

LIFE-HISTORY ADAPTATIONS TO ARBOREALITY IN SNAKES

LÍGIA PIZZATTO,^{1,4} SELMA M. ALMEIDA-SANTOS,² AND RICHARD SHINE³

¹*Pós-Graduação em Ecologia, Depto. de Zoologia, Universidade Estadual de Campinas, CP6109, 13083-970, Campinas, SP, Brazil*

²*Laboratório de Herpetologia, Instituto Butantan, Av. Dr. Vital Brazil, 1500, 05503-900, São Paulo, SP, Brazil*

³*School of Biological Sciences A08, University of Sydney, New South Wales 2006, Australia*

Abstract. If selective forces on locomotor ability and reproductive biology differ among habitats, we expect to see relationships between habitat, morphology, and life-history traits. Comparative (phylogenetically based) analysis of data from 12 pythonid and 12 booid snake species reveals multiple evolutionary shifts in habitat use, notably in the evolution of arboreal habits. Compared to terrestrial and aquatic taxa of the same overall body size, arboreal species have narrower and more laterally compressed bodies and relatively longer tails. Offspring sizes are not affected by arboreality, but presumably reflecting space constraints within their narrow bodies, arboreal species (1) produce smaller clutch sizes relative to maternal body length and (2) have left and right ovaries that overlap little if at all along the length of the body (i.e., the right ovary is positioned anterior to the left ovary) whereas in terrestrial snakes the two ovaries overlap along much of their length. This modification of ovarian morphology in arboreal snakes presumably reduces the degree of bodily distension during vitellogenesis and pregnancy, thus enhancing climbing ability and camouflage among the branches.

Key words: *adaptation; arboreality; Boidae; clutch size; ovarian position; Pythonidae.*

INTRODUCTION

Understanding the adaptive significance of interspecific divergence in life-history traits remains a major challenge for evolutionary biologists. Some of the strongest suggestive evidence in this respect comes from empirical patterns of covariation between morphology, reproductive biology, and general ecology (e.g., habitat use). Such patterns can allow strong inferences about the selective forces that have shaped life-history diversity (Williams 1966, Rose and Lauder 1996). That is, a trait that shows a consistent association with specific environments, habitat types, or other ecological traits, especially if the association results from multiple independent evolutionary origins, is likely to be adaptive to some aspect of that environmental or ecological condition (Harvey and Keymer 1991). Hence, broad phylogenetically based comparisons between life history, morphology, and environment offer a powerful technique to identify such associations and to suggest hypotheses about the selective forces that have generated life-history diversity.

An extensive literature identifies the physical burden of pregnancy as a significant cost of reproduction in many types of animals and suggests that such costs may depend upon the kind of habitats used by the species. Most obviously, the physical distension of the female's body while she is carrying eggs or offspring may impair maternal locomotion. In fishes, for example, embryo

development increases both the body mass and cross-sectional area of gravid females, resulting in both morphological and physiological changes that affect swimming speed and endurance (James and Johnston 1998, Plaut 2002, Ghalambor et al. 2004). Similar decrements to maternal mobility during pregnancy have been reported for snakes (Brodie 1989, Webb 2004), lizards (Shine 1980, 2003, Bauwens and Thoen 1981, Garland 1985, Sinervo 1990, Sinervo et al. 1991, Miles et al. 2000), birds (Lee et al. 1996, Veasey et al. 2001), and even prawns (Berglund and Rosenqvist 1986) and copepods (Winfield and Townsend 1983). Thus, both increased conspicuousness and decreased mobility may render pregnant females more vulnerable to predation (Magnhagen 1991). Females apparently reduce this cost of reproduction in a variety of ways, including changes in behavior (Cooper et al. 1990) and in the magnitude and placement of the reproductive burden (Shine 1988).

The relatively simplified bauplan of snakes makes it easier for investigators to quantify morphology and to compare animals from disparate phylogenetic lineages (Seigel and Ford 1987, Shine 1988). The linear body plan of snakes also facilitates straightforward measurement of the relative position of the clutch or litter within the female's body, a trait that presumably varies interspecifically within many lineages but is not amenable to simple linear quantification in most of them. Shine (1988) took advantage of this opportunity to show that the evolution of aquatic habits within snakes has been consistently associated with the evolution not only of a reduced clutch mass, but also a repositioning of the clutch within the female's body. Apparently reflecting the biomechanical challenges associated with swimming

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Corresponding Editor: D. K. Skelly.

⁴ E-mail: ligia_oceanica@yahoo.com

(especially, the importance of the posterior body in generating propulsion), aquatic snakes carry the clutch in a position more anterior in the body than do their terrestrial counterparts (Shine 1988).

Biomechanical considerations suggest that selection should act also on the relative position of paired structures, such as ovaries and oviducts, within an elongate body. Although most vertebrates exhibit bilateral symmetry in the placement of paired internal organs (e.g., lizards; Fox 1977), elongate taxa frequently exhibit marked deviations from symmetry such that paired organs are of different sizes and one is found anterior to the other, rather than side by side (Gans 1975). For example, such modifications can be seen in the lungs, kidneys, and gonads of many elongate reptiles, including legless lizards (Blackburn 1998) and snakes (Wallach 1998). Presumably, this anterior/posterior positioning reduces maximal distension of the body by arranging the organs such that a slender body form can be maintained (Fox and Dessauer 1962, Greer 1977). This advantage of anterior/posterior displacement is likely to be greatest for organs that are large in size. Side-by-side placement of the female reproductive organs would generate major bodily distension both during vitellogenesis (when yolking follicles increase in size) and pregnancy (when the eggs or offspring must be carried within the female's body, sometimes for several months; Seigel and Ford 1987). The obvious disadvantage of anterior/posterior displacement of ovaries and oviducts, however, is that reduced overlap between the right and left sides inevitably reduces the total volume of reproductive materials (follicles, eggs, offspring) that can be accommodated within a body of a given length. Thus, reducing the degree of overlap between left and right gonads would distribute their reproductive burden more evenly along the female's body, but reduce total reproductive output.

These ideas suggest that selection for slender body form in snakes might impose selection both on reproductive output (clutch size and/or offspring size) and on morphology (relative positioning of the left and right gonads). The independent evolution of arboreal habits in several lineages of snakes offers ideal comparative material to test this prediction. Arboreal snakes consistently are slender-bodied, presumably reflecting the advantages of this body form for effective climbing and/or for camouflage among the branches of a tree (Lillywhite and Henderson 1993). Laterally compressed bodies and enlarged vertebral scales may strengthen the body against bending in the dorsoventral plane and hence facilitate gap-bridging (Pough et al. 1988). Accordingly, we gathered data on a range of arboreal, terrestrial, and aquatic species within two major phylogenetic lineages of morphologically similar snakes (pythons and boas) to examine the predicted links between body shape, fecundity, and ovarian position.

METHODS

The world's largest snakes belong to two major lineages: the oviparous Pythonidae (e.g., black-headed python, carpet python) and the viviparous Boidae (e.g., anaconda, boa constrictor). We examined 1402 preserved adult specimens of 24 species (12 Indo-Australian pythons, 12 boids) in museum collections to quantify body size (snout–vent length [SVL]), mid-body circumference (MC), degree of lateral flattening at the mid-body (LF; defined as body width relative to body height), tail length (distance from the cloaca to the tip of the tail [TL]), clutch/litter sizes (number of oviductal embryos or eggs or of enlarged vitellogenic follicles in the ovary), and offspring sizes (SVLs). Fecundity was assessed via a midventral incision to reveal the ovaries and oviducts, and offspring sizes were assessed based upon full-term oviductal offspring and/or the minimum sizes of specimens collected. All body dimensions were measured using a flexible tape, except for body width and height, which were measured with vernier calipers. Unfortunately, some species (e.g., Asian and African *Python*) are rare in collections, so could not be included in our analysis. (For lists of species, see Appendices A and B.)

We also measured the position of the elongate paired ovaries within adult female snakes. The right ovary was always anterior to the left, but the two ovaries showed substantial overlap in some taxa (up to 8.4% of SVL) whereas they were well-separated in others (by up to 3.9% of SVL). Our overlap measure is based on the distance from the posterior end of the right ovary to the anterior end of the left ovary, divided by the snout–vent length of the specimen. For statistical analysis, we expressed the degree of ovarian separation relative to the widest separation observed in any species (i.e., 3.9% became our zero value); thus, higher values represent greater degrees of ovarian overlap. Sample sizes of pregnant females were too low for quantification of embryo position and overlap in the same way, but the patterns were qualitatively similar to those of ovarian overlap because the embryo-filled oviducts are supported by the same mesenteries within the body cavity (Fox 1977, Blackburn 1998) and, hence, lie adjacent to the ovaries. Close apposition of the oviduct to the ovaries is necessary at ovulation for effective transfer of fertilized oocytes into the oviduct, providing a strong functional reason for expecting that asymmetries in ovarian position will be accompanied by similar asymmetries in oviductal position. In viviparous species, the increasing size of embryos through gestation results in greater abdominal distension of the mother and tighter packing of embryos, but does not significantly expand the proportion of maternal body length occupied by reproductive materials (Appendix C).

To correct for interspecific variation in absolute body sizes, we regressed morphological variables against body size measures to obtain residual scores to serve as size-independent measures of body shape. For example, we regressed mid-body circumference and ovarian overlap

against SVL to obtain residual scores for relative body circumference and relative ovarian overlap and regressed body width against body height to quantify degree of lateral flattening at mid-body. Fecundity measures (clutch size and offspring size) were regressed against maternal SVL to quantify relative reproductive output. Ventral and subcaudal scale counts (i.e., the numbers of scales beneath the body and the tail, respectively) were obtained from published literature (Stull 1932, Hoge 1953, Boulenger 1961, Barker and Barker 1994, Cogger 2000, Dirksen 2002, Henderson 2002, Passos 2003, Vences and Glaw 2003) and were used as indicators of body size and tail size (see Lindell 1994). Relative tail length is highly correlated with the number of subcaudal scales in an interspecific comparison ($r^2 = 0.72$, $P < 0.00001$) and thus, we used scale counts in our analysis instead of length to avoid potential statistical problems associated with use of proportions. There was no such surrogate measure for other body dimensions, so we were forced to use proportions data for analyses of some other traits. We obtained data on microhabitat use for each taxon from published literature, museum records associated with specimen collection, and field experience of ourselves and our colleagues. Based on these data, we estimated the proportion of snakes found in each microhabitat (from 0 = never arboreal, to 1 = always arboreal; see Appendix A). This is a very broad-brush approach, because frustratingly, there are virtually no published data on detailed habitat use by these species (but see Shine and Fitzgerald [1996] and Slip and Shine [1988] for *Morelia spilota*). The hypotheses that predict distinctive morphological and life-history traits in arboreal snakes rely only upon selective forces imposed by climbing and hence should be applicable at the broad scale available from our sources (i.e., all arboreal snakes must climb). Nonetheless, more detailed information would enable a more accurate classification of microhabitat use and potentially could provide deeper insights into the ways in which the challenges imposed by different environments have stimulated adaptive shifts in animals.

We used independent contrast analysis (Felsenstein 1985) to examine interspecific relationships among mean values per species for habitat use (the proportion of snakes found in arboreal sites), adult body size, the number of ventral and subcaudal scales, mid-body circumference relative to SVL (MC), body width relative to body height (LF), ovarian overlap relative to SVL, and relative reproductive output (residuals of clutch size and offspring size vs. maternal SVL). Although female body mass and offspring mass might offer better measures than length, we used SVL because of logistical difficulties associated with draining of preservative liquids and weighing these very large snakes in museum collections. For independent contrast analyses the data on percentage of arboreality were arcsine square-root transformed, all branch lengths were adjusted to 1, and relationships between variables were analyzed by linear regression

forced through the origin (i.e., intercepts adjusted to 0; Martins and Hansen 1996). All independent contrast analyses were performed using the PDAP package (Midford et al. 2005) for Mesquite 1.05 (Maddison and Maddison 2004). We reconstructed the evolution of arboreal habits (where "arboreal" means >50% of the individuals were found in arboreal situations) by linear parsimony, using Mesquite 1.05 (Maddison and Maddison 2004). In morphological comparisons other than those related to fecundity and ovarian position, data for males and females were analyzed together because our aim was to characterize the general body shape for each species. We ran the comparative analyses twice, using two alternative phylogenetic hypotheses. In both cases the pythonid phylogeny was the same and was taken from Kluge (1993). However, we used two different phylogenies for boids: one based on morphology (primarily osteology, thus not including any of the characters used in our own analysis; Kluge 1991) and one that used molecular data also (Burbrink 2005). In both scenarios, we included relationships among the subspecies of *Epicrates cenchria* as clarified by Passos (2003) and considered the two Brazilian *Boa constrictor* subspecies as sister taxa. Kluge (1993) did not resolve relationships among *Antaresia* spp.; we have used the arrangement *A. maculosa* (*A. stimsoni* (*A. childreni*)) but have run all other possible arrangements also, and all give the same results. We used ANCOVA to analyze tail length and reproductive output, with microhabitat use (arboreal, terrestrial, or aquatic) as the factor and SVL as the covariate (Zar 1999).

RESULTS

Our sample of boid and pythonid snakes incorporated multiple independent phylogenetic origins of arboreal habits; the exact number of inferred arboreal origins differed between the two main phylogenetic hypotheses suggested for these animals (see Fig. 1). Our analyses supported the prediction of consistent associations between the evolution of arboreality and the following variables.

Body shape.—Mid-body lateral flatness and circumference declined, relative to SVL, with the evolution of arboreality (Table 1, Fig. 2a, b). That is, lineages that evolved arboreal habits also evolved more slender and flattened body shapes.

Relative tail length.—Relative tail length was greater in arboreal snakes than in their terrestrial or aquatic relatives (ANCOVA: slopes, $F_{2,1282} = 0.12$, $P = 0.889$; intercept, $F_{2,1284} = 581.7$, $P < 0.0001$) and the mean number of subcaudal scales increased with arboreality (Table 1, Fig. 2c). That is, the evolution of arboreality was accompanied by a lengthening of the tail relative to the body and hence an increase in the number of scales under the tail.

Relative clutch size.—Relative clutch size declined with arboreality (Table 1, Fig. 2d). Fecundity differed among snake species as a function of their microhabitat

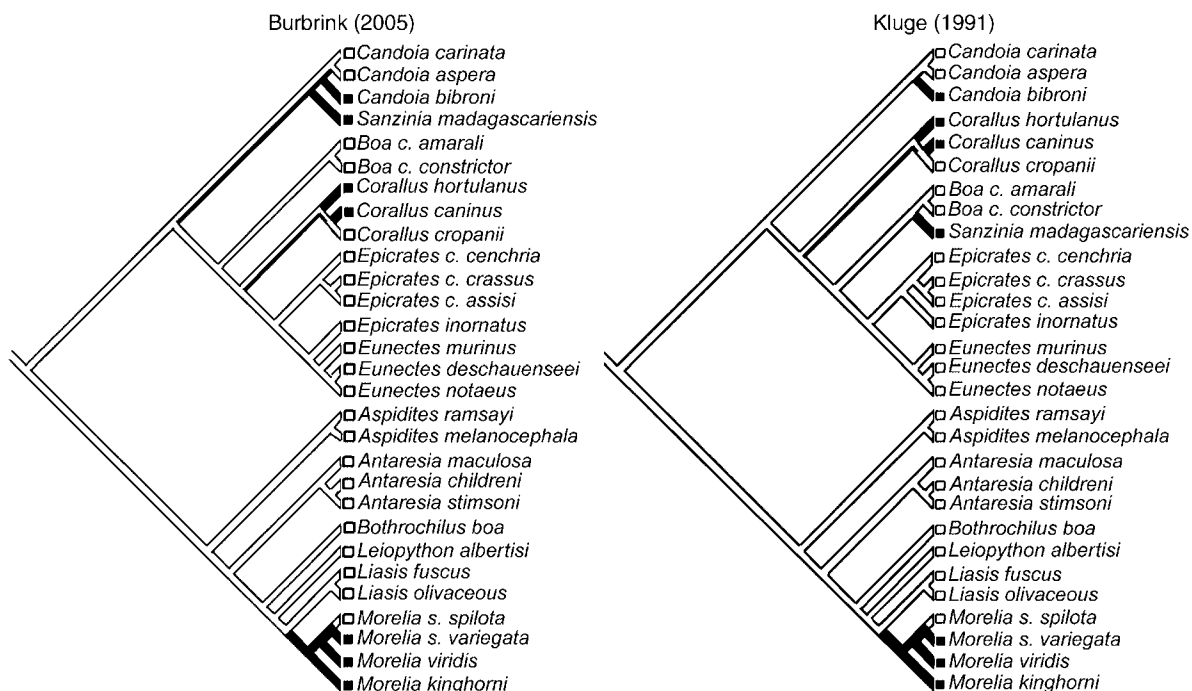


FIG. 1. Reconstruction of evolutionary shifts in the use of arboreal habitats within boid and pythonid snakes, based upon two alternative phylogenetic hypotheses. The relationships among boids differ: the right cladogram is based on Kluge's (1991) hypothesis for boids, whereas the left cladogram shows boid relationships based on Burbrink (2005). Both phylogenetic scenarios include specific hypotheses concerning relationships among *Epicrates cenchria* spp. based on Passos (2003) and among all pythonid species based on Kluge (1993). Open branches indicate non-arboreal snakes; solid branches indicate arboreal snakes. See *Methods* for details.

use (heterogeneity of slopes test, $F_{2,146} = 5.97$, $P < 0.0001$; Fig. 3a). Analysis of the nonoverlap of 95% confidence intervals of the regression slopes for each habitat type revealed that arboreal snakes between 800 and 1700 mm in SVL produced significantly fewer offspring than did terrestrial taxa.

Overlap in ovarian position.—Arboreal snakes exhibited less anterior/posterior overlap in ovarian position than did terrestrial or aquatic snakes (Fig. 3b). The distance between the ovaries increased with the evolution of arboreality under both of the phylogenetic hypotheses that we tested (Table 1, Fig. 2e).

The other variables that we tested were not consistently associated with arboreality (mean SVL, mean number of ventral scales, mean offspring size; Table 1). Thus, evolutionary shifts to arboreal life did not consistently modify either mean adult body length or offspring size.

DISCUSSION

Our data on pythonid and boid snakes support earlier generalizations (based mostly on colubrid taxa) that the evolution of arboreality in snakes is accompanied by significant morphological modifications. Notably, arbo-

TABLE 1. Results of statistical analyses (based on phylogenetically independent contrasts) of associations between the evolution of arboreal habits and snake morphology (body size, body shape, and numbers of ventral and subcaudal scales) and reproductive traits (linear overlap of left and right ovaries, fecundity, and offspring size).

Character	Hypothesis based on Kluge (1991)		Hypothesis based on Burbrink (2005)	
	r^2	P	r^2	P
Mean adult snout–vent length (mm)	0.005	0.713	0.007×10^{-3}	0.989
Mean no. ventral scales	0.020	0.459	0.030	0.340
Mean no. subcaudal scales	0.210	0.013	0.280	0.003
Mid-body circumference	0.260	0.003	0.200	0.018
Lateral flatness of the mid-body	0.430	<0.001	0.590	<0.001
Degree of ovarian overlap	0.199	0.014	0.193	0.016
Litter/clutch size	0.150	0.029	0.130	0.030
Offspring size	0.030	0.417	0.050	0.302

Notes: Two sets of results are shown, from analyses based on two alternative phylogenetic hypotheses for boid and pythonid snakes. Measures of mid-body circumference, overlap between ovaries, litter/clutch size, and offspring size were corrected for body size (SVL, snout–vent length).

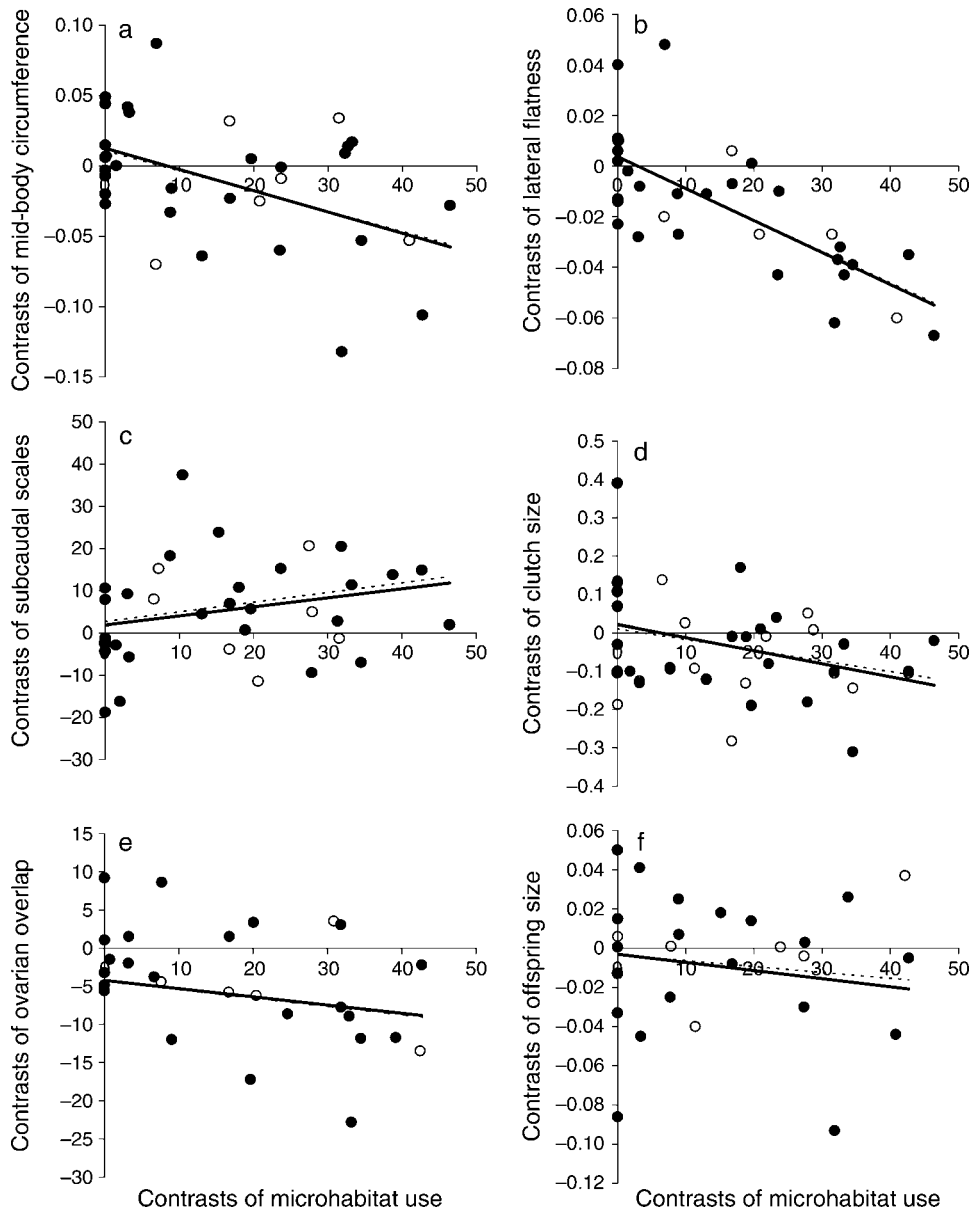


FIG. 2. Relationships between phylogenetically independent contrast scores of (a) mid-body circumference, (b) mid-body lateral flatness, (c) mean number of subcaudal scales, (d) clutch/litter size, (e) degree of ovarian overlap, and (f) offspring size vs. microhabitat use in boid and pythonid snakes. Solid circles and solid lines are results according to a phylogenetic hypothesis based on Kluge (1991); open circles and dashed lines are results according to a phylogenetic hypothesis based on Burbrink (2005). See statistical results in Table 1.

real snakes tend to be slender-bodied (low circumference relative to body length), with a laterally compressed body and a long tail (Vitt and Vangilder 1983, Guyer and Donnelly 1990, Lillywhite and Henderson 1993). Contrary to the suggestion that smaller body sizes are related to arboreality in some snake lineages (Lillywhite and Henderson 1993), the only morphological traits not modified by arboreality among our sample were those relating to overall body size (SVL and the number of ventral scales).

Lillywhite and Henderson (1993) speculated that the slender body shape of arboreal snakes may constrain the female's capacity to carry eggs. Our results strongly support this hypothesis: arboreal pythonid and boid snakes produced smaller clutches than terrestrial and aquatic species, even after controlling for phylogenetic effects. However, offspring size did not differ among the groups, presumably reflecting the importance of selective forces on offspring size unrelated to maternal burdening (Vitt 1986). The most notable adaptation to arboreality

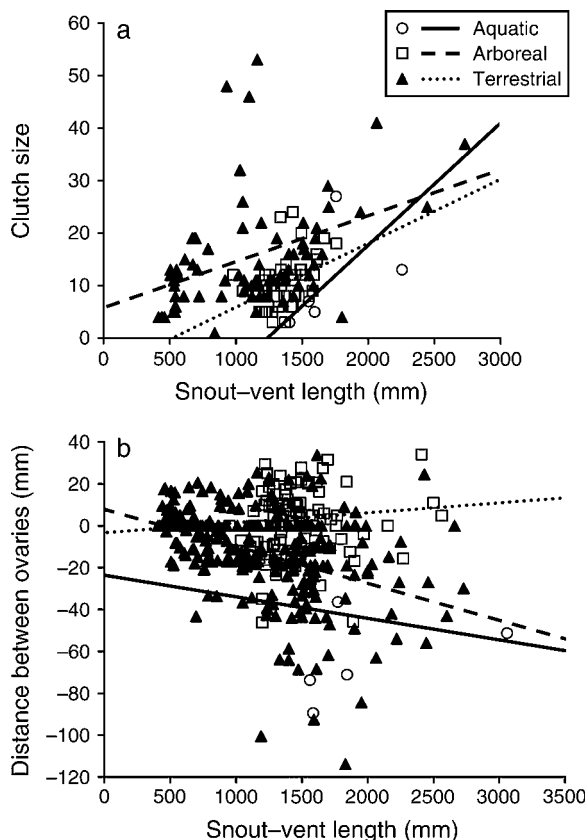


FIG. 3. Relationships between reproductive traits and female body size (snout-vent length, SVL) in aquatic, arboreal, and terrestrial boid and pythonid snakes. The upper panel (a) shows fecundity (clutch or litter size) whereas the lower panel (b) shows distance between ovaries. Untransformed data are shown for clarity, but statistical analysis was based on transformed values (see *Methods*). Negative values represent overlapped ovaries, and positive values represent separated ovaries. Species with mean adult SVL >3.1 m have been deleted from this figure to emphasize the size range common to all three types of snake (arboreal, terrestrial, and aquatic).

revealed by our work involves a shift in the position of the ovaries within the female's body. Increasing reliance upon arboreal habitats was accompanied by an increasing spatial (anterior/posterior) separation in the position of the left and right ovaries within the female's body. This asymmetry in ovarian position may permit arboreal females to minimize their bodily distension during the period when they carry enlarged follicles.

Distension during pregnancy may be important also. Small sample sizes for pregnant specimens in most species prevented us from quantifying the position of the eggs or offspring after ovulation, but we saw the same general trend as with ovarian position. For example, in the terrestrial boa constrictors the embryos in left and right oviducts usually were arranged side by side for much of the mother's body length whereas in the arboreal *Corallus hortulanus* there was no such overlap (L. Pizzatto, *personal observation*; see Appendix C). As noted

above, close apposition of the oviduct to the ovaries is enforced by mesenteries within the body cavity (Fox 1977, Blackburn 1998). An interesting functional consequence of oviductal asymmetry in snakes is that most or all of the eggs in the left oviduct probably are laid before those in the right oviduct (Blackburn 1998). The ability to maintain a relatively slender body shape throughout the reproductive cycle could aid female arboreal snakes in climbing, in supporting the body on thin branches (by spreading mass over a greater body length), in camouflage (by providing a thin branch-like outline), and by facilitating the snake's movement through narrow spaces among branches in its complex three-dimensional habitat (Lillywhite and Henderson 1993).

More generally, ecological factors influencing the evolution of asymmetry within the female reproductive tracts of squamates provide exciting opportunities for broad comparative study (Blackburn 1998) because of the ease with which links between morphology, reproductive biology, and habitat can be investigated. Our results on arboreal snakes accord well with an earlier report that the evolution of aquatic habits in snakes has been consistently associated with a shift in the mass of the clutch and in its position within the female's body (Shine 1988). In both cases, a plausible selective force involves the way in which bodily distension (in position as well as degree) influences locomotor performance. Studies on terrestrial snakes have shown that the mass or volume of the clutch impedes locomotor speeds of pregnant animals (Seigel et al. 1987), but there have been no corresponding analyses of the effects of pregnancy on locomotion in arboreal or aquatic snakes. If indeed the functional significance of modifications of ovarian and oviductal positioning lie in habitat-specific locomotor challenges, the degree to which maternal mobility is impaired by differing degrees and placement of bodily distension should differ between aquatic, terrestrial, and arboreal snakes. Studies on lizards have shown that such distension can be mimicked experimentally by saline injection (Shine 2003), providing a robust opportunity to falsify the adaptive hypotheses that we have proposed.

Are morphological adaptations to arboreal locomotion likely to have modified reproductive morphology in other kinds of animals as well as snakes? Such modifications will be more difficult to quantify in organisms with nonlinear body shapes, but available data hint at similar phenomena in other vertebrate lineages that contain both terrestrial and arboreal species. For example, slender body forms and small clutches have evolved independently several times among arboreal lizards (e.g., Andrews and Rand 1974, Vitt 1986, Henle 1991). It would be interesting to compare arboreal vs. terrestrial taxa in other vertebrate lineages also, notably among anurans and mammals.

Other forms of locomotion may impose even stronger constraints on the position and morphology of reproductive organs. For example, flight imposes severe biomechanical constraints on the amount and distribution of

mass within the body, so that pregnancy may require significant morphological and reproductive adaptations for successful locomotion. Such constraints may explain unusual sexually dimorphic features of volant taxa, such as the relatively larger wingspans of female vespertilionid bats than of conspecific males (Myers 1978) and the larger relative head sizes and gliding membranes of females than males in “flying lizards” of the genus *Draco* (Shine et al. 1998). Similarly, in birds, features of avian reproductive biology, such as the lack of viviparity and occurrence of sequential ovulation, may reflect limitations imposed by flight efficiency (e.g., Blackburn and Evans 1986). Patterns of sexual size dimorphism in birds also may have been affected by limitations that the reproductive burden imposes on flight ability and performance (Andersson and Norberg 1981, Mueller and Meyer 1985). Fossorial taxa that must pass through narrow underground passages present another example of locomotor constraints on bodily distension. Indeed, some elongate fossorial taxa (e.g., the legless lizard *Anniella*, snakes of the genus *Tantilla*, anamalepidid and scolecophidian snakes) have proceeded even further than the arboreal boids and pythonids in this respect, by complete loss of one oviduct (thereby assuring zero overlap; Blackburn 1998).

Such phylogenetically independent convergences generate correlations between ovarian and oviductal morphology on the one hand and ecological factors on the other and offer exciting opportunities to clarify the relationships between an animal's use of habitats, its internal anatomy, its external morphology, and its life-history traits.

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LITERATURE CITED

- Andersson, M., and R. A. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among raptors, with a size scaling of flight performance. *Biological Journal of Linnean Society* 15:105–130.
- Andrews, R., and A. S. Rand. 1974. Reproductive effort in anoline lizards. *Ecology* 55:1317–1327.
- Barker, D. G., and T. M. Barker. 1994. *Pythons of the world*. Volume I. Australia. Advanced Vivarium Systems, Mission Viejo, California, USA.
- Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* 50: 733–743.
- Berglund, A., and G. Rosenqvist. 1986. Reproductive costs in the prawn *Palaemon adspersus*: effects on growth and predator vulnerability. *Oikos* 46:349–354.
- Blackburn, D. G. 1998. Structure, function and evolution of the oviducts of squamate reptiles, with special reference to viviparity and placentation. *Journal of Experimental Zoology* 282:560–617.
- Blackburn, D. G., and H. E. Evans. 1986. Why are there no viviparous birds? *American Naturalist* 128:165–190.
- Boulenger, G. A. 1961. *Catalogue of the snakes of the British Museum (Natural History)*. Volume I. British Museum of Natural History, London, UK.
- Brodie, E. D., III. 1989. Behavioral modification as a means of reducing the cost of reproduction. *American Naturalist* 134: 225–238.
- Burbrink, F. T. 2005. Inferring the phylogenetic position of *Boa constrictor* among the Boinae. *Molecular Phylogenetics and Evolution* 34:167–180.
- Cogger, H. G. 2000. *Reptiles and amphibians of Australia*. Reed New Holland, Sydney, New South Wales, Australia.
- Cooper, W. E., L. J. Vitt, R. Hedges, and R. B. Huey. 1990. Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behavioral Ecology and Sociobiology* 27:153–157.
- Dirksen, L. 2002. *Anakondas*. Monographische revision der gattung *Eumectes* (Wagler, 1830). Natur und Tier-Verlag, Münster, Germany.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Fox, W. 1977. The urogenital system of reptiles. Pages 1–157 in C. Gans and T. S. Parsons, editors. *Biology of the Reptilia*. Volume 6. Morphology. Academic Press, New York, New York, USA.
- Fox, W., and H. C. Dessauer. 1962. The single right oviduct and other urogenital structures of female *Typhlops* and *Leptotyphlops*. *Copeia* 1962:590–597.
- Gans, C. 1975. Tetrapod limblessness: evolution and functional corollaries. *American Zoologist* 15:455–467.
- Garland, T. 1985. Ontogenetic and individual variation in size, shape, and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *Journal of Zoology (London)* 207:425–439.
- Ghalambor, C. K., D. N. Reznick, and J. A. Walker. 2004. Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *American Naturalist* 164:38–50.
- Greer, A. E. 1977. On the adaptive significance of the loss of an oviduct in reptiles. *Proceedings of Linnean Society of New South Wales* 101:242–249.
- Guyer, C., and M. S. Donnelly. 1990. Length–mass relationships among an assemblage of tropical snakes in Costa Rica. *Journal of Tropical Ecology* 6:65–76.
- Harvey, P. H., and A. E. Keymer. 1991. Comparing life histories using phylogenies. *Philosophical Transactions of the Royal Society B* 332:31–39.
- Henderson, R. W. 2002. Neotropical treeboas. Natural history of the *Corallus hortulanus* Complex. Krieger, Malabar, Florida, USA.
- Henle, K. 1991. Life-history patterns in lizards of the arid and semi-arid zone of Australia. *Oecologia* 88:347–358.
- Hoge, A. R. 1953. A new genus and species of Boinae from Brazil. *Xenoboa cropanii*, gen. nov., sp. nov. *Memórias dos Instituto Butanatan* 25:27–34.
- James, R. S., and I. A. Johnston. 1998. Influence of spawning on swimming performance and muscle contractile properties in the short-horn sculpin. *Journal of Fish Biology* 53:485–501.
- Kluge, A. G. 1991. *Boine snake phylogeny and research cycles*. Miscellaneous Publications of the Museum of Zoology of the University of Michigan 178:1–58.

- Kluge, A. G. 1993. *Aspidites* and the phylogeny of Pythonine snakes. *Records of the Australian Museum (Supplement)* 19: 1–77.
- Lee, S. J., M. S. Witter, I. C. Cuthill, and A. R. Goldsmith. 1996. Reduction in scape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proceedings of the Royal Society of London B* 263:619–624.
- Lillywhite, H. B., and R. W. Henderson. 1993. Behavioral and functional ecology of arboreal snakes. Pages 1–48 in R. A. Seigel and J. T. Collins, editors. *Snakes: ecology and behavior*. McGraw-Hill, New York, New York, USA.
- Lindell, L. E. 1994. The evolution of vertebral number and body size in snakes. *Functional Ecology* 8:708–719.
- Maddison, W. P., and D. R. Maddison. 2004. Mesquite: a modular system for evolutionary analysis. Version 1.05. (<http://mesquiteproject.org>)
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology and Evolution* 6:183–186.
- Martins, E. P., and T. F. Hansen. 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. Pages 22–75 in E. P. Martins, editor. *Phylogenies and the comparative method in animal behavior*. Oxford University Press, New York, New York, USA.
- Midford, P. E., T. Garland, Jr., and W. P. Maddison. 2005. PDAP package of Mesquite. Version 1.07. (http://mesquiteproject.org/pdap_mesquite/)
- Miles, D. B., B. Sinervo, and W. A. Frankino. 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. *Evolution* 54:1386–1395.
- Mueller, H. C., and K. Meyer. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the western Palearctic. *Current Ornithology* 2:65–101.
- Myers, P. 1978. Sexual dimorphism in size of vespertilionid bats. *American Naturalist* 112:701–711.
- Passos, P. G. H. 2003. Sistemática do complexo *E. cenchria* (Linnaeus, 1778) com aproximações sobre filogenia de *Epicrates* Wagler, 1830 (Serpentes: Boidae). Thesis. Universidade Federal do Rio de Janeiro, Rio de Janeiro.
- Plaut, I. 2002. Does pregnancy affect swimming performance of female mosquitofish, *Gambusia affinis*? *Functional Ecology* 16:290–295.
- Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitsky, and K. D. Wells. 1988. *Herpetology*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Rose, M. R., and G. V. Lauder. 1996. *Adaptation*. Academic Press, New York, New York, USA.
- Seigel, R. A., and N. B. Ford. 1987. Reproductive ecology. Pages 210–252 in R. A. Seigel, J. T. Collins, and S. S. Novak, editors. *Snakes: ecology and evolutionary biology*. McMillan, New York, New York, USA.
- Seigel, R. A., M. M. Huggins, and N. B. Ford. 1987. Reduction in locomotor ability as a cost of reproduction in snakes. *Oecologia* 73:481–485.
- Shine, R. 1980. “Costs” of reproduction in reptiles. *Oecologia* 46:92–100.
- Shine, R. 1988. Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution* 42:17–27.
- Shine, R. 2003. Effects of pregnancy on locomotor performance: an experimental study on lizards. *Oecologia* 136:450–456.
- Shine, R., and M. Fitzgerald. 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons (*Morelia spilota*) (Serpentes: Pythonidae) in coastal eastern Australia. *Biological Conservation* 76:113–122.
- Shine, R., S. Keogh, P. Doughty, and H. Giragosyan. 1998. Costs of reproduction and the evolution of sexual dimorphism in a ‘flying lizard’ *Draco melanopogon* (Agamidae). *Journal of Zoology* 246:203–213.
- Sinervo, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279–294.
- Sinervo, B., R. Hedges, and S. C. Adolph. 1991. Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *Journal of Experimental Biology* 155:323–336.
- Slip, D. J., and R. Shine. 1988. Habitat use, movements, and activity patterns of free-ranging diamond pythons *Morelia spilota spilota* (Serpentes: Boidae): a radiotelemetric study. *Australia Wildlife Research* 15:515–531.
- Stull, O. 1932. Five new subspecies of the family Boidae. *Occasional Papers of the Boston Society of Natural History* 8:25–30.
- Veasey, J. S., D. C. Houston, and N. B. Metcalfe. 2001. A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. *Journal of Animal Ecology* 70:20–24.
- Vences, M., and F. Glaw. 2003. Phylogeography, systematics and conservation status of boid snakes from Madagascar (*Sanzina* and *Acrantophis*). *Salamandra* 39:181–206.
- Vitt, L. J. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia* 1986:773–786.
- Vitt, L. J., and L. D. Vangilder. 1983. Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia* 4:273–296.
- Wallach, V. 1998. The lungs of snakes. Pages 93–295 in C. Gans and A. S. Gaunt, editors. *Biology of the Reptilia*. Volume 19. Visceral organs. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA.
- Webb, J. 2004. Pregnancy decreases swimming performance of female northern death adders (*Acanthophis praelongus*). *Copeia* 2:357–363.
- Williams, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, New Jersey, USA.
- Winfield, I. J., and C. R. Townsend. 1983. The cost of copepod reproduction: increased susceptibility to fish predation. *Oecologia* 60:406–411.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey, USA.

APPENDIX A

A table showing mean adult body sizes, numbers of ventral and subcaudal scales, and microhabitat use in boid and pythonid snakes (*Ecological Archives* E088-021-A1).

APPENDIX B

A table showing mid-body circumference and lateral flatness, clutch size, and ovarian position in boid and pythonid snakes (*Ecological Archives* E088-021-A2).

APPENDIX C

Photographs showing late-stage embryos within a gravid terrestrial boid snake and early-stage embryos within a gravid arboreal boid snake (*Ecological Archives* E088-021-A3).