



Which proximate factor determines sexual size dimorphism in tiger snakes?

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Diverse interactions between factors that influence body size complicate the identification of the primary determinants of sexual size dimorphism. Using data from a long-term field study (1997–2009), we examined the contributions of the main proximate factors potentially influencing sexual size dimorphism from birth to adulthood in tiger snakes (*Notechis scutatus*). Data on body size, body mass and body condition of neonates, juveniles and adults were obtained by mark–recapture. Frequent recaptures allowed us to monitor reproductive status, diet and food intake, and to estimate survival and growth rates in age and sex classes. Additional data from females held briefly in captivity enabled us to assess reproductive output and the body mass lost at parturition (proxies for reproductive effort). From birth to maturity, individuals of both sexes experienced similar growth and mortality rates. We found no difference in diet, feeding and survival rates between the sexes, nor between juveniles and adults. On maturity, despite comparable diet and food intake by both sexes, the high energy requirements of vitellogenesis and gestation were responsible for a depletion of body reserves and probably resulted in a marked decrease in growth rates. Males were largely exempt from such costs of reproduction, and so could grow faster than females and attain larger body sizes. The absence of niche divergence between the sexes (uniformity of habitat, lack of predators) suggests that the impact of differential energetic investment for reproduction on growth rate is probably the main proximate factor influencing sexual size dimorphism in this species. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 103, 668–680.

ADDITIONAL KEYWORDS: body condition – diet – food intake – growth pattern – sexual dimorphism – survival.

INTRODUCTION

Body size influences all life history traits; therefore, the diversity and interactions of the factors that determine body size have attracted considerable attention (Peters, 1983; LaBarbera, 1989; Bronikowski, 2000; Olsen, Reginato & Wang, 2000; Foellmer & Fairbairn, 2005; McDonnell, Mulkeen & Gormally, 2005; Osmundson, 2006). For analytical reasons, the respective contributions of the major selective forces (i.e. ultimate factors) that determine body size are often distinguished from short-term underlying mechanisms

(i.e. proximate factors). Ultimate selective forces (ecological, sexual or fecundity selection) influence body size across generations (Hedrick & Temeles, 1989; Arnold, 1994; Preziosi & Fairbairn, 1997; Wikelski & Trillmich, 1997; Schulte-Hostedde, Millar & Gibbs, 2002; Badyaev, 2005), whereas underlying physiological regulatory mechanisms (e.g. plasma levels of growth hormones, food intake) operate during ontogeny and determine the actual body size of each individual (Watkins, 1996; Olsen *et al.*, 2000; Badyaev, Whittingham & Hill, 2001; Cox & John-Alder, 2005; Blanckenhorn *et al.*, 2007; Fernandez-Montraveta & Moya-Laran, 2007; Shelby, Madewell & Moczek, 2007; Stillwell & Fox, 2007). However, the interplay between

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the main factors is often complex. For example, multiple genes govern bone growth (Olsen *et al.*, 2000). Consequently, there is no absolute dichotomy between the influences of ultimate vs. proximate factors. Indeed, high food intake (a proximate factor) favours large body size, which, in turn, can provide an advantage in terms of reproductive success (size-dependent fecundity selection represents an ultimate factor). Conversely, food shortage can restrict growth rate even when body size and reproductive success are positively correlated.

Nonetheless, the distinction between ultimate and proximate factors is useful to fathom these intermingled processes, justifying different levels of investigation (e.g. from individuals to populations) and different investigative approaches (Hedrick & Temeles, 1989). Studies on sexual size dimorphism (SSD) have been framed within this general context (Darwin, 1871; Andersson, 1994; Weatherhead *et al.*, 1995; Brown & Weatherhead, 2000). Both the direction and magnitude of SSD are determined in complex ways (Shine, 1989; Madsen & Shine, 1993a; Olsson, Shine & Wapstra, 2002; Badyaev, 2002; Tamate & Maekawa, 2006). The gathering of detailed information on proximate factors that determine body size is thus essential to the understanding of SSD (Bronikowski, 2000; Cox, Skelly & John-Alder, 2003).

The major proximate factors that influence mean adult body size in free-ranging animals include size at birth, growth rates before and after maturity (a complex factor, influenced by thermoregulation and metabolic rate, for instance), maturation schedule, food availability, niche divergence (diet, habitat selection, etc.), energetic costs of reproduction and survival rates. To our knowledge, no mark-recapture field study has collectively assessed these factors. For example, studies have examined the influence of juvenile growth rates on SSD under natural conditions (Badyaev *et al.*, 2001; Le Galliard, Ferrière & Clobert, 2005; Le Galliard *et al.*, 2006) or integrated post-maturity growth patterns, a trait of particular importance in species with indeterminate growth or survival rates (Haenel & John-Alder, 2002; Rutherford, 2004; Le Galliard *et al.*, 2005; Cox & John-Alder, 2007; Rennie *et al.*, 2008). However, other major factors, such as diet and feeding rates (Shine, 1989), have usually not been explored.

A long-term mark-recapture study enabled us to investigate the main proximate factors that could influence SSD in free-ranging tiger snakes (*Notechis scutatus*) and to evaluate their respective influences under natural conditions. In snakes, males are larger than females in about 44% of species (Shine, 1994), with male-male combat seen as the major ultimate selective force for this trait (Shine, 1994). However, the association between ritual combat between males

and SSD is not absolute; females of some species with male-male combat still grow larger than males (e.g. asp viper, Bonnet *et al.*, 1998a), and the magnitude and direction of SSD can vary even among populations within a single species (e.g. carpet python, Pearson, Shine & Williams, 2002; nose-horned viper, Tomovic *et al.*, 2010). Because the energetic cost of reproduction in female snakes is usually higher than that of males (Shine, 2003), females should exhibit lower growth rates than males, and hence a relatively smaller body size (at least in the absence of major ecological niche divergence between the sexes). However, this is clearly not the case, as females are larger than males in around 56% of species, and therefore the energetic cost of reproduction for females and its effect on their growth cannot be a general explanation for snake SSD. The influence of other factors known to affect SSD should be considered, notably the fecundity advantage of larger body sizes in females, or niche divergence between sexes (Shine, 1988, 1989). Because there have been few comprehensive field studies examining the respective contributions of all the main proximate causes involved, we still have an incomplete understanding of the interaction of evolutionary forces influencing SSD. The aim of the current study was to contribute to this knowledge gap.

MATERIAL AND METHODS

STUDY SPECIES AND STUDY SITE

Tiger snakes (*Notechis scutatus*; Elapidae) are large (> 1 m at maturity), viviparous snakes found on the southern mainland and islands of Australia. Adult males are larger than females (Shine, 1987; Schwaner & Sarre, 1990; Bonnet *et al.*, 2002a). From 1997 to 2009, we conducted a mark-recapture study on a large, stable and isolated population of tiger snakes on Carnac Island (32°07'S; 115°39'E) in Western Australia (Bonnet *et al.*, 2002a; Reading *et al.*, 2010). Carnac Island consists of a small limestone plateau with scattered sand dunes, surrounded by sandy beaches and low cliffs (total area, 16 ha). The vegetation of Carnac Island is relatively homogeneous (Abbott, 1980). There are no identified predators of the snakes on this island (Bonnet *et al.*, 2005). Two species of skink (*Egernia kingii*, *Morethia obscura*) and the introduced house mouse (*Mus domesticus*) are common, and represent the major dietary components of neonate and juvenile snakes (Bonnet *et al.*, 1999). The silver gull (*Larus novaehollandiae*) is the most abundant bird species. Adult tiger snakes feed mostly on silver gull chicks (83%), with mice (15%) and lizards (2%) constituting the remainder of the diet (Bonnet *et al.*, 2002a; Aubret *et al.*, 2004a, 2006).

FIELD METHODS

Over the course of 13 years, 690 snakes were individually marked by scale clipping (Bonnet *et al.*, 2002a). The dataset includes a total of 2055 captures and recaptures. Sampling trips were usually undertaken between September and December when the snakes frequently bask, feed intensively, exhibit sexual activity and are easily observed. From late summer (March) to the end of winter (August), cooler environmental conditions are unfavourable for snake activity and they shelter within deep crevices and feed irregularly. For each capture, we recorded snout–vent length (SVL) to the nearest 0.5 cm, and body mass to the nearest gram. During handling, snakes often defecated; large faeces with undigested fragments (bones, feathers, etc.) indicated a recent meal (<1 week). Stomachs were palpated to detect the

presence of prey and, together with the examination of the faeces, enabled us to determine the type of prey consumed in most cases (Bonnet *et al.*, 1999, 2002a; Aubret *et al.*, 2004a). Sex was determined by eversion of hemipenes. After completion of the measurements, each snake was released at its exact point of capture.

On the basis of body size, individuals were classified as neonates, juveniles or adults. In both sexes, we considered individuals of ≥ 70 cm SVL to be sexually mature on the basis of our field observations (the smallest female palpated with developing eggs or embryos in the abdomen, and the smallest male observed courting a female) and through direct gonadal examinations (Shine, 1977, 1978). Individuals with SVL < 24 cm were classed as neonates (see Fig. 1), whereas those between 24 and 70 cm were considered as juveniles, and those larger than 70 cm as adults. We note, however, that the exact size and

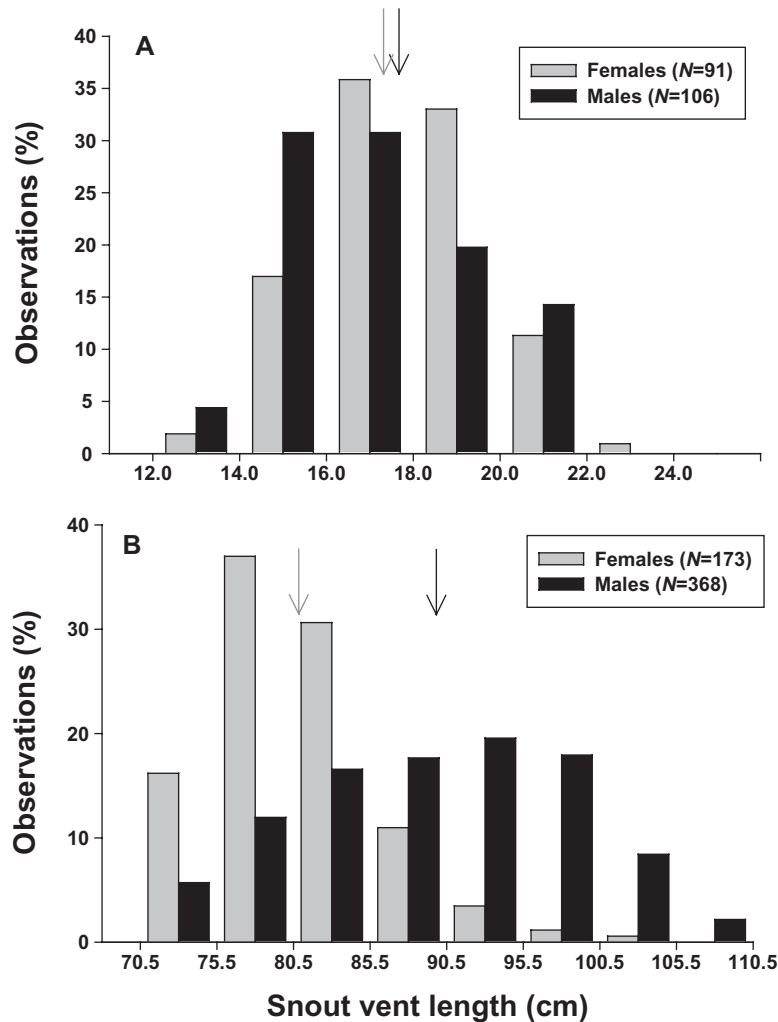


Figure 1. Body size distribution in neonate (A) and adult (B) tiger snakes from Carnac Island. The arrows indicate the respective mean values for females (grey) and males (black).

date at maturation cannot be determined accurately as maturity is a dynamic process subject to individual variation.

On Carnac Island, mating occurred in early spring (September to early October); we directly observed 38 matings, including four occasions where a second male was present (i.e. lying above the other two snakes and displaying the typical jerking courting behaviour). Although, the snake density is very high on Carnac Island (Bonnet *et al.*, 2002a) and individuals are frequently observed, we never saw ritual combat between males. The reproductive status of females was determined by palpation to detect growing follicles (larger than 2 cm) or developing embryos. Vitellogenesis (enlargement of ovarian follicles) was detected by palpation in November and December. Births occurred from March to May (Aubret *et al.*, 2006). Seventeen pregnant females captured in the field in January or February were kept in captivity for different research purposes (e.g. Aubret, Shine & Bonnet, 2004b) until they gave birth. Morphological data were obtained from their neonates. This allowed us to measure neonates immediately after birth in a standardized way, before they had consumed their first meal.

ANALYSES

Body mass and body condition

Body condition (size-adjusted body mass) is strongly correlated with body reserves in snakes, particularly fat bodies, but also with muscle and liver mass (Bonnet *et al.*, 1998a). Body condition was calculated using the residuals from the linear regression of body mass on SVL (both variables were logarithmically transformed for linearity; Hayes & Shonkwiler, 2001). Importantly, the calculation of body condition must take into account recent feeding and reproductive status. Gravid or pregnant females typically exhibiting a high body condition index but possessing limited body reserves represent a particular case. Paradoxical results (i.e. heavy but lean females) are the simple consequence of the massive transfer of nutritional resources from the mother to the follicles. Such animals should only be used in analyses with prudence, notably so as not to misinterpret the relationship between body condition and body reserves (Aubret *et al.*, 2003; Bonnet, Naulleau & Lourdaix, 2003; Bonnet, 2010). Consequently, individuals with obvious prey in the stomach, with enlarged follicles or with developing embryos were excluded from most of the analyses related to body mass (unless the prey was regurgitated).

Growth rate and growth pattern modelling

Growth rate was expressed as the difference in body size (SVL in cm) between recaptures divided by the

time elapsed in days. Growth rates were calculated directly for juveniles and adults, allowing the modelling of sex-specific growth patterns over the life spans of the snakes. In elongated and flexible animals, such as snakes, body size is difficult to measure precisely, and imprecision can generate substantial errors in growth rate calculation (measurement error varied from ± 0.5 cm to ± 2 cm depending on the body size, determined through random repeated measures of the same snake). However, when measured after long intervals of time, the impact of this error is considerably reduced. For example, substantial growth (e.g. > 10 cm annual SVL increase) can only be recorded over long time intervals, but the measurement error remains the same. To limit the impact of measurement errors, two of us (XB and DP) measured almost all ($> 90\%$) of the snakes every year, and restricted the analyses to long time intervals (> 100 days) between captures: 685 ± 457 (SD) days on average (range, 141–3693 days, $N = 846$). Negative values for growth (only observed in adults) were not corrected, because we assumed measurement error would err equally in either direction. Only one measurement per individual was included in the analyses.

Most reptiles, including elapid snakes, exhibit an asymptotic growth pattern (Andrews, 1982; Shine & Charnov, 1992; Webb, Brook & Shine, 2003). Growth patterns of ectotherms have often been characterized using the von Bertalanffy equation which relies on a linear relationship between growth rate and body size (Fabens, 1965; Lester, Shuter & Abrams, 2004). However, a simple linear decrease in the growth rate over time is not realistic and does not properly reflect the rapid growth of juveniles, followed by the slow asymptotic growth of adults of most reptiles (Stamps, 1993; Avery, 1994). Consequently, we used a nonlinear function between growth rate and body size to model the relationship between age and body size. To build the model, we used subsequent measures of body size collected on individual snakes with a time interval of roughly 1 year (380 ± 30 days; range, 310–441 days; $N = 458$) between recapture events. We fitted a Richards equation (Richards 1959), which is a generalization of the von Bertalanffy curve, to the annual growth in body size as a continuous function of initial body size. The growth rate k at any body size SVL was given by the following equation:

$$k_{\text{SVL}} = k_{\text{max}} [1 + e^{(A-\text{SVL})/B}]^{-1}$$

This function used three parameters: A , B and the scaling parameter k_{max} . It was adjusted to allow the growth rate to reach the maximal value (i.e. k_{max}) in small (young) individuals and to decrease until a threshold approaching a null value was reached in

large (old) ones. The inflection point of k corresponded to $SVL = A$, and the rate of change at this point was dependent on the parameter B . We employed nonlinear least-squares estimates using R.2.11.0 to set the value for the parameters, thereby enabling us to use the best fit between the model and the observed data. The mean value m of each parameter and the standard deviation (SD) of the distribution were fitted for male and female individuals separately. The growth pattern of each sex was established a posteriori, inferring the empirical estimate of body size at birth with the continuous function, $SVL_{t+1} = SVL_t + k_{SVL}$, where SVL_t represents the current body size at age t and k_{SVL} is the calculated annual growth rate for each sex at SVL_t . Growth rate modelling enabled us to obtain a picture of potential differences in growth rate between the sexes without relying on the determination of maturity. This provided a complementary view to the analyses of growth rates calculated in juveniles and then in adults.

Survival modelling

We estimated annual survival rates from 1997 to 2009 using the Cormack–Jolly–Seber approach (Lebreton *et al.*, 1992; White & Burnham, 1999). As maturity may influence the survival of individuals, we used a multistate model with ‘juvenile’ and ‘adult’ as states in order to detect potential sex differences in survival rates within these two age classes. We selected a model compatible with the biology of the species; strong seasonal effects and sex differences in catchability have been documented in ectotherms,

including snakes (Bonnet *et al.*, 2002a). Thus, we considered sex, age and time dependence in both survival and capture probabilities [$\phi(\text{sex} \times \text{age} \times t)$ $p(\text{sex} \times \text{age} \times t)$]. A classical model selection procedure was then performed [Akaike Information Criterion (AICc), Lebreton *et al.*, 1992; Burnham & Anderson, 1998]. When δAICc exceeded two between two models, we considered that their respective estimates were significantly different; otherwise parameters were estimated using a model averaging procedure (Buckland, Burnham & Augustin, 1997; Burnham & Anderson, 1998; Anderson & Burnham, 1999). All estimates and AICc values were computed using the program MARK (White & Burnham, 1999).

RESULTS

BODY SIZE

At birth, the mean body sizes of males ($SVL = 17.9 \pm 1.9$ cm, $N = 106$) and females ($SVL = 17.3 \pm 2.1$ cm, $N = 91$) were not statistically significantly different (Fig. 1; Table 1). Similarly, in juveniles, the mean body size was not different in males compared with females (mean $SVL = 52.5 \pm 13.5$ cm, $N = 71$ in females vs. mean $SVL = 55.3 \pm 13.1$ cm, $N = 63$ in males; Table 1).

In contrast, adult males attained markedly larger mean and absolute body sizes than females (mean $SVL = 89.4 \pm 8.8$ cm, $N = 368$ vs. mean $SVL = 80.7 \pm 5.5$ cm, $N = 173$, respectively; Table 1). Overall, sexual divergence of SVL increased from birth to adulthood, with clear dimorphism only apparent in adults (Fig. 1).

Table 1. Comparisons between the sexes of body size [snout–vent length (SVL), cm], body condition (size-adjusted body mass) and annual growth rate in neonate, juvenile and adult tiger snakes

Dependent variable	Covariable	Random factor	Direction	<i>F</i>	d.f.	<i>P</i>
Neonate body size	–	Mother		4.16	1, 16	0.052
Neonate body condition	SVL	Mother		0.13	1, 16	0.677
Juvenile body size	NA	–		1.29	1, 132	0.126
Juvenile body condition (slope)	SVL	–		0.626	1, 92	0.431
Juvenile body condition (intercept)	SVL	–	F > M	4.099	1, 93	0.050
Juvenile growth rate (slope)	SVL	–		0.227	1, 52	0.636
Juvenile growth rate (intercept)	SVL	–		1.924	1, 53	0.171
Adult body size	NA	–	M > F	141.23	1, 540	0.001
Adult body condition (slope)	SVL	–		1.590	1, 333	0.209
Adult body condition (intercept)	SVL	–	F > M	9.74	1, 334	0.001
Adult growth rate (slope)	SVL	–		0.967	1, 300	0.324
Adult growth rate (intercept)	SVL	–	M > F	50.733	1, 301	0.001

General linear models were performed using sex as the main factor, maternal identity as a random factor, when appropriate, and body size as covariate to estimate body condition and growth rate (e.g. second line: mixed model ANCOVA with maternal identity as a random factor, neonate body mass as the dependent variable, sex as the main factor and neonate SVL as the covariate). Data were log-transformed prior to the analyses. Direction indicates significant cases in which the trait under focus (size, growth, etc.) is larger in one sex. F, female; M, male; NA, ?.

BODY CONDITION

Body reserves can influence growth rate and hence body size (Aubret *et al.*, 2003). Consequently, it was necessary to examine the influence of this factor in the different age classes. At birth, the respective body conditions of males and females were not different [size-adjusted body masses were 4.8 ± 1.5 g in females ($N = 96$) and 4.9 ± 1.4 g in males ($N = 106$); Table 1]. We found a weak sex difference in juveniles [adjusted body masses were 118.4 ± 79.2 g in females ($N = 49$) and 104.0 ± 60.8 g in males ($N = 47$); Table 1]. Therefore, the possible influence of body reserves progressively stored before maturity on subsequent adult growth rates may have advantaged females over males.

Adult females were in better condition than males [least mean squares adjusted body masses were 407.9 ± 94.3 g in females ($N = 84$) and 386.8 ± 142.9 g in males ($N = 253$); Table 1]. If reproductive females were retained in the analysis (with growing follicles or embryos, but excluding those snakes with prey in the stomach), the observed sex difference in body condition was more apparent [the adjusted body masses of females increased to 425.2 ± 96.2 g ($N = 133$)]. The mass of the mother plus the mass of the follicles (or embryos) provides a measure of the nutritional status of the mother; this is represented by the actual maternal somatic mass + the mass of resources invested into the litter. Importantly, the body condition values of the post-parturient females

(adjusted mean body mass: 316.6 ± 39.6 g, $N = 6$) and nonreproductive females caught in spring (= post-parturient females from previous year; adjusted mean body mass: 314.1 ± 59.9 g, $N = 4$) were particularly low compared with reproductive females and with adult males [ANCOVA with body mass as the dependent variable, SVL as a covariate and adult category (post-parturient female, vitellogenic female, male) as the factor: $P < 0.01$; all *post hoc* tests with $P < 0.01$], indicating a strong depletion of body reserves from early vitellogenesis to parturition.

GROWTH RATES BEFORE AND AFTER MATURITY

Growth rates were strongly dependent on body size (correlation between growth rate and SVL; $r = -0.74$, $P < 0.001$, $N = 360$ using a single value per individual; $r = -0.70$, $P < 0.001$, $N = 849$ including pseudoreplicates; Fig. 2). In juveniles, the growth rates of males and females were not significantly different (Fig. 3; Table 1). On average, juveniles gained 0.33 ± 0.16 mm day⁻¹ (range, 0.09–0.88 mm, $N = 56$), corresponding to an SVL increase of 5 to 32 cm per year. The mean growth rate of adults was almost five-fold lower than that of juveniles: 0.07 ± 0.08 mm day⁻¹ (range, -0.09–0.50 mm; 0 to 18 cm SVL increase per year; $N = 304$). After maturity, we observed strong differences in growth rate between males and females (Fig. 3). Adult males (1.01 ± 0.76 mm, $N = 218$) exhibited a higher growth

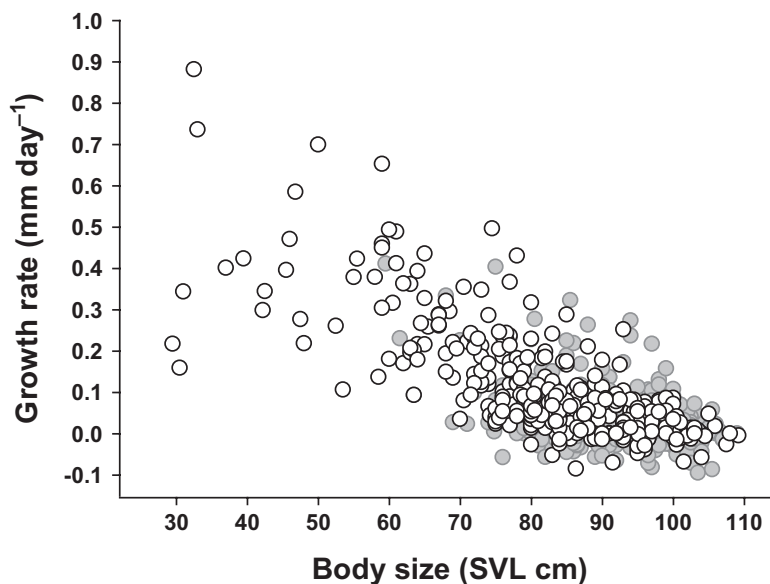


Figure 2. Individual growth rates with respect to snout–vent length (SVL) of tiger snakes obtained through long-term mark–recapture on Carnac Island. Open circles indicate data based on one observation per individual. Grey filled circles indicate data for which there is more than one observation on the same individual (see text for details). Few pseudoreplicates were collected in juveniles (SVL < 70 cm) owing to their rapid growth.

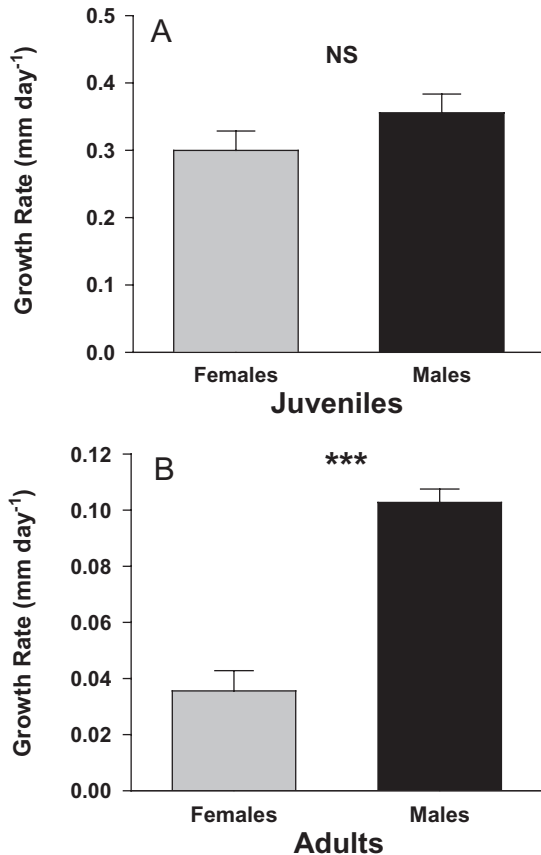


Figure 3. Growth rates of male (black bars, mean \pm SD) and female (white bars) tiger snakes. A, Juveniles: means did not differ. B, Adults; means differed $P < 0.001$.

rate than females (0.36 ± 0.78 mm, $N = 86$) (Table 1). The incorporation of pseudoreplicates in order to increase the power of the analyses did not change the results.

Growth rate modelling provided complementary results (Fig. 4). The fitting procedure yielded a mean maximum growth rate of 30.2 cm year⁻¹ for females and 21.8 cm year⁻¹ for males; the inflection points (parameter A) for females and males were 57.2 cm SVL and 70.2 cm SVL, respectively. The growth rate reached a plateau at body sizes of 98 cm SVL (estimated age of 14 years) and 86 cm SVL (estimated age of 11 years) for males and females, respectively. The slope at point A (parameter B) was -8.7 for females and -8.6 for males. Thus, the growth rate decreased more abruptly in females than in males, although these rates converged as each sex approached its maximum body size (Fig. 4). Several young snakes marked in the field approximately 6 months after birth (SVL < 33.0 cm) reached maturity in 2 years (68 cm $<$ SVL < 80 cm), suggesting that the estimated 2.5-year value for maturity was realistic in both

sexes. Recapture data and growth rate modelling also revealed important interindividual variations.

FEEDING RATE AND DIET

Owing to the infrequent feeding of most snakes (usually 1 week is required to digest a meal, as indicated by multiple palpations; Brischox, Bonnet & Shine, 2007), the proportion of fed vs. unfed snakes captured provided a reasonable index of feeding rate. The respective percentages of females and males with a recent meal were similar in both juvenile (41% of females, $N = 82$ observations vs. 43% of males, $N = 68$ observations; $\chi^2 = 0.021$, $df = 1$, $P = 0.884$) and adult (28% of females, $N = 408$ observations vs. 32% of males, $N = 1030$ observations; $\chi^2 = 2.516$, $df = 1$, $P = 0.113$) snakes. Further analyses considering the main types of prey ingested (lizard, mice and chicks) failed to detect a sex difference in juvenile (females fed on 10.0% lizards, 86.7% mice and 3.3% chicks; males fed on 10.7% lizards, 78.6% mice and 10.7% chicks; $\chi^2 = 1.266$, $df = 2$, $P = 0.531$; $N = 58$ identified prey) and adult (females fed on 0.0% lizards, 27.1% mice and 72.9% chicks; males fed on 0.3% lizards, 19.35% mice and 80.4% chicks; $\chi^2 = 3.194$, $df = 2$, $P = 0.205$; $N = 423$ identified prey) diets.

RELATIVE LITTER MASS

In six reproductive females captured shortly before parturition, the mean relative litter mass (the ratio of litter mass divided by post-parturition maternal mass) was 26.5%. The maternal mass dropped from 403.2 ± 81.6 to 304.0 ± 39.1 g after parturition. Subsequently, the post-parturient females were in poor body condition with large longitudinal skin folds visible on the posterior part of the body.

SURVIVAL RATES

The two models with the lowest AICc values were [$\phi(\text{age} \times \text{sex}) p(t \times \text{sex})$] and [$\phi(\text{age}) p(t \times \text{sex})$], with over 90% support in the data (Table 2). These models diverged by less than two in their AIC values, showing no significant sex effect on the survival rates within age classes. However, significant divergence between adult and juvenile survivorship was detected, as δAICc was 10.3 between the model with an age effect and the constant survival model. The estimates from model averaging gave juvenile survival rates of 0.498 (SE = 0.105) in females and 0.640 (SE = 0.089) in males, whereas, for adults, the rates were 0.787 (SE = 0.017) in females and 0.781 (SE = 0.014) in males. Capture probabilities were time and sex dependent; males were more catchable than females at any given period; δAICc was 3.36

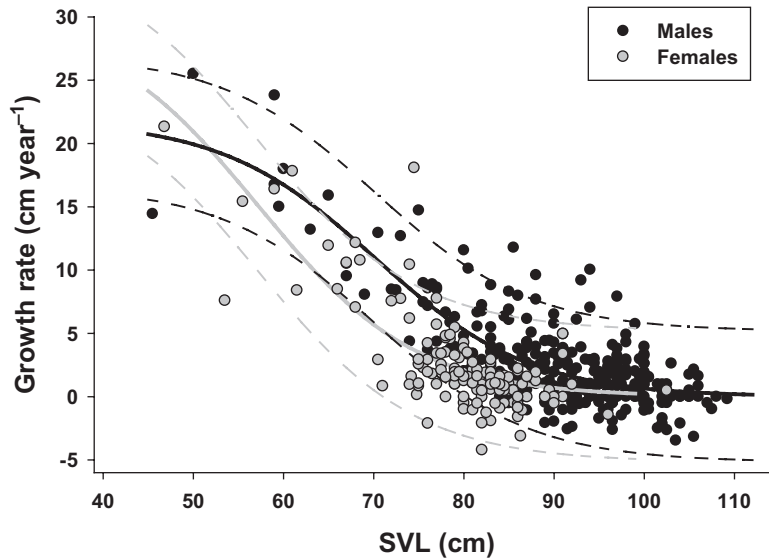


Figure 4. Growth rates of male (black filled symbols and black lines) and female (grey filled symbols and grey lines) tiger snakes modelled using Richard's equation (individual data were selected for homogeneity in the time elapsed between capture and recapture, 380 ± 30 days; each data point represents a different individual). The full line indicates the best fit between data and modelling; the broken lines provide confidence intervals (95%).

Table 2. Characteristics of the different models used to examine survival rates (ϕ) in tiger snakes

Model	AICc	δ AICc	AICc weights	Likelihood	<i>N</i>	Deviance
$\phi(\text{age} \times \text{sex}) p(t \times \text{sex})$	5160.4149	0.0000	0.48682	1.00000	30	2825.7844
$\phi(\text{age}) p(t \times \text{sex})$	5160.7170	0.3021	0.41857	0.85980	28	2830.2646
$\phi(\text{age} \times \text{sex}) p(t)$	5163.7768	3.3619	0.09064	0.18620	18	2854.0286
$\phi(.) p(t \times \text{sex})$	5170.7165	10.3016	0.00282	0.00580	27	2842.3484
$\phi(\text{sex}) p(t \times \text{sex})$	5172.5235	12.1086	0.00114	0.00230	28	2842.0710
$\phi(t \times \text{age} \times \text{sex}) p(t)$	5187.5049	27.0900	0.00000	0.00000	62	2784.2901
$\phi(\text{age} \times \text{sex}) p(t \times \text{sex})$	5187.5686	27.1537	0.00000	0.00000	73	2759.9963
$\phi(t \times \text{age} \times \text{sex}) p(t \times \text{age})$	5190.8856	30.4707	0.00000	0.00000	74	2761.0785
$\phi(t \times \text{age} \times \text{sex}) p(t \times \text{age} \times \text{sex})$	5209.9529	49.5380	0.00000	0.00000	95	2732.4047
$\phi(t \times \text{age} \times \text{sex}) p(.)$	5289.3165	128.9016	0.00000	0.00000	51	2910.0529

ϕ was held constant (\cdot), varied with time (t), with sex (sex), with age (age) or in interaction (\times) between these factors. Similarly, the probabilities of capture p were constant (\cdot), varied with time (t), with sex (sex), with age (age) or in interaction (\times) between these factors. N indicates the number of parameters estimated.

between the model with sex effect on capture [$\phi(\text{age} \times \text{sex}) p(t \times \text{sex})$] and the model with time dependence only [$\phi(\text{age} \times \text{sex}) p(t)$].

DISCUSSION

Comparative studies have demonstrated the variation in the direction and degree of SSD across taxa, but have also revealed broad trends (Emlen, Hunt & Simmons, 2005; Fairbairn, Blanckenhorn & Székely, 2007; Cox, Stenquist & Calsbeek, 2009). For instance, the reason why SSD tends to be male biased in endotherms (birds and mammals; Cabana *et al.*, 1982;

Arak, 1988), but reversed in most ectotherms (Shine, 1988, 1989; Fairbairn, 1997), remains largely unexplained, although the greater importance of sexual selection for large size of male endotherms probably plays a role (Clutton-Brock, Harvey & Rudder, 1977; Székely, Lislevand & Figuerola, 2007). Similarly, Rensch's rule (i.e. that in male-biased lineages, SSD tends to be more pronounced in larger species) has been validated in a wide variety of clades, but not in others (Abouheif & Fairbairn, 1997; Fairbairn, 1997, 2005; Blanckenhorn *et al.*, 2007; Webb & Freckleton, 2007; Stephens & Wiens, 2009). The variety of interacting potential factors known to influence the evolution of

SSD complicate understanding (Blanckenhorn *et al.*, 2007; Høye *et al.*, 2009); consequently, Stephens & Wiens (2009) cautioned that 'although global analyses of SSD across large clades may be particularly appealing due to their comprehensive nature . . . they may be problematic when different processes occur within different subclades'. This is particularly important in studies of ectothermic vertebrates, because they exhibit greater variation in the extent of SSD, mean body sizes and individual growth rates among and within lineages and populations compared with endotherms (Shine, 1994; Bonnet *et al.*, 2001; Fairbairn *et al.*, 2007). Incidentally, our data illustrate a clear dispersion of body sizes and growth rates (Figs 1–4) as a result of fluctuations of foraging success between individuals and years (Bonnet, Pearson; unpubl. data). Therefore, the identification of the proximate factors that determine the direction and intensity of SSD remains an important prerequisite for comparative studies seeking to understand the influence of ultimate forces (Cox *et al.*, 2003; Cox, Butler & John-Alder, 2007).

In arthropods exhibiting female-biased SSD, differential growth rates between the sexes are the major proximate determinants of SSD, whereas differences in development time play a secondary role (Blanckenhorn *et al.*, 2007). In vertebrate taxa that are male biased, differential growth rates between the sexes rather than differences in maturation time also determine SSD (this study; Beaupre, Duvall & O'Leile, 1998; Beaupre, 2003; Taylor *et al.*, 2005). Our data suggest that differential selection between the sexes acting at birth or during the juvenile phase, or niche divergence in adults, are not responsible for SSD observed in adults. Both sexes were similar in size and body condition at birth, followed almost indistinguishable growth trajectories and, as adults, both sexes exhibited equivalent food intake, fed on the same prey and were not subject to differential predation. Before maturity, females tended to store larger body reserves than males, without decreasing growth rates (and sizes). Our results suggest that, at maturity, a differential reproductive investment between males and females is responsible for the observed male-biased SSD (see also Beaupre, 2003; Taylor *et al.*, 2005).

Adult female tiger snakes invested significant quantities of body reserves and consumed food to produce offspring which, by inference, resulted in decreased growth rates. This relationship has been documented in other viviparous vertebrates (Madsen & Shine, 1993b; Bonnet, Naulleau & Mauget, 1994; Luiselli, Capula & Shine, 1996; Bonnet *et al.*, 2002b; Moyes *et al.*, 2006; Penn & Smith, 2007). The marked depletion of maternal body reserves during reproduction means that body reserves stored prior to reproduction (resulting in the observed better body

condition of females at this stage) were transferred to the follicles during vitellogenesis, and thus were not available for growth (all post-parturient females were emaciated with large skin folds).

Males do not seem to bear strong costs to reproduce. On Carnac Island, they do not move widely in search of mates (reproductive females are easy to locate) and they do not fight rivals. Perhaps because of this reduced activity, males do not show marked depletion of body reserves, reduced growth rates or mortality, as observed in many other taxa (e.g. Madsen & Shine, 1993b; Bonnet, Naulleau, Shine & Lourdais, 1999b; Bonnet, Naulleau & Shine, 1999c; Moore & Wilson, 2002; Shine, 2003; Burton-Chellew *et al.*, 2007). Whatever energetic costs are associated with spermatogenesis, they are probably modest compared with the requirements of vitellogenesis and gestation. In addition, in the absence of strong physical male competition, the possible selective advantage of a larger body size does not appear to be a strong determinant for SSD in the studied population (Shine, 1994).

Experiments altering the consequences of reproductive effort for both sexes would be very helpful (Bronikowski, 2000): for instance, feeding experiments to examine to what extent females are limited in their growing capacities relative to males, notably to determine whether the observed difference in adult growth rate persists in the absence of reproductive constraints (Prenter, Elwood & Montgomery, 1999; Lourdais *et al.*, 2003; Taylor & DeNardo, 2005; Le Galliard *et al.*, 2006). In captivity and in the absence of reproduction, female tiger snakes are able to grow and incorporate resources into somatic tissues at much higher rates than observed in the field. For example, a captive unmated female with an SVL of 78.0 cm and a body mass of 324 g was able to reach 91.5 cm SVL and 700 g body mass in 3 years. Her growth rate was 1.23 mm day⁻¹, compared with a maximum of 0.43 mm day⁻¹ in wild adults, and the heaviest free-ranging female weighed 635 g. Similarly, experiments based on endocrinal manipulations (e.g. exogenous administration of agonistic vs. antagonistic hormones) would be useful, because sex-specific hormones have a strong influence on energy allocation and growth rates in both sexes (Lerner & Mason, 2001; Cox & John-Alder, 2005; Cox, Zilberman & John-Alder, 2006; John-Alder, Cox & Taylor, 2007; Shelby *et al.*, 2007).

A recent review of the causes of SSD in three species of lizard from the genus *Sceloporus* (John-Alder *et al.*, 2007) suggested that the costs of reproduction experienced by males may actually drive the development of SSD in lizard species where females are larger. These results led to different conclusions from those for viviparous snakes, where maternal reproductive costs may play a major role. Such divergence further

illustrates that patterns across species and lineages are likely to reflect a complex interplay of proximate energetic constraints and ultimate selective pressures on growth and body size. Compared with snakes, lizards tend to be 'income breeders' (Warner *et al.*, 2008), having relatively low energetic reproductive investment, but males pay high reproductive costs. In this group of reptiles, the effect of maternal reproductive effort might be less than that of viviparous snakes, in which females produce high reproductive effort (Shine & Charnov, 1992). Other field studies (albeit usually lacking at least one major factor, such as neonate data, for example) have revealed a range of outcomes. For instance, males are smaller in two percid fish as a result of decreasing feeding activity (Rennie *et al.*, 2008). In this case, SSD results from differential foraging activity and maturity schedule, rather than from divergent reproductive efforts. In an Iguanian lizard, most of the male-biased SSD resulted from a greater post-maturity growth rate in males relative to females, with an additional influence of lower female survival (Watkins, 1996).

Overall, our results and those of other workers suggest that the physiological processes (and thus underlying combinations of alleles) that regulate female reproductive effort (follicle recruitment, follicular growth and gestation) are the best proximate candidates to interpret SSD in viviparous snakes. Perhaps the greater reproductive effort of females explains why males are larger in many species. It would be interesting to examine whether the intensity of female reproductive effort relative to male investment influences SSD. There are also species in which females invest in a large reproductive effort (e.g. most natricine snakes), but nonetheless remain the larger sex despite intensive intrasexual selection among males driven by very low operational sex ratios (Luiselli *et al.*, 1996; Brown & Shine, 2002); however, higher feeding frequency in female than male water snakes has been reported (Jones *et al.*, 2009). This is also the case in the asp viper (Bonnet *et al.*, 2000), although males represent the larger sex in most viperid snakes (Shine, 1994). Thus, various combinations of sexual selection, selection for fecundity and costs of reproduction can be imagined to lead to alternative evolutionary patterns (for instance, is male-to-male combat the determinant for the evolution of large males, or is it a by-product of intense costs of reproduction in females?). In the absence of extensive field data, the elucidation of the causes of SSD may remain imprecise even when framed within known phylogeny, because the complicating factors mentioned above may be retained in the analyses unless they can be identified and modelled. Experiments (performed in the laboratory or in the field) that offer the possibility to understand causal factors should be compared with

results from field studies. Ideally, various approaches should be combined, but there is, as yet, no study in which the contributions of the main proximate factors have been simultaneously investigated in the field, in the laboratory and through modelling. This is a useful direction for further study.

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