

Sex differences in body composition, performance and behaviour in the Colombian rainbow boa (*Epicrates cenchria maurus*, Boidae)

O. Lourdais^{1,2}, R. Shine³, X. Bonnet¹ & F. Brischox¹

¹ Centre d'Etudes Biologiques de Chizé, CNRS, Villiers en Bois, France

² Conseil Général des Deux Sèvres, Niort, France

³ School of Biological Sciences, University of Sydney, Australia

Keywords

sexual dimorphism; musculature; body composition; snakes.

Correspondence

Olivier Lourdais. CEBC-CNRS UPR 1934, 79 360 Villiers en Bois, France.

Tel: +33 (0) 5 49 09 96 16

Fax: +33 (0) 5 49 09 65 26

Email: Lourdais@cebc.cnrs.fr

Received 24 November 2004; accepted 6 September 2005

doi:10.1111/j.1469-7998.2006.00057.x

Abstract

Although most analyses of sexual dimorphism focus on overall body size (sexual size dimorphism), males and females of the same species may differ profoundly in their morphology, performance and behaviour even if the two sexes attain similar adult sizes. Thus, similarity in size may mask major sex-based divergences in traits such as musculature and fat stores. Although female Colombian rainbow boas *Epicrates cenchria maurus* are slightly longer than males, we show that males are more muscular than females and, accordingly, males outperform same-sized females in tests of strength. Musculature may enhance success in male–male combat. The two sexes also differ in body shape: the wider abdomens of females may allow more space to store fat and/or embryos. Lastly, male boas reacted more overtly to handling (via defecation and striking) than did females. These sex differences in morphology, performance and behaviour plausibly reflect ecological differences between the sexes in the wild, with males under sexual selection for increased physical strength and females under fecundity selection for enhanced reproductive output.

Introduction

In all sexually reproducing species, males and females differ significantly in morphology. In some cases this difference is limited to the gonads and associated structures, but in many taxa males and females differ in many other traits as well to the point that, in a few cases, taxonomists initially have described conspecific adults of each sex as different species (Shine, 1993). The most obvious dimension for such divergence is body size, and an extensive literature documents and attempts to explain interspecific and intraspecific variation in the degree of sexual size dimorphism (SSD) (Head, 1995; Wikelski & Trillmich, 1997; Loison *et al.*, 1999; Beaupre, 2002; Blondel *et al.*, 2002). This topic has been popular with evolutionary biologists ever since Darwin (1871), because restricting comparisons to males and females within a single population greatly simplifies the problem of identifying causal agents (selective forces) that might have generated such phenotypic evolution. At least three different selective processes might be at work in generating sexual dimorphism: sexual selection, fecundity selection and natural selection (Andersson, 1994). There is strong empirical evidence for the action of all three selective processes listed above. For example, larger males may win combat bouts against their smaller rivals, and thus obtain

additional mating opportunities (sexual selection: Darwin, 1871). Similarly, larger body size may be associated with higher reproductive output in females, with larger animals producing more or larger offspring (fecundity selection: Darwin, 1871). Last, males and females may be exposed to different selective forces if they forage in different places or on different items (natural selection). It is worth noting that, besides selective processes, the evolution of SSD might also be dependent on genetic, physiological or environmental constraints operating in different ways for males and females (Beaupre, 2002; Blondel *et al.*, 2002; Taylor & DeNardo, 2005).

A similarity in mean adult body sizes between the sexes (i.e. an absence of SSD) does not imply a lack of any sex difference in selective regimes, because the equality in body sizes might be due either to constraint (e.g. body size may be under such strong energy constraints that even intense selection does not result in significant SSD) or to balancing selection (e.g. fecundity selection on females balances sexual selection on males). Selective forces on the two sexes will often take very different forms, and will affect many aspects of the phenotype other than adult body size. Accordingly, several studies have shown major differences in body shape and body composition between the two sexes that reflect their different reproductive roles (Andersson, 1994; Bonnet

et al., 1998, 2001a; Malmgren & Tholleson, 1999; Olsson *et al.*, 2002). Because evolutionary divergence in traits such as body composition can occur without major changes in body size, species that lack SSD may nonetheless exhibit important sex differences in traits such as body composition.

Some of the best examples of sexual divergence in traits other than mean adult body size may come from animal taxa with simplified external morphology (Bonnet *et al.*, 1998). This simplification reduces the number of axes along which males and females may vary, and hence facilitates direct comparison between conspecific animals of each sex. Snakes are useful study organisms in this respect (Bonnet *et al.*, 1998). For example, although body size is an important determinant of fighting ability in species with male–male combat (Shine, 1978, 1993; Andersson, 1994; Schuett, 1997), musculature may also be important. Although the high frequency of male–male combat suggests that sex differences in musculature may be common among vertebrates, such a difference is easier to quantify in the relatively simple morphology of a snake than it would be in a species where the sexes differ substantially in shape as well as size (Bonnet *et al.*, 1998). Similarly, maternal body size, an important determinant of (or constraint on) reproductive output (Shine, 1988, 1992), is relatively easy to measure in elongate animals such as snakes. Combined with abdominal width, it can provide an index of abdominal fat stores, which are important in the reproductive effort of capital breeding species (O. Lourdais, X. Bonnet, F. Brischox & L. Baratin, unpubl. data). Such a situation greatly simplifies the assessment of sex differences in body composition (Bonnet *et al.*, 1998).

In the present study, we document sex differences in body composition, performance and behaviour in the Colombian rainbow boa *Epicrates cenchria maurus*, a constricting snake species that shows only minor sexual dimorphism in mean adult body size.

Methods

Study species and maintenance

Epicrates cenchria maurus are medium-sized [up to 1500 mm snout–vent length (SVL)], non-venomous, constricting snakes from South and Central America (Ross & Marzec, 1990; Matz, 2001). The species is viviparous and females give birth to 5–15 young after a 2–3-month gestation period. Before vitellogenesis, females accumulate substantial abdominal fat stores. SSD in the genus *Epicrates* is relatively slight; Fitch's (1981) review lists one taxa (*angulifer*) as having females larger than males, two taxa (*fordi*, *striatus*) as having males larger than females, and one taxon (*gracilis*) as having no obvious SSD. There have been no published accounts of SSD in *E. c. maurus*. Males fight each other during the breeding season (O. Lourdais, pers. obs.), as in other *Epicrates* species (Tolson, 1983; Tolson & Henderson, 1993). The snakes in our study (19 females, plus 20 males) were obtained in 2001 from a long-term captive snake colony. Snakes were maintained in the laboratory in separ-

rate cages (50 × 50 × 20 cm) that provided free access to a heat source (temperature range in the cage: 28–33 °C). Water was available *ad libitum*, and snakes were fed rats (mean mass = 150 g) once a month.

Variables measured

Our aim was to assess sexual dimorphism in a suite of variables, including morphology, body composition (relative musculature and energy stores), physical performance and defensive behaviour. Because of an elongate morphology, simple external variables can be used to provide an index of musculature and fat stores in snakes. All measurements were taken after an 8-month feeding period and while snakes were not reproductive. Hence all individuals were well fed and in good body condition at the time of data collection.

Body size and body composition

In order to reduce measurement error, all snakes were anaesthetized using isoflurane (Abbott Laboratories, Abbott Park, IL, USA) before measurement sessions. This anaesthetic induced complete muscular relaxation. Apart from the standard size descriptors [SVL, total body length (BL) and body mass (BM)], we also measured:

(1) *Width of the epaxial musculature*: Because male *E. c. maurus* wrestle with each other during the breeding season, we may expect a more developed musculature in males than in females. In snakes, the epaxial muscles lying beside the vertebral column are of primary importance in locomotion (Cundall, 1987) and constriction (Moon, 2000). We measured the width of the epaxial muscles at four positions between the head and the vent (20, 40, 60 and 80% of the snake's SVL). Magnetic resonance imaging (MRI) of epaxial musculature in *E. c. maurus* has verified that external measurements of muscle width with calipers provide accurate estimates of muscle size (Lourdais *et al.*, 2004; Lourdais, Brischox & Barantin, 2005).

(2) *Abdominal fat stores*: Female boas store fat for later use in reproduction. In another study on this species, we showed that abdominal width is significantly correlated with fat stores (O. Lourdais *et al.*, unpubl. data). To examine possible differences in body shape, we measured body width at four equally spaced points between the head and the vent (20, 40, 60 and 80% of the snake's SVL).

(3) *Body composition*: We examined the determinants of body mass for each sex using stepwise backward multiple regression including SVL, a musculature index and an abdominal fat index as factors. For each individual, the musculature index was calculated as follows. First, we calculated total musculature as the sum of width measurements in each of four body sections. Then, we calculated an index of musculature as the residual value from the general linear regression of total musculature against SVL (ln transformed). The same procedure was used to provide an index of abdominal fat (including only body sections 3 and 4, where fat stores are located).

Physical performance

Our predictions about musculature in male snakes rely upon the assumption that increased musculature results in increased strength. We measured the strength of male and female boas in three contexts designed to mimic biologically realistic challenges. The validity of these estimators is established in a related paper (Lourdais, Brischox & Barantin, 2005). Measurements were taken after complete recovery from anaesthesia and with at least 2 days between successive measurements.

(1) *Escape from a predator*: *Epicrates cenchria maurus* react to handling, especially attempts to stretch their bodies, by vigorous and extended body contraction. We quantified the strength of these tractions using a dynamometer connected to the snakes' tails (Pesola, Baar, Switzerland). Snakes were stretched and then touched at mid-body to stimulate body contractions. A drag pointer on the dynamometer recorded the maximum tension during a 5-min period of repeated stretching and contraction. The procedure was harmless and detailed information on the method is available in a related manuscript (Lourdais, Brischox & Barantin, 2005).

(2) *Prey handling*: We measured the intensity of muscular contraction during prey constriction using a compressible lure (10 cm long \times 2 cm diameter water-filled rubber balloon surrounded by mouse-scented cloth: Lourdais, Brischox & Barantin, 2005). The lure was connected to an open water column via a rigid plastic tube (5 mm in diameter). Snakes readily bit and coiled around the lure, which was then wiggled for 10 s to simulate normal prey reaction. Displacements of the water column were videotaped so that maximal displacement (cm) could be subsequently measured.

(3) *Climbing ability*: When held by the tail, *E. c. maurus* climb up their own bodies towards the hand of the operator. Each snake was removed from its cage and placed on the ground. The snake was then lifted by the tip of the tail so that its head was positioned *c.* 30 cm off the ground. We measured the length of time required for the snake's head to reach the operator's hand on three consecutive trials. The same operator always carried out the procedure in the same area (O. Lourdais).

Defensive behaviour

During our performance trials, the snakes often reacted to our handling by biting, discharging their anal glands, or refusing to attack the lure. We quantified these behaviours as detailed below.

(1) *Chemical defence*: Extrusion of strongly odoriferous cloacal gland materials is a common anti-predator tactic in snakes (Graves & Duvall, 1984, 1988; Greene, 1988). At the end of our 5-min trials of traction, the cloacal region of each snake was visually inspected for musk discharge.

(2) *Bite*: After the defence trial, each snake was placed back into its individual cage. The cage was kept open and bites were then elicited by moving a piece of cloth a short distance (20 cm) in front of the snake. We counted the number of bites during a 60-s stimulation trial for each

individual. In order to minimize disturbances, the test was not replicated.

(3) *Escape from the lure*: When the lure was presented, some snakes adopted a defensive posture by hiding their heads beneath their coils or by moving away from the lure. We recorded whether or not a snake refused to attack the lure at the first presentation.

Statistics

All statistics were performed with Statistica 6.0. Differences in musculature and abdominal width were examined using one-factor analysis of covariance (ANCOVA) with musculature or abdominal width as the dependent variable, sex as a fixed factor and SVL as the covariate. In each case, we tested the equality of slopes between males and females. To facilitate an intuitive understanding of any differences detected, we also conducted analysis of variance (ANOVA) on these data after restricting the analysis to males and females over a common range of body sizes. Sex differences in physical performance and defensive behaviour were examined using one-factor ANOVA. Finally, the frequencies of defensive behaviours were compared using contingency-table (Yates corrected chi-square) analysis. Unless otherwise stated, all values are presented in the text as the mean \pm 1SD.

Results

Body size and body composition

Body size and body mass

Female boas averaged larger than males (mean values for SVL, 119.26 ± 7.60 vs. 108.84 ± 6.08 cm, $F_{1,37} = 35.47$, $P < 0.0001$; for body mass, $1154.85 + 176.8$ vs. $885.67 + 141.4$ g, $F_{1,37} = 27.72$, $P < 0.0001$). Mass relative to SVL did not differ between the sexes (ANCOVA: effect of sex: $F_{1,36} = 0.34$, $P = 0.56$; homogeneity of slopes: $F_{1,35} = 0.27$, $P = 0.60$). Females had shorter tails relative to SVL than did males (mean adjusted values for tail length: 13.91 ± 1.43 vs. 16.70 ± 1.40 cm; ANCOVA: effect of sex: $F_{1,36} = 27.75$, $P < 0.0001$; homogeneity of slopes: $F_{1,35} = 0.41$, $P = 0.52$). Although females attained larger average sizes, there was substantial overlap between the two sexes, with SVLs of nine males and eight females within the range of 110–117 mm. The following analyses are based both on the total sample and on the subset of snakes within this restricted size range.

Musculature

Male boas were more muscular than females for each body section considered (see Table 1). Musculature width varied across different sections of the body, peaking in section 2 (Table 1). The same conclusions were obtained when analysis was restricted to males and females over the range of common body sizes (Fig. 1).

Table 1 Sex differences in dorsal muscles and body diameter (mm) of 20 male and 19 female rainbow boas *Epicrates cenchria maurus* measured at four equidistant points between the head and the vent (1–4 starting from the head)

Body section	Males	Females	F	P-value
Epaxial muscles width				
1	19.40 ± 1.22	18.11 ± 1.56	5.78	0.0215
2	21.20 ± 1.12	20.12 ± 1.25	5.23	0.028
3	20.02 ± 1.01	18.29 ± 1.17	18.76	0.0001
4	18.53 ± 1.33	16.67 ± 1.29	13.68	0.0007
Body width				
1	28.79 ± 2.60	28.59 ± 2.85	0.04	0.83
2	35.29 ± 3.42	34.51 ± 4.06	0.33	0.56
3	38.56 ± 4.76	37.73 ± 4.88	0.21	0.64
4	32.64 ± 3.27	36.45 ± 2.73	8.45	0.0063

P-values were obtained from separate analysis of covariance (ANCOVA) analyses using musculature width or body diameter as the dependent variable and sex as the factor. Values are reported as size-adjusted means ± SD. Tests for equality of slopes were non-significant (all $P > 0.20$).

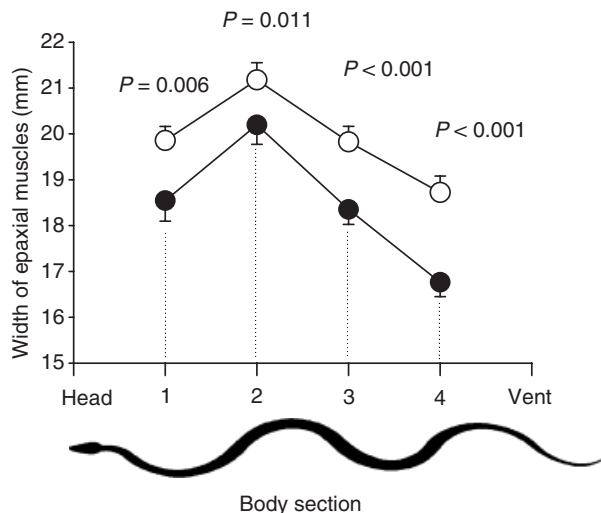


Figure 1 Musculature profiles measured in nine male (●) and eight female (○) rainbow boas with similar body sizes. Dorsal muscle widths (mm) were measured at four equidistant points between the head and the vent (one to four starting from the head). P-values were obtained from ANOVA analysis using musculature width as the dependent variable and sex as the factor.

Body width

At the same SVL, females had wider abdomens than did males (section 4; see Table 1). The sex difference in abdomen width was also evident in individuals of similar body sizes (mean values for abdomen width, 36.60 ± 3.44 vs. 33.04 ± 2.69 mm; $F_{1,15} = 5.42$, $P = 0.0355$).

Body composition

SVL was the primary determinant of body mass in both sexes, explaining 64% (male) and 67% (female) of the

variation observed (Table 2). However, residual variation in body mass was mostly due to musculature index in males and abdominal index in females (Table 2).

Physical performance

Traction strength

Male boas exerted greater contractile strength than did females ($F_{1,37} = 5.80$, $P = 0.021$, Fig. 2). The difference was even greater when considering only individuals of similar body sizes (mean values for traction strength, 110.14 ± 17.49 vs. 63.46.00 ± 9.96 N; $F_{1,15} = 44.06$, $P < 0.0001$).

Prey handling

No significant differences in maximal constriction pressure were evident between the sexes (mean constriction values, 23.52 ± 7.14 vs. 21.6 ± 4.57 mm for females and males, respectively; $F_{1,33} = 0.83$, $P = 0.37$). Larger females exerted more pressure on the lure ($r^2 = 0.36$; $F_{1,15} = 8.42$, $P < 0.01$). Males and females of similar body sizes also exerted similar constriction pressures (mean constriction values, 21.41 ± 6.74 vs. 21.93 ± 4.54 mm for females and males, respectively; $F_{1,15} = 0.04$, $P < 0.85$) and wrapped around the lure for similar periods of time (mean constriction duration, 108.23 ± 44.7 vs. 106.44 ± 43.06 s for females and males, respectively; $F_{1,33} = 0.01$, $P = 0.90$).

Climbing ability

When suspended by the tail, males took less time to reach the hand of the operator than did females (2.93 ± 1.02 vs. 8.84 ± 4.01 s; $F_{1,37} = 34.75$, $P < 0.0001$; for same-sized animals, $F_{1,15} = 13.98$, $P < 0.002$, Fig. 3).

Defensive behaviour

Chemical defence

Male snakes often reacted to handling by expelling the contents of their anal glands, whereas this behaviour was less common in females (nine of 20 vs. three of 19). This difference however was not significant (Yates corrected $\chi^2 = 2.65$, d.f. = 1, $P = 0.10$).

Response to the lure

Defensive responses to the lure occurred more frequently in males than in females (eight of 20 vs. four of 19), but this difference was not statistically significant (Yates corrected $\chi^2 = 0.85$, d.f. = 1, $P = 0.35$).

Defensive strikes

Males were more prone to bite than females (11 of 20 vs. four of 19; Yates corrected $\chi^2 = 3.42$, d.f. = 1, $P = 0.065$),

Variable	Step	Change in r^2	F	$\beta \pm \text{SE}$	P -value
<i>Males: $r=0.93$; $r^2=0.87$; $n=20$; $F_{3,16}=36.87$; $P<0.00001$</i>					
BL	1	0.62	29.47	0.84 ± 0.09	0.00006
MUSC	2	0.22	22.63	0.39 ± 0.09	0.0002
ABDO	3	0.04	4.59	0.20 ± 0.09	0.047
<i>Females: $r=0.96$; $r^2=0.93$; $n=19$; $F_{3,15}=60.62$; $P<0.00001$</i>					
BL	1	0.67	35.43	0.80 ± 0.07	0.00003
ABDO	2	0.18	20.54	0.31 ± 0.08	0.0004
MUSC	3	0.06	12.94	0.28 ± 0.08	0.003

The best model was obtained by including all three independent variables. BL accounted for most of the variance observed in body mass in males and females. The residual variance was mainly explained by musculature (males) or abdominal width (females). See text for statistics.

Table 2 Influences of body length (BL), musculature condition (MUSC) and abdominal width (ABDO) on body mass for male and female rainbow boas *Epicrates cenchria maurus*

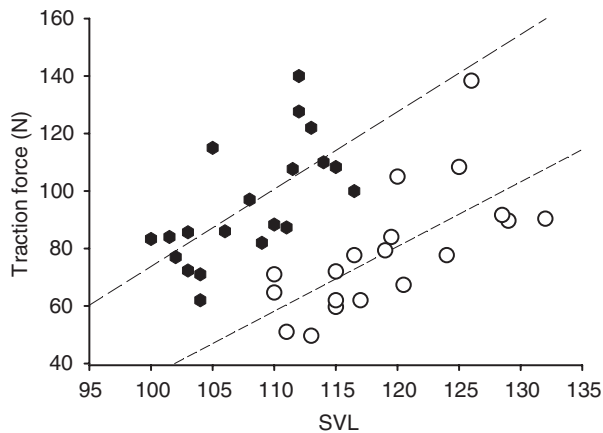


Figure 2 Relationship between maximal contraction strength (N) and snout-vent length of 20 male (●) and 19 female (○) rainbow boas. Each point represents an individual snake.

and the number of bites elicited was higher in males (5.69 ± 2.98 vs. 2.25 ± 1.25 ; $F_{1,15} = 4.88$, $P = 0.043$).

Discussion

Although showing relatively slight sexual dimorphism in mean adult body size, male and female rainbow boas nonetheless differ substantially in many other traits. Although males and females exhibit similar body mass at the same body length, this equivalence masks an underlying difference in body composition: males have more muscle mass whereas females apparently store more abdominal fat. Thus, variables related to body composition are useful tools in an integrated approach to studying sexual dimorphism. Notably, it permits a focus on specific aspects of body plan that may be driven by a limited number of predictable selective forces (Bonnet *et al.*, 1998). Below, we consider in more detail the likely functional significance of the sexual dimorphism that we have documented in rainbow boas.

First, female *E. c. maurus* tended to be longer, and as a consequence were heavier than males. Limited abdominal space may constrain reproductive investment in terms of either offspring number or total clutch mass (Vitt &

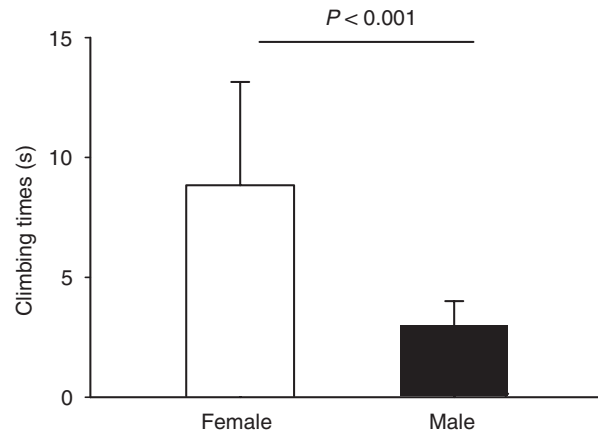


Figure 3 Climbing ability of 20 male (black bars) and 19 female (white bars) rainbow boas. When suspended by the tail, males took less time to reach the hand of the operator than did the females. Error bars represent standard deviation.

Congdon, 1978; Shine, 1988; Qualls & Andrews, 1999). In support of this putative constraint, many reptile species show a strong relationship between maternal body size and reproductive output (Fitch, 1981; Shine, 1988). In this context, fecundity selection is likely to favour large body size in females. Indeed, comparative analyses have shown a significant link between the degree of sexual size dimorphism in snakes and the intensity of fecundity selection (as indicated by the rate at which fecundity increases with maternal body size; Shine, 1993). However, fecundity selection will operate on other aspects of maternal body structure as well. For example, female snakes typically have shorter tails (relative to SVL) than do conspecific males, and this is due at least partly to a tendency for the cloaca to be positioned at a more posterior body segment in females than in males (King, 1989; Shine, 2000; Shine & Shetty, 2001). This sex difference in cloacal position, also detected in the rainbow boa, essentially creates a longer abdomen relative to total length, and thus enhances abdominal volume in females. Large body size can enhance male mating success, especially in species with male–male combat. Although male–male combat occurs in *E. c. maurus*, the limited SSD

suggests a balanced situation whereby sex-specific selective forces result in relatively little sex divergence in mean adult body sizes (Rivas & Burghardt, 2001). Such a situation can mask the degree and direction of selective forces acting on variables other than body size. In this context, studies on variables other than body size can clarify the study of sexual dimorphism (Bonnet *et al.*, 1998, 2001a).

Using such an integrative approach, we found that males had thicker epaxial musculature than did same-sized females in each of the four body sections that we measured, and these differences were associated with 30% higher values for traction strength in males. These differences in musculature are consistent with the mating system of the species, where males undertake intensive locomotor activities during mate searching, and sometimes engage in prolonged combat bouts with rivals before mating (Shine, 1993; Tolson & Henderson, 1993). Intensive searching trips and the form of combat bouts (wrapping around one's rival and constricting strongly, perhaps to impede respiration by the other snake and thus induce hypoxic stress; Shine, Langkilde & Mason, 2003) are likely to favour individuals that are stronger and hence have greater muscle mass. Sexual divergence in musculature may be one of the most widespread forms of dimorphism in living organisms and has previously been documented in different snake lineages (Schwaner & Sarre, 1990; Bonnet *et al.*, 1998, Bonnet, Ineich & Shine, 2005).

The sexes also differed in abdominal width relative to SVL, with females having wider abdomens. This sexual dimorphism reflects the concentration of fat storage in the posterior region (O. Lourdais *et al.*, unpubl. data). Like females of many other ectothermic species, female rainbow boas accumulate fat prior to its expenditure during vitellogenesis (i.e. capital breeding; Jöhnsson, 1997; Bonnet, Bradshaw & Shine, 1998). Body fat provides a major source of energy and materials during reproduction, and females with more body fat produce larger offspring (O. Lourdais *et al.*, unpubl. data). Although the quantity of abdominal fat store is tightly linked to foraging success in nature, our experimental conditions minimized this source of variation because both males and females were regularly fed. The sex difference in fat stores likely reflects sex differences in physiological adaptations for energy storage. Thus, a similarity in body condition (mass relative to SVL) between the sexes masked significant sex differences in body composition. In keeping with this interpretation, our multiple regression analyses showed sex differences in the determinants of body mass variation. That is, male body condition was driven mostly by variation in muscularity, whereas female body condition was driven mostly by variation in fat storage.

Finally, we also examined differences in behaviour, including prey handling and climbing abilities. Interestingly, the differences we observed in musculature were not associated with differences in constriction maxima or constriction duration. By contrast, climbing time was significantly different, with males reaching the hand of the operator more rapidly than females. Such differences may be related to musculature but may also involve sex differences in physio-

logy and reaction to disturbance. For example, defensive reactions tended to be more frequent in males. The sex difference in anti-predator responses of our snakes may reflect sexual selection, with males retaliating more frequently either because of direct (non-adaptive?) physiological differences or because their frequent mate-searching movements may often bring them into encounters with predators in situations (away from cover) where active retaliation is the most effective form of defence (Duvall, King & Gutzweiler, 1985; Shine *et al.*, 2000).

In summary, the relatively minor sex divergence in mean adult body sizes in rainbow boas masks more subtle sexual dimorphism in anatomy (and thus performance) as well as behaviour. These divergences are likely to reflect sexual selection on males (notably, for success in physical combat with rival males) as well as fecundity selection on females. Among vertebrates, squamate reptiles show dramatic intraspecific variation in adult body size (at both intra- and inter-population levels) reflecting plasticity in growth trajectories (Bonnet *et al.*, 2001b). In this context SSD may be generated by proximate (ecological) factors, and several studies have shown inter-population variation in SSD depending on local food availability (Shine, 1990, 1991; Forsman, 1991; Madsen & Shine, 1993; Pearson, Shine & How, 2002a; Pearson, Shine & Williams 2002b). Because of this 'variability' in SSD, our study emphasizes the advantages of taking an integrative approach, and of incorporating measurements of variables other than body size to quantify the direction and degree of sexual dimorphism. Additional studies under natural conditions are required to examine how variations in traits such as musculature or internal organization affect individual fitness.

Acknowledgements

We thank Emily Taylor and Jean-Pierre Vacher for helpful comments on the manuscript. Sabrina Servanty helped during data collection. We are grateful to Gilbert Matz for providing the snake colony. Financial support was provided by the Conseil Général des Deux-Sèvres, the CNRS and the Australian Research Council.

References

- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Beaupre, S.J. (2002). Modeling time–energy allocation in vipers: individual responses to environmental variation and implications for populations. In *Biology of the vipers*: 463–481. Schuett, G.W., Hoggren, M., Douglas, M.E. & Greene, H.W. (Eds). Eagle Mountain, UT: Eagle Mountain Publishing.
- Blondel, J., Perret, P., Anstett, M.C. & Thebaud, C. (2002). Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *J. Evol. Biol.* **15**, 440–450.

- Bonnet, X., Bradshaw, S.D. & Shine, R. (1998). Capital versus income breeding: an ectothermic perspective. *Oikos* **83**, 333–341.
- Bonnet, X., Ineich, I. & Shine, R. (2005). Terrestrial locomotion in sea snakes: the effects of sex and species on cliff-climbing ability in sea kraits (Serpentes, Elapidae, *Laticauda*). *Biol. J. Linn. Soc.* **85**, 433–441.
- Bonnet, X., Lagarde, F., Henen, B.T., Corbin, J., Nagy, K.A., Naulleau, G., Balhoul, K., Chastel, O., Legrand, A. & Cambag, R. (2001a). Sexual dimorphism in steppe tortoises: influence of the environment and sexual selection on body shape and mobility. *Biol. J. Linn. Soc.* **72**, 357–372.
- Bonnet, X., Shine, R., Naulleau, G. & Thiburce, C. (2001b). Plastic vipers: environmental influences on the size and shape of Gaboon vipers, *Bitis gabonica*. *J. Zool. (Lond.)* **255**, 341–351.
- Bonnet, X., Shine, R., Naulleau, G. & Vacher-Vallas, M. (1998). Sexual dimorphism in snakes: different reproductive roles favour different body plans. *Proc. Roy. Soc. Ser. B* **265**, 1–5.
- Cundall, D. (1987). Functional morphology. In *Snakes: ecology and evolutionary biology*: 210–252. Seigel, R.A., Collins, J.T. & Novak, S.S. (Eds). New York: Macmillan.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: John Murray.
- Duvall, D., King, M.B. & Gutzweiler, K.J. (1985). Behavioral ecology and ethology of the prairie rattlesnake. *Nat. Geo. Res.* **1**, 80–111.
- Fitch, H.S. (1981). Sexual size differences in reptiles. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **70**, 1–72.
- Forsman, A. (1991). Variation in sexual size dimorphism and maximum body size among adder populations – effects of prey size. *J. Anim. Ecol.* **60**, 253–267.
- Graves, B. & Duvall, D. (1984). An alarm pheromone from the cloacal sacs of prairie rattlesnakes. *Am. Zool.* **24**, 17A.
- Graves, B. & Duvall, D. (1988). Evidence of an alarm pheromone from the cloacal sacs of prairie rattlesnakes. *Southwestern Nat.* **33**, 339–345.
- Greene, H.W. (1988). Antipredator mechanisms in reptiles. In *Biology of the Reptilia. Vol. 16*: 1–152. Gans, C. & Huey, R.B. (Eds). New York: Alan R. Liss.
- Head, G. (1995). Selection on fecundity and variation in the degree of sexual dimorphism among spider species (class Araneae). *Evolution* **49**, 776–781.
- Jönsson, K.I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66.
- King, R.B. (1989). Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? *Biol. J. Linn. Soc.* **38**, 133–154.
- Loison, A., Gaillard, J.M., Pelabon, C. & Yoccoz, N.G. (1999). What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* **1**, 611–633.
- Lourdais, O., Brischoux, F. & Barantin, L. (2005). How to assess musculature and performance in a constricting snake? A case study in the Colombian rainbow boa (*Epicrates cenchria maurus*). *J. Zool. (Lond.)* **265**, 43–51.
- Lourdais, O., Brischoux, F., DeNardo, D. & Shine, R. (2004). Protein catabolism in pregnant snakes (*Epicrates cenchria maurus*, Boidae) compromises musculature and performance after reproduction. *J. Comp. Physiol. B* **174**, 383–391.
- Madsen, T. & Shine, R. (1993). Phenotypic plasticity in body sizes and sexual dimorphism in European grass snakes. *Evolution* **47**, 321–325.
- Malmgren, J.C. & Tholleson, M. (1999). Sexual size and shape dimorphism in two species of newts, *Triturus cristatus* and *T. vulgaris* (caudata: Salamandridae). *J. Zool. (Lond.)* **249**, 127–136.
- Matz, G. (2001). Biologie de la reproduction de *Epicrates maurus* Gray, 1849. *Situla*, **3**, 10–15.
- Moon, B.R. (2000). The mechanics and muscular control of constriction in gopher snakes (*Pituophis melanoleucus*) and a king snake (*Lampropeltis getula*). *J. Zool. (Lond.)* **252**, 83–98.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* **56**, 1538–1542.
- Pearson, D., Shine, R. & How, R. (2002a). Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). *Biol. J. Linn. Soc.* **77**, 113–125.
- Pearson, D., Shine, R. & Williams, A. (2002b). Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**, 418–426.
- Qualls, C.P. & Andrews, R.M. (1999). Maternal body volume constrains water uptake by lizard eggs *in utero*. *Func. Ecol.* **13**, 845–851.
- Rivas, J.A. & Burghardt, G.M. (2001). Understanding sexual dimorphism in snakes: wearing snakes's shoe. *Anim. Behav.* **62**, F1–F6.
- Ross, R.A. & Marzec, G. (1990). *The reproductive husbandry of pythons and boas*. Stanford, CA: Institute for Herpetological Research.
- Schuett, G.W. (1997). Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim. Behav.* **54**, 213–224.
- Schwane, T.D. & Sarre, S.D. (1990). Body size and sexual dimorphism in mainland and island tiger snakes. *J. Herpetol.* **24**, 320–322.
- Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia* **33**, 269–278.
- Shine, R. (1988). The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. *Am. Nat.* **131**, 124–131.
- Shine, R. (1990). Proximate determinants of sexual differences in adult body size. *Am. Nat.* **135**, 278–283.
- Shine, R. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Am. Nat.* **138**, 103–122.
- Shine, R. (1992). Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* **46**, 828–833.

- Shine, R. (1993). Sexual dimorphism in snakes. In *Snakes: ecology and behavior*: 49–86. Seigel, R. & Collins, J. (Eds). New York: McGraw-Hill.
- Shine, R. (2000). Vertebral numbers in male and female snakes: the roles of natural, sexual and fecundity selection. *J. Evol. Biol.* **13**, 455–465.
- Shine, R., Langkilde, T. & Mason, R.T. (2003). Cryptic forcible insemination: male snakes exploit female physiology, anatomy and behavior to obtain coercive matings. *Am. Nat.* **162**, 653–667.
- Shine, R., Olsson, M.M., LeMaster, M.P., Moore, I.T. & Mason, R.T. (2000). Effects of sex, body size, temperature and location on the antipredator tactics of free-ranging gartersnakes (*Thamnophis sirtalis*, Colubridae). *Behav. Ecol.* **11**, 239–245.
- Shine, R. & Shetty, S. (2001). The influence of natural selection and sexual selection on the tails of sea-snakes (*Laticauda colubrina*). *Biol. J. Linn. Soc.* **74**, 121–129.
- Taylor, E.N. & Denardo, D.F. (2005). Sexual size dimorphism and growth plasticity in snakes: an experiment on the Western diamond-backed rattlesnake (*Crotalus atrox*). *J. Exp. Zool.* **303A**, 598–607.
- Tolson, P.J. (1983). Captive propagation and husbandry of the Cuban boa, *Epicrates angulifer*. In *Sixth annual reptile symposium on captive propagation and husbandry*: 285–293. Marcellini, D.L. (Ed.). Thurmont, MD: Zoological Consortium.
- Tolson, P.J. & Henderson, R.W. (1993). *The natural history of West Indian boas*. Portishead, UK: R & A.
- Vitt, L.J. & Congdon, J.D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards – resolution of a paradox. *Am. Nat.* **112**, 595–608.
- Wikelski, M. & Trillmich, F. (1997). Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* **51**, 922–936.