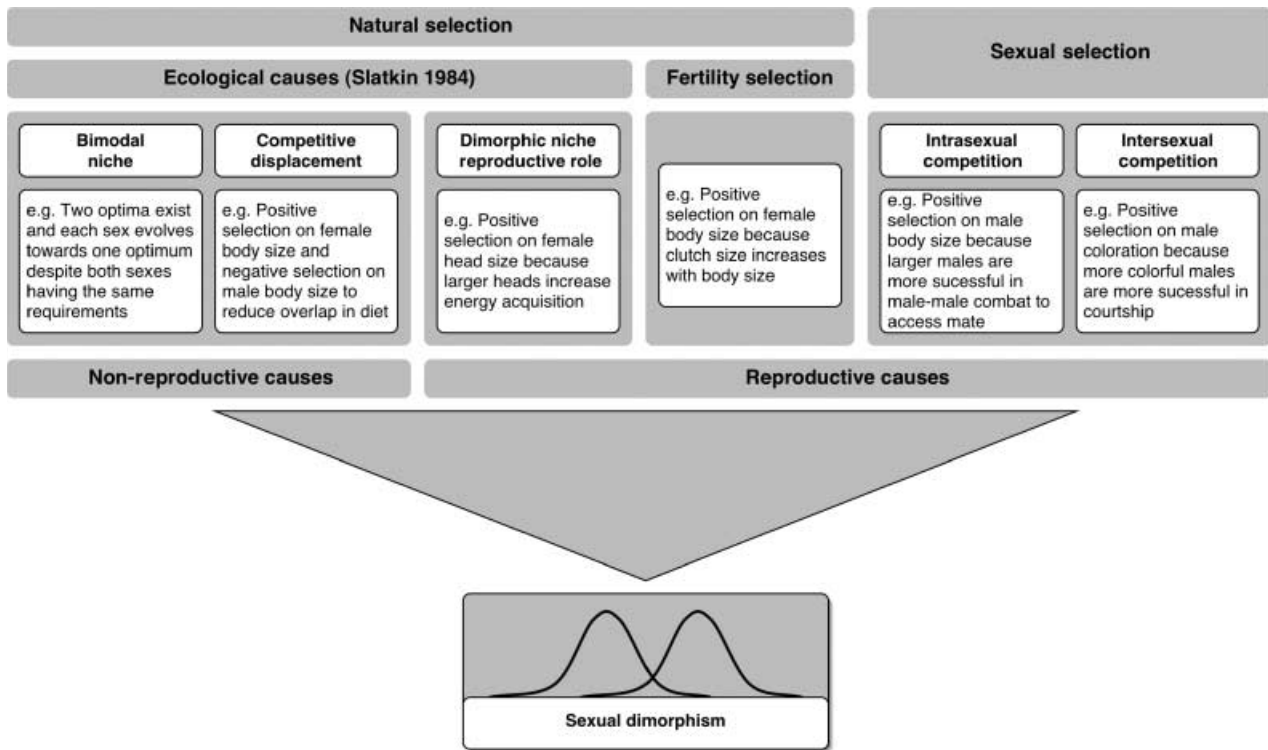


Fig. 1. Ultimate causes for sexual dimorphism with examples.

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 & Rypstra 2002) or the dimorphic niche hypothesis (Slatkin 1984; Hedrick & Temeles 1989). The RRH falls under the umbrella of ecological dimorphism (Fig. 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 turtles as an example, we 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 2000, 2006b). 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 2006b) although exclusive molluscivory can also occur in males (White & Moll 1992). In addition, northern map turtles exhibit the most extreme female-biased sexual size dimorphism in chelonians (Gibbons & Lovich 1990), with females averaging eight to ten times the mass of males. 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, O'Reilly & Richmond 2002). Thus, selection for large head dimensions in female turtles may arise to overcome partly 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.

## Methods

### STUDY SPECIES AND STUDY SITE

We 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 we measured maximum plastron length (PL) with a forestry calliper ( $\pm 0.5$  mm) and head width (HW) with a digital calliper ( $\pm 0.01$  mm). We marked turtles individually by drilling small holes in the marginal scutes.

### BITE FORCE ANALYSIS AND PREY HARDNESS

Bite force was measured in 52 turtles with an isometric Kistler force transducer (type 9023, Kistler Inc., Wintherthur, Switzerland) connected to a Kistler charge amplifier (type 5058a, Kistler Inc.).

We induced turtles to bite forcefully on the free ends of the bite force device (following Herrel & O'Reilly 2006). We measured bite force five times for each turtle, with a short rest (30–40 s) 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.

We 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 faeces 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 (G. Bulté, unpublished data). We collected faeces by keeping turtles individually overnight in plastic bins filled with lake water. Water containing faeces was filtered and the solid phase was preserved in ethanol until examination under a dissecting scope. For each sample, we measured the largest operculum.

To reconstruct snail hardness, we 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 strong predictor of SL ( $R^2 = 0.95$ ,  $F_{(1,88)}$ ,  $P < 0.0001$ :  $SL = -0.878 + 1.906 \times OL$ ). We 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 faeces 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 PL, we used cyclical regressions to partition the data (Thomson *et al.* 1996). This approach involves a series of linear regressions (in our 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, we investigated the relationship between head size and two important measures of fitness: body condition and reproductive output. We 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, Marshall & Uetz 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, Millar & Hickling 2005). Among animals, body condition is correlated with important reproductive traits, such as testis size (Schulte-Hostedde *et al.* 2005) and reproductive output (Brown & Shine 2005; Litzgus, Bolton & Schulte-Hostedde 2008). We calculated body condition only for individuals captured within 3 weeks of emergence from hibernation (i.e. c. 15 April to 7 May). Turtles captured during that

period have empty stomachs, thereby eliminating the confounding effect of digestive status on mass.

For our second measure of fitness, we measured reproductive output in 61 females. We used mean hatchling size as our metric of maternal fitness because body size is an important trait for hatchling survival in turtles (Janzen, Tucker & Paukstis 2000). We 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.

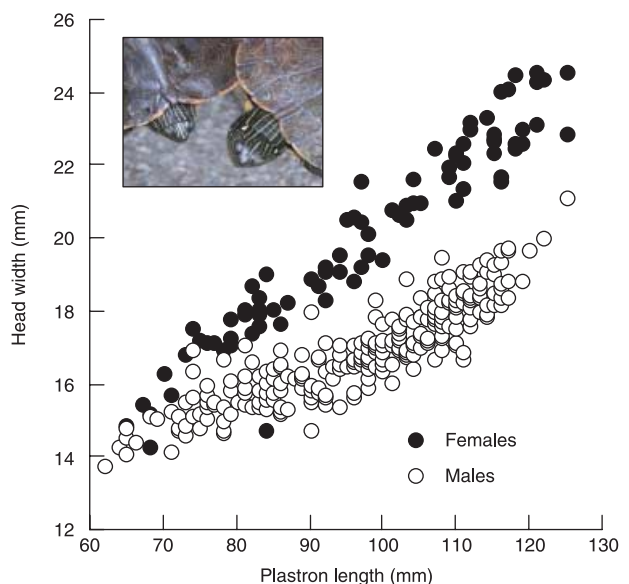
#### STATISTICAL ANALYSES

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. We 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, Cary, North Carolina).

## Results

#### SEXUAL DIMORPHISM IN BODY SIZE AND TROPHIC MORPHOLOGY

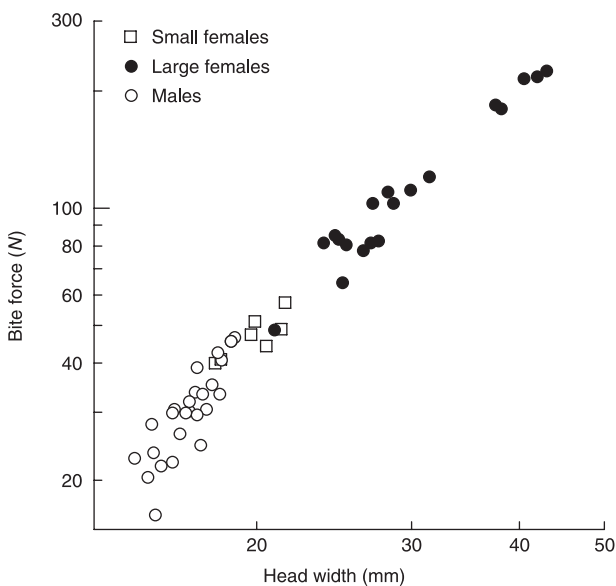
Females ranged from 65 to 253 mm PL (mean = 179,  $n = 351$ ), whereas males ranged from 62 to 125 mm PL (mean = 97,  $n = 267$ ). Allometric scaling of HW to PL indicated that turtles were also very dimorphic in head size (Fig. 2, Table 1). We compared HW as a function of PL in males and females using ANCOVA. To avoid comparing largely non-overlapping PL ranges, we restricted the analysis to



**Fig. 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.

**Table 1.** Scaling relationships of head width, bite force, and prey hardness as a function of body size and head size. Data are log<sub>10</sub> 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	<i>n</i>	Slope (95% CI)	Intercept (95% CI)	<i>R</i> <sup>2</sup>
Plastron length	Head width	Female	351	0.85 (0.83 to 0.87)	-0.37 (-0.43 to -0.36)	0.97
		Male	267	0.52 (0.49 to 0.55)	0.19 (0.13 to 0.24)	0.78
Plastron length	Bite force	Female	26	1.93 (1.59 to 2.35)	-2.19 (-3.06 to -1.47)	0.79
		Male	26	1.96 (1.54 to 2.49)	-2.38 (-3.43 to -1.56)	0.67
Head width	Bite force	Female	26	2.09 (1.95 to 2.25)	-1.04 (-1.26 to -0.83)	0.97
		Male	26	3.62 (2.91 to 4.49)	-2.93 (-4.01 to -2.07)	0.73
Plastron length	Maximum prey hardness	Female	24	2.64 (2.38 to 2.94)	-4.07 (-4.73 to -3.48)	0.94
		Male	11	1.91 (1.25 to 2.94)	-2.85 (-4.88 to -1.52)	0.66
Head width	Maximum prey hardness	Female	21	2.99 (2.48 to 3.61)	-2.65 (-3.59 to -1.88)	0.84
		Male	12	4.13 (2.83 to 6.04)	-4.14 (-6.49 to -2.53)	0.70



**Fig. 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.

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 with positive allometry with HW in males, but did not deviate from the expected slope of two (see Meyers, Herrel & Birch 2002) in females (Fig. 3, Table 1). We 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:  $R^2 = 0.27$ ,  $F_{(1,25)} =$

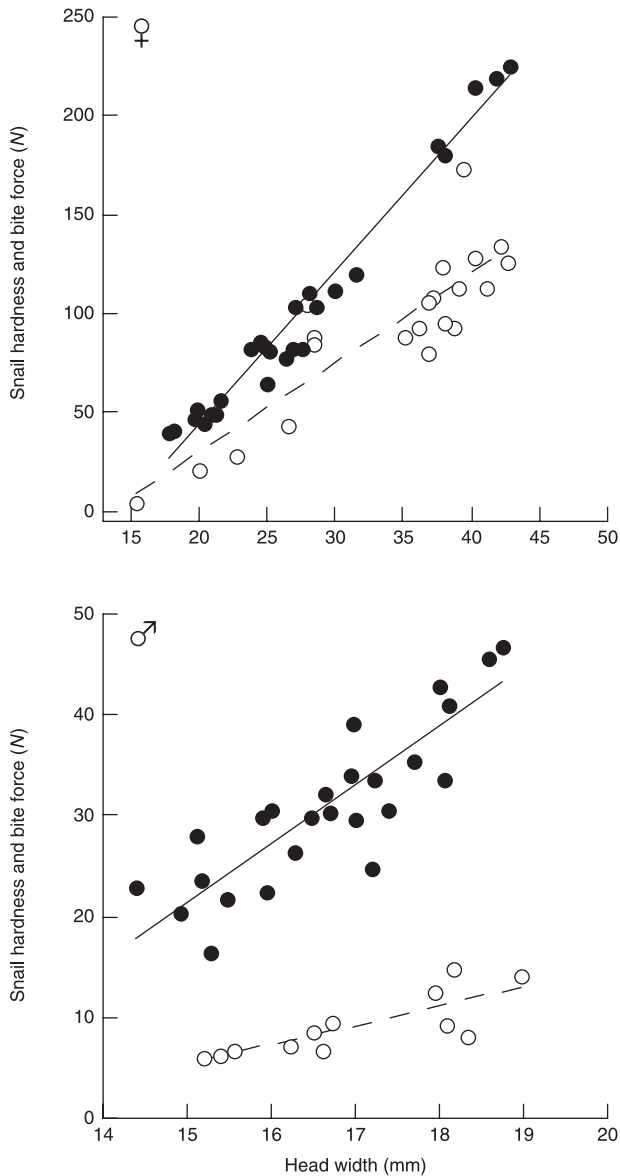
23.99,  $P < 0.0001$ ; sex:  $R^2 = 0.23$ ,  $F_{(1,25)} = 20.70$ ,  $P < 0.0001$ ). The slopes were the same ( $R^2 = 0.02$ ,  $F_{(1,25)} = 1.82$ ,  $P = 0.19$ ) for both sexes, however, suggesting that the difference in absolute bite force between the sexes over the same range of body size is due to differences in HW not PL.

#### PREY HARDNESS

We examined the faeces 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, we 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, we used 11 (for PL) and 12 (for HW) data points out of 44. In both sexes, we 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), we found that females consumed snails that were significantly closer to their maximum bite force capacity ( $60\% \pm 4.22\%$ ) compared to males ( $28\% \pm 1.43\%$ ,  $t$ -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. 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% (SD = 3.29%), indicating that the within clutch variance in hatchling mass is small. We 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

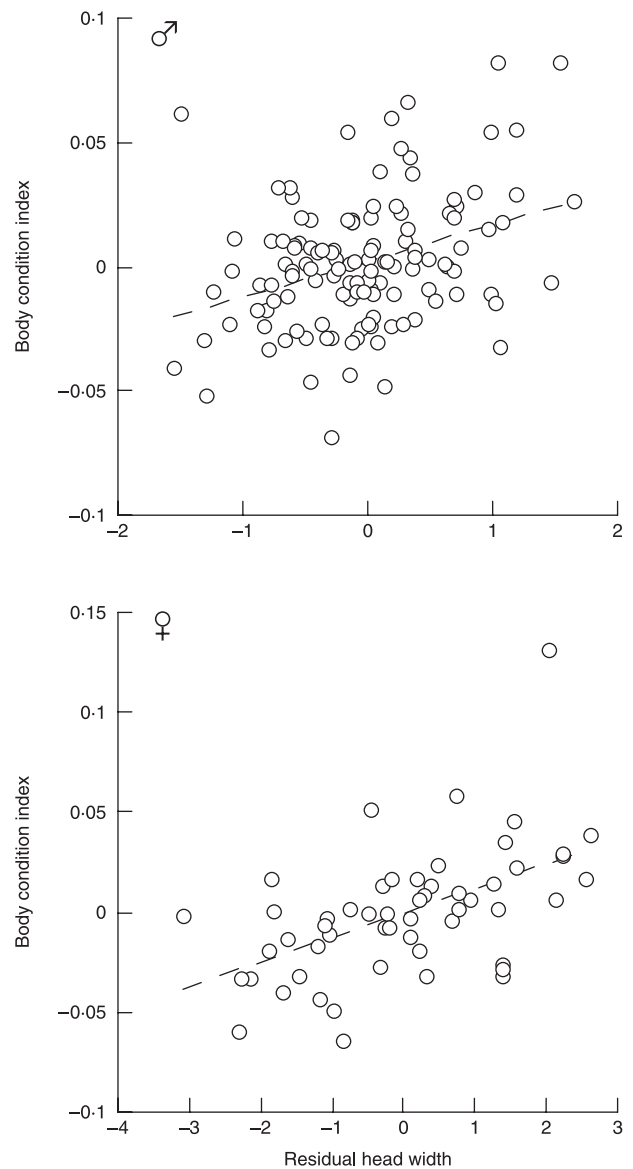


**Fig. 4.** Female (top) northern map turtles in lake Opinicon, Ontario, ingest snails closer to their maximum biting capacity than males (bottom). Open symbols denote snail hardness and filled symbols denote bite force.

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

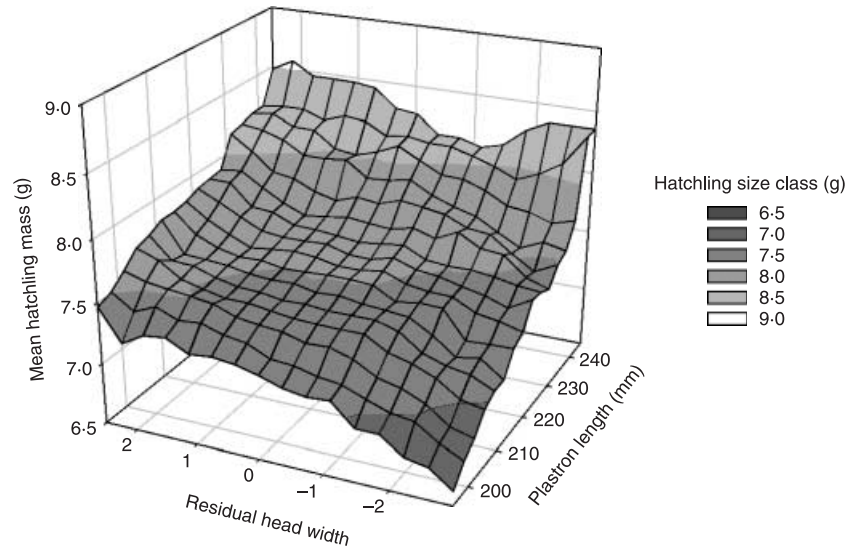
Sexual dimorphism has received substantial attention from evolutionary ecologists (Hedrick & Temeles 1989; Fairbairn 1997; Blanckenhorn 2005). In the absence of sexual selection, sexual dimorphism can theoretically evolve to accommodate the reproductive roles of each sex (Slatkin 1984), but few empirical data exist to support this hypothesis. Our findings offer clear support for the RRH of TMD, which states that



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

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 HW and fitness in durophagous turtles. The relationships between our measures of fitness and relative HW 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. We 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, we demonstrated that females with relatively larger heads were able to produce larger offspring. We assume here that head size has a



**Fig. 6.** Mean offspring mass increases with both body size (plastron length) and relative head width in northern map turtles from lake Opinicon, Ontario.

strong genetic basis, a reasonable assumption in this group of turtles (Lindeman 2000), 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 durophagous 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. Our 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: (i) growth for achieving a larger body size (Shine 1988); (ii) maintenance, because metabolic rate increases with body size (Andrews & Pough 1985) and (iii) egg production because more, or larger, eggs are more energetically costly (Nagle, Burke & Congdon 1998). Thus, selection on energy intake and fertility may be inextricably linked: without a concomitant increase in energy intake, females cannot realize the fertility 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. Our 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 & Sharkey 2001), which suggests that modifications of the trophic morphology occurred in females only in response to durophagy.

Although our 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 our study population. We conducted detailed dietary analyses (G. Bulté, unpublished data) 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, Fitzsimmons & Gibbons 1995; Lindeman 2006a).

Our study demonstrates the fitness advantage of HW and bite force in females. We 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 & Moll 1992) 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 (Lindeman 1999) and head growth may be constrained by the inhibitory effect of testosterone (Shine & Crews 1988). Interestingly, we 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 our 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 2000). However, TMD is more pronounced in molluscivorous species (Lindeman 2000). 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 favouring large heads in females (see also Lindeman & Sharkey 2001).

Our study provides 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. Our data also underscore that the evolution of morphology (head shape), body size, energetics and fertility may be inextricably linked.

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