# Predicted and observed maximum prey size – snake size allometry

R. B. KING†

*Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA*

### Summary

**1.** For gape-limited predators such as snakes, it should be possible to predict the relationship between maximum prey size and body size from the relationship between maximum prey size and gape size and between gape size and body size. Such predictions were generated for Water Snakes, *Nerodia sipedon* L., using a data subset and then tested with a larger data set.

**2.** Gape size was computed based on jaw length and width and cyclical regression was used to identify prey of maximum size for snakes of a given gape or mass.

**3.** Predicted and observed maximum prey cross-section–snake mass allometry were in good agreement. Predicted maximum prey mass–snake mass allometry somewhat exceeded observed allometry which did not differ from 1.

**4.** Observed minimum prey size–snake size allometry was significantly greater than 0, indicating that larger snakes drop small prey from their diets.

**5.** Gape size–body size allometry in two other natricine snakes (*Thamnophis sirtalis*, *Storeria dekayi*) suggest that patterns of ontogenetic change in prey size should differ among species in predictable ways.

**6.** Sex differences in gape size–snake size allometry suggest that sex differences in maximum prey size should increase with increasing snake size, even when linear measures of head dimensions do not.

*Key-words*: Gape size, *Nerodia sipedon*, sexual dimorphism, *Storeria dekayi*, *Thamnophis sirtalis*

*Functional Ecology* (2002) **16**, 766–772

## Introduction

Among predators that swallow prey whole, gape size sets an upper limit on the size of prey that can be consumed. Such predators often exhibit distinctive adaptations for subduing and swallowing prey. In snakes, general adaptations for swallowing large prey include a flexible connection between the anterior tips of the mandibles, movable units in the skull, and articulation of the mandible to highly mobile quadrate bones rather than directly to the skull (Cundall & Greene 2000). More specialized adaptations include vertebral processes that aid in breaking egg shells and the use of venom to subdue prey and speed digestion (Gans 1974; Greene 1997).

Snakes frequently show ontogenetic, sexual, geographical and phylogenetic variation in head dimensions relative to body size (e.g. Greene 1983; Forsman 1991; Shine 1991b; King 1997; King *et al.* 1999a) and snake body size–prey size relationships might be expected to vary accordingly. Within species, prey size typically increases with increasing body size (Shine 1991a; Arnold 1993). However, species differ in whether this pattern results from larger snakes (1) adding larger prey to their diets while continuing to consume small prey (an ontogenetic 'telescope') or (2) switching to larger prey and omitting small prey (an ontogenetic shift, cf. Figure 3·1 in Arnold 1993). Variation in relative head dimensions within and among taxa has demonstrable effects on swallowing performance: larger-headed individuals and taxa swallow prey of a given size more quickly and with fewer jaw protractions (Pough & Groves 1983; Forsman & Lindell 1993). Young snakes typically have larger heads relative to body size than do older larger individuals and one interpretation of this pattern is that it allows young snakes, in which prey size is already constrained by small body size, to consume larger prey than might otherwise be possible (King *et al.* 1999a). Males and females also typically differ in relative head dimensions (most commonly, females exceed males), perhaps as a consequence of selection arising from pre-existing differences in foraging habits or prey selection (Shine 1991b, 1993). Sex differences in relative head dimensions have been attributed to an inhibitory effect of testosterone on head growth in male snakes (Shine & Crews 1988). Individual differences in relative head dimensions have

†Author to whom correspondence should be addressed. E-mail: rbking@niu.edu

been attributed to underlying genetic variation and to phenotypic plasticity in response to prey size (King 1997; Queral-Regil & King 1998; Bonnet *et al*. 2001).

These observations suggest that information on the relationship between prey size and snake gape size and the relationship between gape size (or a correlate of gape size) and snake body size could be used to predict maximum prey size–snake size allometry. Such predictions are generally lacking, perhaps in part because many analyses of prey size–snake size relationships have focused on mean (not maximum) prey size (examples in Arnold 1993). Here, I use cyclical regression to identify prey of maximum size consumed by Water Snakes, *Nerodia sipedon* Linnaeus. I then use the observed relationship between maximum prey size and an index of gape size from a data subset to predict allometric relationships between maximum prey size and snake mass. These predictions are tested using a larger data set. I also use cyclical regression to identify prey of minimum size and test whether large Water Snakes continue to consume small prey or switch to larger prey. Finally, I use maximum prey size–snake size allometry in Water Snakes together with gape index–body size allometry in Garter Snakes (*Thamnophis sirtalis* Linnaeus) and Brown Snakes (*Storeria dekayi* Holbrook) to explore the ecological implications of ontogenetic changes and sexual dimorphism in snake head dimensions more generally. Garter Snakes and Brown Snakes are taxonomically allied with Water Snakes (Lawson 1987; de Queiroz & Lawson 1994) but attain smaller adult body size and, in the populations studied here, feed primarily on soft-bodied invertebrate terrestrial prey such as earthworms rather than aquatic vertebrate prey (salamanders, fish) as consumed by Water Snakes (King & Lawson 2001).

## Materials and methods

Prey items were recovered opportunistically from Lake Erie Water Snakes (*Nerodia sipedon insularum*) at study sites in Erie and Ottawa County, Ohio, USA (King 1986, 1993; King *et al*. 1999b). Prey were identified and measured to obtain mass, height and width. Prey cross-sectional area was computed as the area of an ellipse with major and minor axes equal to prey height and width:

Prey cross-sectional area = π(prey width)(prey height)/4. eqn 1

Snakes were classified by sex and measured to obtain mass, jaw length (distance from the posterior edge of the posterior-most superlabial scale to the anterior tip of the rostrum; King *et al*. 1999a), and jaw width (widest part obtained while applying pressure on the posterior portion of the head to spread the quadrates and mandibles laterally; Miller & Mushinsky 1990). An index of gape cross-sectional area was computed as the area of an ellipse with major and minor axes equal to jaw length and jaw width. This index is based on the

expected contributions of head width and length to swallowing ability (cf. Figure 2 in Arnold 1983; an alternative index was used by Miller & Mushinsky 1990):

Gape index = π(jaw length)(jaw width)/4. eqn 2

A total of 114 prey (fish and salamanders) were recovered from 86 individual Water Snakes. However, not all measurements were obtained for all prey or snakes from which prey were obtained. Both mass and cross-sectional area were obtained for 102 prey, both prey cross-section and snake gape index were obtained for 31 prey from 29 snakes, and both prey mass and snake gape index were obtained for 33 prey from 30 snakes. Body size and head dimensions were also obtained from snakes from which no prey were recovered for a total of 422 males and 409 females. It is these data on which predicted allometric relationships between maximum prey size and snake mass are based. Both prey cross-section and snake mass were obtained for 87 prey from 64 snakes and both prey mass and snake mass were obtained for 94 prey from 69 snakes. It is this more inclusive data set on which tests of predicted prey size–snake mass allometry are based.

Identification of the maximum prey size consumed by snakes of a given size was accomplished using repeated cycles of linear regression to subdivide data (Thomson *et al*. 1996). For example, in determining the relationship between maximum prey cross-section and snake gape index, an initial regression analysis was used to divide the data set in two. Points falling above the regression line represent prey with large cross-section given snake gape index and points falling below the line represent prey with small cross-section given snake gape index. Subsequent cycles of regression were used to further partition data and more narrowly identify prey of maximum size. Depending on sample size, three or four regression cycles were used to identify prey of maximum size. (This technique can also be used to identify observations with minimum values for some parameter. It and related techniques for identifying extreme observations are discussed in Nelson & Gregory 2000.)

All variables were transformed using natural logarithms prior to analysis. Because there was no clear dependent–independent relationship between prey mass and prey cross-section or between snake mass and snake gape index, reduced major axis regression (Sokal & Rohlf 1995, pp. 541–549) was used to determine allometric coefficients for these relationships. Simple linear regression was used to determine allometric relationships between prey characteristics (dependent variable) and snake size (independent variable). SPSS 10·0 was used for all analyses.

Morphological measurements of Garter Snakes and Brown Snakes were obtained at study sites in Erie and Ottawa County, Ohio, as part of other studies (King 1997; King *et al*. 1999a; King & Lawson 2001). In these species, jaw width was measured without applying
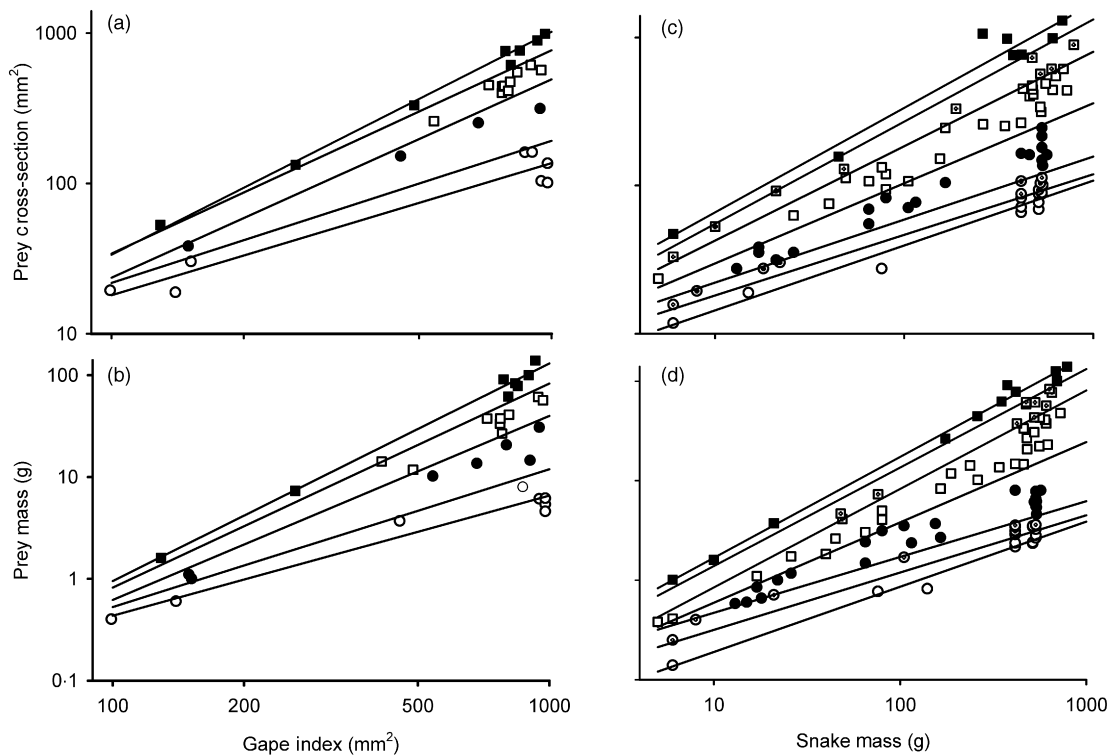
**Fig. 1.** Allometric relationships between (a) prey cross-section and Water Snake gape index, (b) prey mass and Water Snake gape index, (c) prey cross-section and Water Snake mass, and (d) prey mass and Water Snake mass. Prey of maximum size (filled squares and uppermost line in each graph) were identified using cyclical regression to subdivide data. The middle line in each graph represents the least-squares regression for all data. Successively higher (lower) lines represent the least-squares regression for data having positive (negative) residuals in the prior regression cycle. Different data subsets are represented by different symbols.

pressure to flatten the head (in contrast to Water Snakes). However, gape indices computed using either measure of jaw width were highly correlated in Water Snakes ($r = 0.992$ in 422 males and 0.995 in 409 females), suggesting that one measure can be substituted for the other without affecting conclusions.

## Results

### PREDICTED MAXIMUM PREY SIZE–SNAKE SIZE ALLOMETRY

Three cycles of regression were used to identify prey of maximum size in determining the relationship between maximum prey cross-section and snake gape index (Fig. 1a). The resulting allometric coefficient was 1·484 ($n = 9$ of 31 prey, 95% confidence limits = 1·337 and 1·631, $r^2 = 0.99$, $F_{1,7} = 567.79$, $P < 0.001$). Similarly, three cycles of regression were used to determine the relationship between maximum prey mass and snake gape index (Fig. 1b), giving an allometric coefficient of 2·139 ($n = 9$ of 33 prey, 95% confidence limits = 1·948 and 2·329, $r^2 = 0.98$, $F_{1,7} = 706.27$, $P < 0.001$). Allometric coefficients relating snake gape index and snake mass, obtained using reduced major axis regression, were 0·511 for males ($n = 422$, 95% confidence limits = 0·503 and 0·521, $r = 0.99$, $P < 0.001$) and 0·530 for females ($n = 409$, 95% confidence limits = 0·523 and 0·536, $r = 0.99$, $P < 0.001$) (Fig. 2).
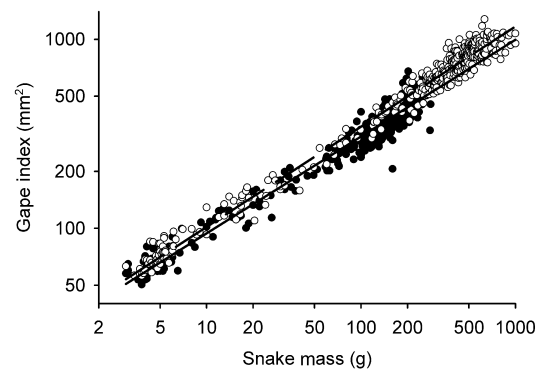
**Fig. 2.** Allometric relationship between gape index and mass in male (filled circles and solid line) and female (open circles and dashed line) Water Snakes determined using reduced major axis regression.

Confidence intervals for males and females did not overlap, indicating that allometric coefficients relating gape index and snake mass differ significantly between sexes (this conclusion was unchanged when females exceeding 502 g, the mass of the largest male, were excluded from analysis). The predicted allometric relationship between maximum prey cross-section and snake mass was obtained by taking the product of the allometric coefficient relating prey cross-section and gape index (1·484) and the allometric coefficient relating gape index and snake mass (0·511 for males, 0·530 for females):

males: maximum prey cross section = male snake mass$^{(0.758)}$,

females: maximum prey cross section = male snake mass$^{(0.786)}$. 
eqn 3

Similarly, the predicted allometric relationship between maximum prey mass and snake mass was obtained by taking the product of the allometric coefficient relating prey mass and gape index (2·139) and the allometric coefficient relating gape index and snake mass (0·511 for males, 0·530 for females):

males: maximum prey mass = male snake mass$^{(1.095)}$,

females: maximum prey mass = male snake mass$^{(1.133)}$. 
eqn 4

### OBSERVED MAXIMUM PREY SIZE–SNAKE SIZE ALLOMETRY

Four cycles of regression were used to identify prey of maximum size in determining the relationship between maximum prey cross-section and snake mass (Fig. 1c). The resulting allometric coefficient was 0·706 ($n = 8$ of 87, $r^2 = 0.96$, $F_{1,6} = 143.30$, $P < 0.001$). 95% confidence limits of this coefficient (0·562, 0·850) included predicted allometric coefficients for both males (0·758) and females (0·786), hence predicted and observed allometric coefficients did not differ significantly. Similarly, four cycles of regression were used to determine the relationship between maximum prey mass and snake mass (Fig. 1d), giving an allometric coefficient of 1·015 ($n = 11$ of 94, $r^2 < 0.99$, $F_{1,9} = 1696.16$, $P < 0.001$). 95% confidence limits of this coefficient (0·959, 1·071) did not include predicted allometric coefficients for males (1·095) or females (1·133), hence predicted and observed allometric coefficients differed significantly. However, the magnitude of this difference is small. 95% confidence limits did include 1, indicating that the observed relationship between maximum prey mass and snake mass did not differ significantly from isometry.

### OBSERVED MINIMUM PREY SIZE–SNAKE SIZE ALLOMETRY

The allometric coefficient relating minimum prey cross-section and snake mass (Fig. 1c) was 0·438 ($n = 11$ of 87 prey, 95% confidence limits = 0·385 and 0·492, $r^2 = 0.97$, $F_{1,10} = 336.93$, $P < 0.001$). The allometric coefficient relating minimum prey mass and snake mass (Fig. 1d) was 0·655 ($n = 9$ of 94 prey, 95% confidence limits = 0·589 and 0·721, $r^2 = 0.99$, $F_{1,7} = 550.45$, $P < 0.001$). Confidence intervals indicate that both allometric coefficients were significantly greater than 0, thus as snake size increased, minimum prey size also increased.

### ONTOGENETIC CHANGES AND SEX DIFFERENCES IN SNAKE HEAD DIMENSIONS

Allometric coefficients relating gape index to snake mass were lower in Garter Snakes and Brown Snakes than in Water Snakes (Table 1). Sex differences in allometric coefficients were nearly significant in Garter Snakes (95% confidence intervals overlap by just 0·001) but were not significant in Brown Snakes (Table 1). Assuming that the allometric coefficient relating gape index to maximum prey mass in Garter snakes and Brown Snakes is the same as that observed in Water Snakes (2·139), predicted maximum prey mass–snake mass allometry can also be computed for Garter Snakes and Brown Snakes (Table 1). Predicted maximum prey mass–snake mass allometry differs among species. Brown Snakes are expected to show negative allometry, Garter Snakes are expected to show slightly positive (females) or slightly negative (males) allometry, and Water Snakes are expected to show positive allometry (Table 1, Fig. 3) (although as noted above, the observed allometric coefficient in Water Snakes, 1·015, did not differ significantly from isometry).

Sex differences in predicted maximum prey mass–snake mass allometry mean that female Water Snakes and Garter Snakes are expected to consume larger prey than similarly sized males. For example, the predicted

**Table 1.** Observed gape index–snake mass allometry and predicted maximum prey mass–snake mass allometry in three species of natricine snakes

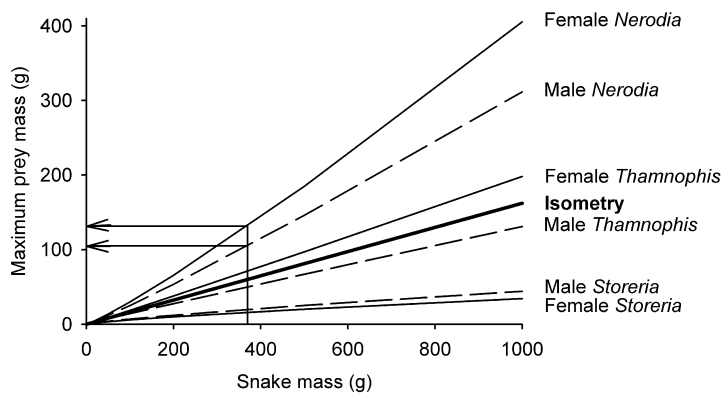| Species | Sex | $n$ | Observed gape index–snake mass allometry (95% CI) | Predicted prey mass–snake mass allometry |
|---|---|---|---|---|
| *Nerodia sipedon* | Males | 422 | 0·511 (0·503, 0·521) | 1·95 |
| | Females | 409 | 0·530 (0·523, 0·536) | 1·133 |
| *Thamnophis sirtalis* | Males | 167 | 0·453 (0·436, 0·471) | 0·969 |
| | Females | 367 | 0·481 (0·470, 0·492) | 1·029 |
| *Storeria dekayi* | Males | 41 | 0·374 (0·316, 0·443) | 0·811 |
| | Females | 69 | 0·362 (0·310, 0·415) | 0·775 |

**Fig. 3.** Predicted allometric relationship between maximum prey mass and snake mass for Water Snakes (*Nerodia*), Garter Snakes (*Thamnophis*) and Brown Snakes (*Storeria*). For each species, solid lines represent females and dashed lines represent males. Isometry (allometric coefficient = 1) is represented by a heavy solid line. Arrows illustrate the maximum prey mass predicted for a male and female Water Snake each weighing 370 g (the maximum mass observed among male Water Snakes, R. B. King unpublished data).

maximum prey size consumed by a 370-g male Water Snake (the maximum mass attained by any male in this study) was only 80% of that consumed by a 370-g female (Fig. 3). Because adult females exceed males in body size (King *et al*. 1999a), sex differences in gape index are expected to accentuate differences in maximum prey size arising as a consequence of differences in body size alone. Given a mean adult body mass of 151 g in males and 408 g in females (R. B. King & A. Queral Regil unpublished data), expected maximum prey size of an average male would be 33% that of an average female in the absence of sexual dimorphism in gape index–body size allometry but just 27% that of an average female given the dimorphism observed here.

Sexual dimorphism in head dimensions and gape index are reversed in Brown Snakes (see also King 1997). As a consequence, male Brown Snakes are expected to consume larger prey than similarly sized females. As in Water Snakes and Garter Snakes, adult female Brown Snakes exceed males in body size (King 1997). Hence, sex differences in gape index of Brown Snakes are expected to reduce differences in maximum prey size arising from differences body size alone.

## Discussion

The observed allometric relationship between maximum prey cross-section and snake mass (Fig. 1b) agreed with that predicted from the relationship between maximum prey cross-section and gape index (Fig. 1a) and between gape index and snake mass (Fig. 2) (observed allometric coefficient = 0·706, predicted allometric coefficient = 0·758 in males and 0·786 in females). However, the observed allometric relationship between maximum prey cross-section and snake gape index (1·484) exceeded what might be expected based on first principles. Specifically, the gape index used here was intended as a measure of the cross-sectional area of a snake's gape and consequently, maximum

prey cross-section was expected to vary isometrically with gape index. There are several possible explanations for the higher allometric coefficient observed here. One likely explanation is that jaw length and jaw width only partly determine gape. Jaw length was measured using an external landmark (the posterior edge of the posterior-most upper labial scale) because this facilitates measurement on intact live animals. However, mandible and quadrate bone length both show positive allometry with skull length in natricine snakes (Rossman 1980) that may not be reflected in the position of this landmark. In addition, the stretch capacity of soft tissues connecting the mandible tips is an important determinant of snake gape (cf. Figures 9·11 and 9·12 in Cundall & Greene 2000). Although the nature of the soft tissues connecting the mandible tips varies taxonomically (Young 1998), data on the elasticity of this connection and on ontogenetic variation in elasticity are lacking. A second possible explanation is that the smaller snakes included in this analysis (and perhaps more generally) fed on smaller prey than they were physically capable of consuming. Such a pattern would seem unexpected given the premium on rapid growth in young snakes (e.g. to survive first hibernation, to outgrow potential predators, to reach reproductive maturity). However, consuming large prey reduces locomotory performance (Garland & Arnold 1983), potentially increasing the risk of predation for small snakes. Direct measures of maximum gape size of snakes differing in body size are needed to distinguish between these alternatives. Importantly, despite possible shortcomings of the gape index used here, knowledge of maximum prey size–gape index allometry still allows meaningful prediction of maximum prey size–snake size allometry.

The observed allometric relationship between maximum prey mass and snake mass (Fig. 1d) was somewhat smaller in magnitude than that predicted from the relationship between maximum prey mass and gape index (Fig. 1b) and between gape index and snake mass (Fig. 2) (observed allometric coefficient = 1·015, predicted allometric coefficient = 1·095 in males and 1·133 in females). The reason for this discrepancy is not clear. Possibly, partial digestion of some prey resulted in an underestimate of maximum prey mass, especially in larger snakes. Alternatively, prey consumed by small and large snakes may have differed in shape. Size-related shifts in prey taxa have been reported previously among the Water Snakes included in this analysis (King 1993). However, prey taxa were similar in shape, all having a fusiform morphology. A plot of prey mass *vs* prey cross-section suggests that neither partial digestion nor prey taxon biased the results presented here: partially digested prey were not noticeably lighter given their cross-section nor did prey taxa differ noticeably in cross-section–mass relationship (Fig. 4). The allometric coefficient relating prey mass and prey cross-section, obtained using reduced major axis regression, was 1·457 and did not differ from 1·5 (95%
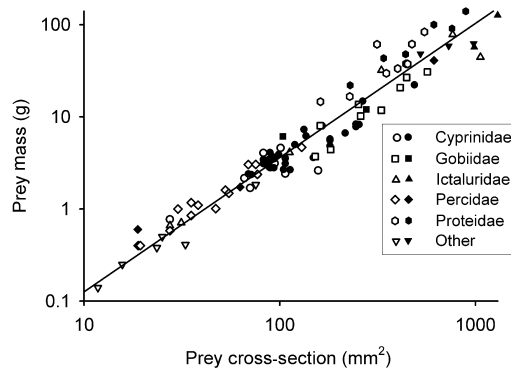
**Fig. 4.** Relationship between prey mass and prey cross-section determined using reduced major axis regression. Different symbols represent prey belonging to different families (see King 1993 and King *et al.* 1999b for species identification of prey). Closed symbols represent complete prey, open symbols represent partially digested prey.

confidence limits = 1·387 and 1·526, $r^2 = 0·971$, $P < 0·001$), the expected allometric coefficient relating mass and cross-section. It should be noted that there was very little variation in prey mass among prey with a given cross-section (Fig. 4). In species feeding on more diverse prey, separate analyses of maximum prey size–snake size allometry might be necessary for each prey type.

Sex differences in gape index–snake mass allometry lead to the prediction that maximum prey size–snake size allometry of female Water Snakes should exceed that of males. No attempt was made to test this prediction because males were poorly represented, especially among larger snakes (22 of 69 Water Snakes from which prey were recovered were male, the largest male was 238 g). However, the prevalence of sex differences in snake head dimensions (Shine 1991b), and presumably gape, suggests that such tests would be of interest provided data were sufficient to determine maximum prey size separately for males and females. King *et al.* (1999a) note that given the relative constancy in the degree of sexual dimorphism in head dimensions from neonates to adults, efforts to understand the fitness consequences of this dimorphism might profitably focus on neonates. In contrast, the present analysis suggests that despite ontogenetic constancy in head dimorphism, sex differences in maximum prey size are expected to increase in magnitude with increasing snake size (Fig. 3).

Garter Snakes and Brown Snakes had lower allometric coefficients relating gape index to body mass than did Water Snakes (Table 1). As a consequence, Garter Snakes and Brown Snakes also had lower predicted maximum prey mass–snake mass allometric coefficients than did Water Snakes. Coefficients for Garter Snakes were close to isometry whereas those for Brown Snakes suggest negative allometry between prey mass and snake mass (Table 1). These predictions assume that relationship between prey mass and gape index in Garter Snakes and Brown Snakes is the same as that of

Water Snakes. This assumption may not be true because, at least in the Lake Erie area, Garter Snakes and Brown Snakes feed primarily on earthworms (R. B. King unpublished data), a far more elongate prey than the fish and salamanders consumed by Water Snakes. Data on the relationship between cross-section and mass for these prey (cf. Fig. 4) and on the relationship between prey mass and gape index for Garter Snakes and Brown Snakes (cf. Fig. 1b) would be useful to further evaluate variation in gape index–snake mass allometry among species.

As noted above, direct measures of snake gape size and the elasticity of soft tissues connecting the mandible tips are needed. In addition, validation of the utility of cyclical regression in identifying prey of maximum size (e.g. by feeding captive snakes successively larger prey) would strengthen interpretation of the analyses presented here. Finally, information on gape size, prey dimensions and prey size–snake size allometry is needed for additional species specializing on other prey types. It seems likely that the marked difference in predicted prey size–snake size allometry among Water Snakes, Garter Snakes and Brown Snakes is partly an artefact of assuming constant gape size–prey mass allometry across species. Despite these limitations, this study demonstrates the potential utility of cyclical regression in identifying prey of maximum (minimum) size, thus providing information needed to predict and assess maximum prey size–snake size allometry. This study also demonstrates that information on sex and species differences in gape size may be useful in predicting patterns of dietary divergence. For example, one unexpected result of this analysis is that despite the fact that sexual dimorphism in relative head dimensions remains relatively constant as snakes grow (King *et al.* 1999a), sex differences in maximum prey size should increase.

## Acknowledgements

## References

Arnold, S.J. (1983) Morphology, performance, and fitness. *American Zoologist* **23**, 347–361.

Arnold, S.J. (1993) Foraging theory and prey-size–predator-size relations in snakes. *Snakes: Ecology and Behavior* (eds R.A. Seigel & J.T. Collins), pp. 87–115. McGraw-Hill, New York.

Bonnet, X., Shine, R., Naulleau, G. & Thiburce, C. (2001) Plastic vipers: influence of food intake on the size and shape of Gaboon vipers (*Bitis gabonica*). *Journal of Zoology* **255**, 341–351.

Cundall, D. & Greene, H. (2000) Feeding in snakes. *Feeding: Form Function, and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 293–333. Academic Press, San Diego, CA.

Forsman, A. (1991) Adaptive variation in head size in *Vipera berus* L. populations. *Biological Journal of the Linnean Society* **43**, 281–296.

Forsman, A. & Lindell, L.E. (1993) The advantage of a big head: swallowing performance in adders, *Vipera berus*. *Functional Ecology* **7**, 183–189.

Gans, C. (1974) *Biomechanics: an Approach to Vertebrate Biology*. J. B. Lippincott Co, Philadelphia, PA.

Garland, T. Jr & Arnold, S.J. (1983) Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* **1983**, 1092–1096.

Greene, H. (1983) Dietary correlates of the origin and radiation of snakes. *American Zoologist* **23**, 431–441.

Greene, H. (1997) *Snakes: the Evolution of Mystery in Nature*. University of California Press, Berkeley, CA.

King, R.B. (1986) Population ecology of the Lake Erie water snake, *Nerodia sipedon insularum*. *Copeia* **1986**, 757–772.

King, R.B. (1993) Microgeographic, historical, and size-correlated variation in water snake diet composition. *Journal of Herpetology* **27**, 175–185.

King. R.B. (1997) Variation in brown snake (*Storeia dekayi*) morphology and scalation: sex, family, and microgeographic differences. *Journal of Herpetology* **31**, 335–346.

King, R.B. & Lawson, R. (2001) Patterns of population subdivision and gene flow in three sympatric natricine snakes. *Copeia* **2001**, 602–614.

King, R.B., Bittner, T.D., Queral-Regil, A. & Cline, J.H. (1999a) Sexual dimorphism in neonate and adult snakes. *Journal of Zoology* **247**, 19–28.

King, R.B., Queral-Regil, A., Bittner, T.D., Kerfin, J.M. & Hageman, J. (1999b) *Nerodia sipedon insularum* (Lake Erie water snake) diet. *Herpetological Review* **30**, 169–170.

Lawson, R. (1987) Molecular studies of thamnophiine snakes. I. The phylogeny of the genus *Nerodia*. *Journal of Herpetology* **21**, 140–157.

Miller, D.E. & Mushinsky, H.R. (1990) Foraging ecology and prey size in the mangrove water snake, *Nerodia fasciata compressicauda*. *Copeia* **1990**, 1099–1106.

Nelson, K.J. & Gregory, P.T. (2000) Activity patterns of garter snakes, *Thamnophis sirtalis*, in relation to weather conditions at a fish hatchery on Vancouver Island, British Columbia. *Journal of Herpetology* **34**, 32–40.

Pough, F.H. & Groves, J.D. (1983) Specializations of the body form and food habits of snakes. *American Zoologist* **23**, 443–454.

de Queiroz, A. & Lawson, R. (1994) Phylogentic relationships of the garter snakes based on DNA sequence and allozyme variation. *Biological Journal of the Linnean Society* **53**, 209–229.

Queral-Regil, A. & King, R.B. (1998) Evidence for phenotypic plasticity in snake body size and relative head dimensions in response to amount and size of prey. *Copeia* **1998**, 423–429.

Rossman, C.E. (1980) Ontogenetic changes in skull proportions of the diamondback water snake, *Nerodia rhombifera*. *Herpetologica* **36**, 42–46.

Shine, R. (1991a) Why do large snakes eat larger prey items? *Functional Ecology* **5**, 493–502.

Shine, R. (1991b) Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* **138**, 103–122.

Shine, R. (1993) Sexual dimorphism in snakes. *Snakes: Ecology and Behavior* (eds R.A. Seigel & J.T. Collins), pp. 49–86. McGraw-Hill, New York.

Shine, R. & Crews, D. (1988) Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. *Evolution* **42**, 1105–1110.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman, New York.

Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers and rocks. *Ecology* **77**, 1698–1715.

Young, B.A. (1998) The comparative morphology of the intermandibular connective tissue in snakes (Reptilia: Squatmata). *Zoologischer Anzeiger* **237**, 59–84.