*Herpetologica*, 46(3), 1990, 283–290

# BIOLOGICAL ASPECTS OF THE ADAPTIVE RADIATION OF AUSTRALASIAN PYTHONS (SERPENTES: BOIDAE)

RICHARD SHINE AND DAVID J. SLIP[1]

*Zoology Department, The University of Sydney,*
*N.S.W. 2006, Australia*

ABSTRACT: More than 1000 specimens representing 13 species of Australasian pythons were dissected to provide an overview of the natural history of this group. Although the species examined span a wide range of adult body sizes, morphologies, and habitats, several consistent ecological features were evident. Females generally exceed males in average adult body size and mature at a higher proportion of mean adult snout–vent length (SVL). Males outnumber females in museum collections. Cloacal spurs tend to be larger in males than in conspecific females and to be larger (relative to body size) in larger species. Reproductive biology is conservative, with all taxa apparently oviparous and with maternal attendance at the nest. Female reproductive cycles are strongly seasonal but differ among species and areas. The high proportion of non-reproductive adult-size females suggests a generally low reproductive frequency. Mean clutch sizes of 5–16 eggs were recorded, with hatchling size highly correlated with mean adult SVL interspecifically and with incubation period (based upon data from reproduction in captivity) dependent upon hatchling size. Australasian pythons consume a wide range of vertebrates, with a shift from reptiles to mammals in larger species and in larger individuals within a species. Overall, the adaptive radiation of pythons in Australia has involved retention of many primitive features, but the invasion of an arid continent has favored greater utilization of reptilian prey and (consequently?) the evolution of smaller body size.

*Key words:* Serpentes; Boidae; Pythoninae; Feeding; Reproduction; Allometry; Life history; Australia

To many people, the word "python" conjures up an image of a large heavy-bodied snake draped over a tree-limb in a tropical rainforest, lying in wait for some unwary large mammal. The reality of the pythonine radiation is very different. About two-thirds of all species of pythons are endemic to Australasia, and many of these species are not particularly large or heavy-bodied, or arboreal, or restricted to forested habitats, or tropical in distribution, or primarily mammal-eaters. The popular image of pythons stems mainly from the better-known Asian and African pythonines, which tend to fit this stereotype in many cases (e.g., Fitzsimons, 1930; but note the fossorial African *Calabaria*). Except for the recent radiotelemetric work of Slip and Shine (1988*a*,*b*,*c*) on diamond pythons, *Morelia spilota spilota*, from south-eastern coastal Australia, the only published information so far available on the biology of pythons is fragmentary and anecdotal.

The present study is based primarily on dissections of museum specimens and aims to provide an overview of the general ecology of the Australian pythonine radiation. Such information may serve as a useful comparison to data available for Asian and African pythons and to snakes of other families. Quantitative data on this poorly-known lineage may also help to clarify some questions of current interest in the field of reptilian life-history evolution. In particular, we use this new data set to examine the roles of allometry, phylogenetic conservatism, and species-specific adaptation in determining interspecific variance in ecological attributes (e.g., Dunham et al., 1988; Shine, 1989).

Evolutionary–ecological interpretations such as these ultimately rely upon a phylogenetic framework. Fortunately, despite the lack of detailed study of Australasian pythonine phylogeny, the major lineages are distinct even though affinities between them are in some cases obscure. By far the most speciose and diverse lineage is the *Liasis* group. Snakes of this group are primarily terrestrial rather than arboreal and are found in a continuum of habitats from

---

[1] PRESENT ADDRESS: Antarctic Division, Channel Highway, Kingston, Tasmania, Australia 7150.

northern tropical rainforests (*Liasis albertisii*), through seasonally inundated areas (*L. fuscus*), to more xeric regions (three lineages: the small species of the *L. childreni* group, the large *L. olivaceus*, and the highly modified semifossorial *Aspidites*). The only other geographically widespread group is *Morelia*. Although morphologically less diverse than *Liasis*, this lineage of semiarboreal pythons has produced at least one giant form (*M. oenpelliensis*) in the tropics. Another giant tropical species (*M. amethistina*) and the green tree python (*Chondropython viridis*) may be only distantly related to the rest of the *Morelia* group (Mengden, Shine, and Cogger, unpublished). Immunological and electrophoretic data suggest that the Australasian pythons comprise a relatively recent monophyletic radiation, presumably entering mainland Australia from Asia when the two continents collided in the mid-Miocene (G. Mengden and T. Schwaner, personal communication; see Smith and Plane, 1985, for an alternative hypothesis). A similar origin has been postulated for another major radiation of Australian snakes, the terrestrial proteroglyphs (Schwaner et al., 1985).

## MATERIALS AND METHODS

We examined all available pythons in collections of the major Australian museums: the Northern Territory Museum, the South Australian Museum, the Western Australian Museum, the Museum of Victoria, the Queensland Museum, and the Australian Museum. Road-killed pythons found during our fieldwork were also dissected, and data on, for example, body sizes and prey items were obtained from pythons that we captured and released during fieldwork. The sample of *Morelia spilota* used consisted entirely of carpet pythons (*M. s. variegata*) and did not include any of the diamond pythons (*M. s. spilota*) for which data have previously been presented (Slip and Shine, 1988*a*,*b*, 1989). In the case of preserved animals, we first recorded snout–vent length (SVL) and then made a midventral incision to examine gonads and gut contents. Males were classed as mature if the testes were large and turgid or if the efferent ducts were opaque and thickened. Females were classed as mature if they were gravid, had thickened oviducts, or had ovarian follicles >10 mm. Clutch sizes were counted or estimated from enlarged ovarian follicles. Any gut contents were removed and subsequently identified; most mammalian remains were identified by microscopic analysis of fur, in conjunction with available guides (Brunner and Coman, 1974) and with a reference collection of fur from potential prey species. Spurs on either side of the snake's vent were measured with vernier calipers. Data on incubation periods from clutches laid in captivity were assembled by literature review and personal communication with private keepers (N. Charles, personal communication).

## RESULTS

Data were obtained from 1082 specimens of 13 species of pythons (Table 1). Samples of the New Guinea taxa were difficult to obtain, and some (*L. boeleni*, *L. mackloti*, *L. papuanus*) were not represented in our sample. Similarly, we did not obtain enough of the Australian *M. oenpelliensis* or *M. bredli* for analysis. Nonetheless, our sample includes representatives of all of the major lineages and is more extensive than any previous data base on these animals. Judging by data in museum registers, most of the pythons that we examined had been collected while moving about at night, with only occasional records of diurnal activity.

Table 1 shows that mean adult body size ranged from <0.5 m in *L. perthensis* to >2 m in *L. amethistina*, with values for the larger species undoubtedly being underestimates because of the bias against preserving extremely large specimens entire. Most species attain sexual maturity at approximately 70–75% of mean adult SVL, with the ratios for males being consistently lower than for conspecific females ($t_{11} = -2.02$, one-tailed $P < 0.05$). No correlation between this ratio and absolute body size was evident ($P > 0.05$ for both sexes).

Sexual differences in body size are relatively minor in the Australian pythons but show a consistent tendency for adult females to average slightly larger than males both at sexual maturation (testing the ratio of female to male SVL against a null hypothesis of 1.0; $t_{11} = -4.87$, $P < 0.001$)

TABLE 1.—Sample sizes and body sizes of Australasian pythons. Snout–vent length (SVL) in cm.

| Species | Total sample size | Adult males | | | | Adult females | | | | SVL of smallest collected |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $n$ | $\bar{x}$ SVL | (SD) | Extremes | $n$ | $\bar{x}$ SVL | (SD) | Extremes | |
| *Aspidites melanocephalus* | 97 | 35 | 156.1 | (32.3) | 95–218 | 19 | 159.3 | (19.9) | 101–184 | 55.0 |
| *A. ramsayi* | 64 | 15 | 148.2 | (37.5) | 100–220 | 10 | 158.3 | (24.8) | 129–195 | 39.0 |
| *Chondropython viridis* | 33 | 8 | 100.3 | (11.1) | 84–116 | 4 | 128.5 | (28.7) | 99–160 | 30.4 |
| *Liasis albertisii* | 12 | 5 | 130.0 | (19.9) | 116–165 | 3 | 140.7 | (23.2) | 115–160 | 40.3 |
| *L. boa* | 25 | 11 | 82.4 | (16.0) | 66–120 | 0 | — | (—) | — | 18.0 |
| *L. childreni* | 189 | 59 | 68.8 | (15.2) | 39–99 | 25 | 71.8 | (9.7) | 48.5–94 | 22.6 |
| *L. maculosus* | 111 | 38 | 77.2 | (17.7) | 50–112 | 24 | 84.1 | (12.5) | 62–110 | 24.0 |
| *L. perthensis* | 52 | 5 | 44.9 | (6.6) | 39–56 | 4 | 47.3 | (2.5) | 45–50.7 | 17.2 |
| *L. stimsoni* | 89 | 21 | 87.6 | (21.1) | 55.2–127 | 20 | 85.2 | (12.1) | 65–106 | 23.5 |
| *L. fuscus* | 87 | 19 | 130.5 | (31.8) | 97–220 | 24 | 147.1 | (27.0) | 105–212 | 42.2 |
| *L. olivaceus* | 82 | 23 | 175.9 | (37.9) | 100–252 | 24 | 190.1 | (36.6) | 108–255 | 44.0 |
| *Morelia amethistina* | 43 | 10 | 191.7 | (65.0) | 129–345 | 2 | 232.5 | (7.8) | 227–238 | 75.0 |
| *M. spilota variegata* | 194 | 50 | 129.8 | (34.9) | 72–240 | 32 | 150.9 | (37.6) | 88–245 | 32.0 |

and at mean adult body size ($t_{11} = -3.56$, $P < 0.005$). The difference in mean adult body size between the sexes ranged from 0–39%, and averaged 13% larger in females. Not surprisingly, mean adult body sizes of males and females were highly correlated when all species were included in the analysis ($n = 12$ species, Pearson's $r = 0.98$, $P < 0.001$), with no consistent allometric relationship between absolute body size and the degree of dimorphism ($n = 11$, $r = 0.01$, $P = 0.97$): that is, there was no trend for larger species to be either more or less dimorphic than were smaller taxa. However, we note that the bias against preserving very large specimens may influence the apparent degree of size dimorphism in collections of museum specimens.

Measurements on spur dimensions showed a slight but statistically insignificant trend for larger spurs in males than in conspecific females of most species. One exception was *Chondropython viridis*, in which spurs were very much larger in males than in females (analysis of covariance: slopes $F_{2,13} = 13.10$, $P < 0.01$). Overall, mean spur length in adult males was highly correlated with mean SVL ($r = 0.81$, $P < 0.01$: Fig. 1a), but with a marginally significant tendency for spurs to be larger (relative to SVL) in larger species of pythons than in smaller taxa (regressing relative spur length against mean SVL, df = 9, $r = 0.63$, $P = 0.05$).

The sex ratio of adult pythons in museum collections was consistently skewed towards males (Table 1), with an average of 68% of the sample being male (range = 44.2–100.0%, SD = 14.7; against a null hypothesis of 50%, $t_{12} = 3.38$, $P < 0.01$). Adult sex ratio was not significantly correlated with mean SVL of adult males in an interspecific comparison ($n = 13$, $r = 0.05$, $P = 0.88$). However, the bias against preserving very large specimens may affect these data on sex ratio.

Dissection of gravid specimens with hard-shelled oviductal eggs, and observations of reproduction in captivity, indicate that oviparity is the reproductive mode for all of the species of pythons listed in Table 1 with the possible exception of some members of the *L. childreni* group for which no specific data are available. Observations on reproduction in captivity similarly suggest that females of all of the Australasian taxa of pythons coil around the clutch until hatching, although again no specific data are available for some members of the *L. childreni* group, or for *A. ramsayi* (Charles et al., 1985; Shine, 1988; N. Haskins, personal communication, for *L. olivaceus*).

Considerable variation is evident in the seasonal timing of reproduction in Australian pythons, with enlarged ovarian follicles and oviductal eggs being recorded in most months of the year. In combination with published records (Charles et al., 1985), these data suggest geographic variation in the timing of reproduction in *L. fuscus* (oviposition in October–November in Queensland, but in August–October in the Northern Territory). *Morelia* and *Aspidites* appear to be more consistent, with

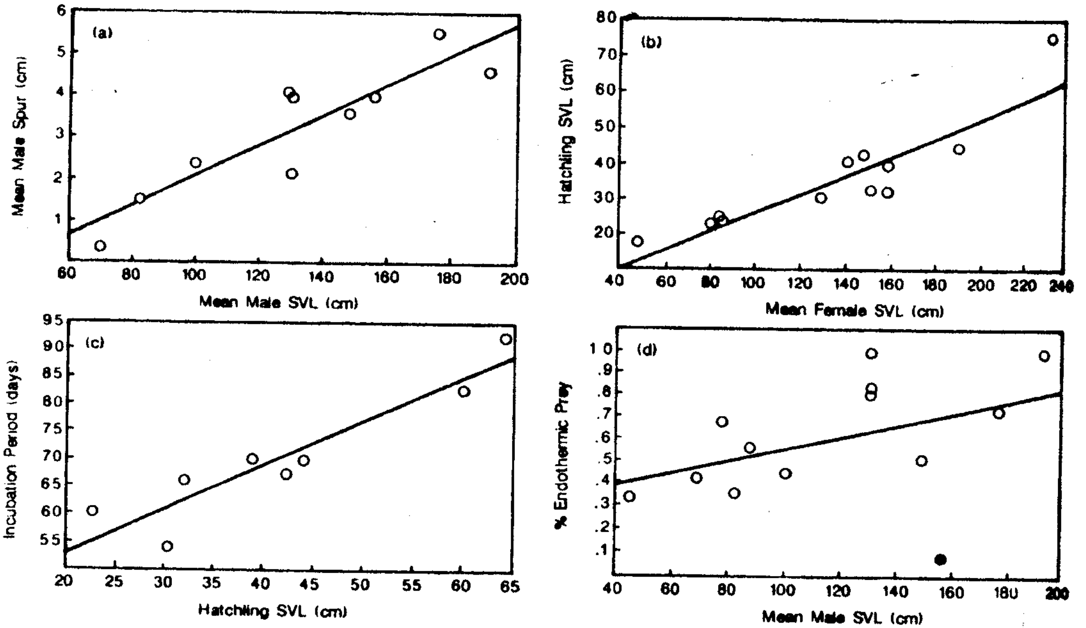

FIG. 1.—Interspecific relationships between SVL (in cm) and other morphological and ecological traits in Australasian pythons. Each point is a mean for a single species, and all regressions are fitted by least squares. (a) The mean length of male spurs is highly correlated with mean adult male body length, (b) mean hatchling body size is highly correlated with mean conspecific maternal SVL, and (c) incubation period at 30 C is correlated with the size of the resulting hatchling. In (d), the proportion of the diet (in terms of the numbers of prey items recorded) composed of ectothermic vertebrates increases with mean adult SVL in most Australian pythons (circles), although the reptile-specialist *Aspidites melanocephalus* does not fit this trend (dot).

records of enlarged ovarian follicles or oviductal eggs in October, November, December, and January in both genera. No reproductive females were recorded in large samples from other months of the year. The ambiguity about reproductive seasonality, and the possibility of extended breeding seasons in tropical pythons, prevent us from estimating the proportion of adult-size females reproductive in any given year. However, the very high proportions of non-reproductive females collected at all times of year suggest that many female pythons do not reproduce annually.

Clutch sizes of from 3–38 eggs were recorded, with no consistent patterns evident from analysis (Table 2). Sample sizes were insufficient to examine possible relationships between fecundity and maternal size within species. Mean clutch size was not significantly correlated with mean adult SVL in an interspecific comparison ($n$ = 10, $r$ = 0.41, $P$ = 0.23), suggesting that the interspecific variance in mean clutch size was not due to any simple allometric effect. Closer inspection also failed to reveal any phylogenetic conservatism: each genus (*Aspidites*, *Liasis*, *Morelia*) contained both "high-fecundity" and "low-fecundity" species.

Offspring size (as estimated by SVL of the smallest specimen collected) was highly correlated with mean maternal SVL in an interspecific comparison ($n$ = 12, $r$ = 0.91, $P < 0.01$; Fig. 1b). Larger species of pythons tended to have neonates which were smaller relative to maternal SVL than were the offspring of smaller species, but this trend did not attain statistical significance ($n$ = 12, $r$ = 0.36, $P$ = 0.25). Incubation periods of python eggs from clutches laid in captivity ranged from 54–92.5 days (species means), and were highly correlated with mean SVL's of hatchlings in an interspecific comparison ($n$ = 8, $r$ = 0.94, $P < 0.001$; Fig. 1c).

Table 3 provides data on the prey species identified from guts of Australasian python species. Many records of mammalian prey were based on a few hairs in the hindgut, which may overemphasize the importance of mammals compared to other groups (especially amphibians) which would be more difficult to identify from fully-digested remains. No invertebrate prey items were recorded, but a wide variety of vertebrates was consumed. Frogs were a significant food source in the *L. childreni* group but not for the larger pythons. The reptilian prey cover a broad range of diurnal and nocturnal taxa, and a wide range of body sizes. They were consumed by almost all species of pythons, but particularly by *Aspidites melanocephalus* (92% of items: Table 3). Birds were also eaten by several species of pythons, although less frequently than were reptiles or mammals. Murids (especially *Mus* and *Rattus*) were the most significant mammalian dietary items, although possums, bandicoots, rabbits, and bats were also identified from the alimentary tracts of the snakes.

These dietary data were analyzed in terms of the total number of prey items of each vertebrate Class (Amphibia, Reptilia, Aves, Mammalia) in each species of python. Significant interspecific differences were apparent in this respect (4 × 13 contingency $\chi^2 = 187.45$, 36 df, $P < 0.001$), prompting further analysis. An obvious possibility is that dietary composition is a function of snake size: larger species may be more likely to consume mammals and birds rather than amphibians and reptiles, because prey items in the former groups tend to be larger than those in the latter. Analysis supported this hypothesis. The proportion of the diet composed of endothermic vertebrates (birds and mammals) was highly correlated with mean adult SVL in an interspecific comparison if the reptile-specialist *Aspidites melanocephalus* was omitted ($n = 12$, $r = 0.73$, $P < 0.01$), although not if *A. melanocephalus* was included ($n = 13$, $r = 0.43$, $P = 0.14$; Fig. 1d). A size-related dietary shift in the proportion of endothermic prey was also apparent within as well as among species: the mean SVL of specimens containing endothermic prey was significantly higher than that of snakes with ectothermic prey in *Chondropython viridis, Liasis boa, L. maculosus, L. stimsoni, L. fuscus,* and *Morelia spilota* ($P < 0.05$ in each case). In two additional species, the same trend was evident but did not attain statistical significance (*Aspidites ramsayi, L. olivaceus*: $P < 0.08$).

TABLE 2.—Clutch sizes of Australasian pythons. Counts are based on oviductal eggs or ovarian follicles >5 mm diameter.

| Species | $n$ | Clutch size | |
|---|---|---|---|
| | | $\bar{x}$ (SD) | Extremes |
| *Aspidites melanocephalus* | 6 | 7.8 (4.1) | 3–14 |
| *A. ramsayi* | 3 | 14.3 (2.1) | 12–16 |
| *Chondropython viridis* | 4 | 12.3 (5.3) | 6–19 |
| *Liasis childreni* | 4 | 6.5 (4.0) | 3–12 |
| *L. maculosus* | 5 | 12.6 (4.6) | 8–19 |
| *L. perthensis* | 3 | 4.7 (0.6) | 4–5 |
| *L. fuscus* | 10 | 10.3 (6.9) | 3–24 |
| *L. olivaceus* | 6 | 15.9 (7.9) | 8–30 |
| *Morelia amethistina* | 2 | 11.5 (0.8) | 11–12 |
| *M. spilota variegata* | 5 | 16.2 (12.9) | 6–38 |

## DISCUSSION

Clearly, the taxonomic and morphological diversity of the Australasian pythons is accompanied by a considerable diversity in ecological attributes. This apparent diversity presumably would be augmented if more data were available for some of the poorly represented tropical species, especially giant forms such as *Morelia oenpelliensis* and *Liasis papuanus*. For example, anecdotal reports indicate that these species may take very large prey (e.g., a 22.7 kg wallaby in a 27.2 kg *L. papuanus*: Parker, 1982). Despite the lack of specific data, some aspects of the natural history of these larger taxa may be estimated by reference to the general allometric relationships established in our analyses (e.g., Fig. 1). It appears that a knowledge of mean adult body sizes for any species of Australasian python provides reasonable grounds for inferences on characteristics as diverse as the probable offspring size, incubation period, spur size, and broad dietary composition of the taxon (Fig. 1). This result reinforces the major influence of absolute body size on many aspects of an organism's biology. For example, the consistency with which larger body sizes correlate with a shift from reptilian to mammalian prey items, both intraspecifically and interspecifically, suggests that the primary reason why most pythons eat mammals is not any special adaptation of the Pythoninae so much as a consequence

TABLE 3.—Prey items recorded from alimentary tracts of pythons examined. One record of a prey item from *L. albertisii* (a *Rattus* sp.) is omitted to save the need for a column for this species.

| Prey items | *childreni* | *maculosus* | *perthensis* | *stimsoni* | *melanocephalus* | *ramsayi* | *viridis* | *boa* | *fuscus* | *olivaceus* | *amethistina* | *spilota* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AMPHIBIA—spp. | 9 | 2 | | 2 | | | | | | | | 2 |
| Hylidae | | | | | | | | | | | | |
| *Litoria* spp. | 1 | | | | | | | | | | | |
| *L. nasuta* | 1 | | | | | | | | | | | |
| Myobatrachidae | | | | | | | | | | | | |
| *Limnodynastes* spp. | 2 | | | | | | | | | | | |
| *L. ornatus* | 1 | | | | | | | | | | | |
| REPTILIA | | | | | | | | | | | | |
| Lacertilia—spp. | | 2 | | 1 | | | | | | | | |
| Agamidae—spp. | | | | 2 | 6 | 5 | | | | 2 | | |
| *Chlamydosaurus kingii* | | | | | 1 | | | | | 1 | | |
| *Ctenophorus caudicinctus* | | | | | 1 | 1 | | | | | | |
| *Diporiphora lalliae* | | | | 1 | | | | | | | | |
| *Lophognatus gilberti* | | | | | 1 | | | | | | | |
| *Pogona* sp. | | | | | 1 | | | | | | | |
| *P. barbata* | | | | | | | | | | | | 1 |
| *P. minor* | | | | | | 1 | | | | | | |
| *P. vitticeps* | | | | | 1 | | | | | | | |
| Gekkonidae—spp. | | | 1 | | | 1 | 1 | | | | | |
| *Gehyra* sp. | | 2 | 1 | | | | | | | | | |
| *G. australis* | | | | 1 | | | | | | | | |
| *G. nana* | 1 | | | | | | | | | | | |
| *Heteronotia binoei* | 3 | | | | | | | | | | | |
| *Phyllurus milii* | | | | | | | | | | | | 1 |
| Scincidae—spp. | 5 | 6 | 1 | 4 | 14 | 3 | 4 | 9 | 2 | 1 | | 11 |
| *Ctenotus* spp. | 1 | | | | | | | | | | | 1 |
| *Egernia napoleonis* | | | | | | | | | | | | 1 |
| *Menetia greyi* | | 1 | | | | | | | | | | |
| *Morethia ruficauda* | | | | | | | | | | | | 1 |
| *Sphenomorphus douglasi* | 1 | | | | | | | | | | | |
| *S. isolepis* | | | 1 | | | | | | | | | |
| *Tiliqua scincoides* | | | | | 2 | 1 | | | | | | |
| Varanidae—spp. | | | | | 10 | 2 | | | 1 | | | |
| *Varanus acanthurus* | | | | | 1 | | | | | | | |
| *V. gouldii* | | | | | | 1 | | | | | | |
| *V. tristis* | | | | | 1 | | | | | | | |
| Serpentes—spp. | | | | | 3 | 1 | | | | 1 | | |
| Elapidae—spp. | | | | | 1 | | | | | | | |
| *Pseudechis australis* | | | | | 1 | | | | | | | |
| Reptile eggs | | | | | 1 | 1 | | | | | | |
| AVES—spp. | 1 | | | | 1 | 1 | | | 4 | 5 | | 8 |
| Passerine spp. | | 1 | | | | | | | | | | |
| Finch | 1 | | | | | | | | | | | 1 |
| Chicken | | | | | | | | | 1 | | | |
| Bird eggs | | | | | | | | | 2 | | | |
| MAMMALIA—spp. | | 5 | 1 | 6 | 3 | 5 | | | 7 | 4 | | 9 |
| Marsupials | | | | | | | | | | | | |
| *Acrobates pygmaeus* | | | | | | | | | | | 1 | |
| *Circatetus nanus* | | | | | | | | | | | | 1 |
| *Isoodon macrourus* | | | | | | | | | 1 | | | |
| *Trichosurus vulpecula* | | | | | | | | | | | | 1 |
| Eutherians | | | | | | | | | | | | |
| Muridae—spp. | | 1 | | | | 1 | | | | | | |
| *Melomys cervinipes* | | | | | | | 1 | | | | | |
| *Zyzomys argurus* | | | | | | | | | 1 | | | |
| *Mus domesticus* | 11 | 13 | 1 | 7 | | 5 | 2 | 2 | 3 | | | 44 |
| *Rattus* spp. | 2 | 2 | | | | 2 | 1 | 3 | 2 | 4 | 2 | 8 |
| *R. colletti* | | | | | | | | | 2 | | | 3 |

TABLE 3.—Continued.

| Prey items | childreni | maculosus | perthensis | stimsoni | melanocephalus | ramsayi | viridis | boa | fuscus | olivaceus | amethistina | spilota |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *R. fuscipes* | | 1 | | | | | | | | | | 1 |
| *R. norvegicus* | | 1 | | | | | | | | | | 1 |
| *R. rattus* | | | | 1 | | | | | 1 | | | |
| *R. villosissimus* | 1 | | | | | | | | | 1 | | |
| *Oryctolagus cuniculus* | | | | | | 1 | | | 1 | | | |
| Bats—spp. | 1 | | | | | | | | | | | |
| *Taphozous* spp. | 1 | | | | | | | | | | | |

of the fact that most pythons are unusually large snakes (in comparison with sympatric colubrids, elapids, and the like). The apparent prevalence of mammalian prey in the diets of Asian and African pythons (Branch and Haacke, 1980; Fitzsimons, 1930) is consistent with this interpretation.

How do our data compare with previously published work on other Australasian pythons, and particularly with the results of detailed studies on the ecology of the southernmost (i.e., temperate-zone) Australian python, *Morelia s. spilota* (Slip and Shine, 1988*a*,*b*,*c*)? In general terms, agreement is good. Our broader data base suggests that *M. s. spilota* is probably relatively typical of Australian pythons in showing larger minimum and mean adult body sizes in females than males, cloacal spurs slightly larger in males relative to SVL, a predominance of males rather than females in museum collections, a strongly seasonal schedule of female reproduction, a probably less-than-annual reproductive frequency in adult females, and a diverse diet with a preponderance of reptiles in smaller snakes and mammals in larger ones (see references in Slip and Shine, 1988*a*,*b*,*c*). Many of these characteristics are also shared by Australian proteroglyphous snakes (elapids) that occupy the same habitats as the pythons (e.g., Shine, 1985), and indeed by many snakes of other families in other continents (e.g., Seigel and Ford, 1987).

Despite these consistencies, and an overall pattern of adherence to general allometric relationships, much interspecific variance in ecological traits remains unexplained. For example, the lack of a consistent interspecific correlation between maternal body length and fecundity in our data may reflect sampling error in our study, variance induced by spatial or temporal fluctuations in resource availability, or evolutionary adjustments of fecundity relative to body length in this group. Further data should resolve this question.

Overall, these data illuminate the ways in which a lineage of snakes has become ecologically and morphologically modified as it has radiated throughout a continent. These changes have occurred within a general framework of conservatism: many of the consistent features of pythons worldwide (e.g., large size, heavy build, large head, lack of venom, oviparity) were probably widespread also in the earliest snakes (Greene, 1983). Many of the distinctive features of the Australian pythons may be due to the sparse vegetative cover over most areas of the continent, and the predominance of ectothermic rather than endothermic vertebrates (e.g., Morton and James, 1988). Hence, arboreality is rare in Australian snakes, and most of the potential prey items are reptiles and amphibians rather than mammals and birds. The scarcity of large endothermic prey may have favored the evolution of smaller body sizes in Australian pythons (Fig. 1d). Within one specialized reptile-eating lineage (*Aspidites*), the dietary shift is reflected in major morphological modifications (Smith, 1981): the heat-sensing labial pits have been lost and relative head size has been reduced, because prey are small and elongate and hence easier to swallow. This kind of influence of prey type on the evolution of predator size and shape is particularly evident in Australian snakes because of the restricted array of available prey types in most habitats. The relative scarcity of endothermic prey seems to have profoundly influenced the adaptive radiations of both boid and elapid snakes in this continent (e.g., Shine, 1980).

*Acknowledgments.*—P. Harlow, L. Wilkins, and A. Roberts helped with data analysis, R. Lambeck with dissections, R. Hore with microscopy of faecal samples, and N. Charles and M. Fitzgerald with samples and advice on captive animals. The work would have been impossible without the enthusiastic cooperation of the curators and staff of the various museums involved. G. M. Mengden and H. G. Cogger kindly allowed us to cite their unpublished phylogenetic work. P. Harlow and H. G. Cogger provided comments on the manuscript. The Australian Research Council supported the study financially.

## LITERATURE CITED

BRANCH, W. R., AND W. D. HAACKE. 1980. A fatal attack on a young boy by an African rock python *Python sebae*. J. Herpetol. 9:243–248.

BRUNNER, H., AND B. COMAN. 1974. The Identification of Mammalian Hair. Inkata Press, Melbourne.

CHARLES, N., R. FIELD, AND R. SHINE. 1985. Notes on the reproductive biology of Australian pythons, genera *Aspidites, Liasis* and *Morelia*. Herpetol. Rev. 16:45–48.

DUNHAM, A. E., D. B. MILES, AND D. N. REZNICK. 1988. Life history patterns in squamate reptiles. Pp. 441–552. *In* C. Gans and R. B. Huey (Eds.), Biology of the Reptilia, Vol. 16. Alan R. Liss, New York.

FITZSIMONS, F. W. 1930. Pythons and Their Ways. G. G. Harrap, London.

GREENE, H. W. 1983. Dietary correlates of the origin and radiation of snakes. Am. Zool. 23:431–441.

MORTON, S. R., AND C. D. JAMES. 1988. The diversity and abundance of lizards in arid Australia: A new hypothesis. Am. Nat. 132:237–256.

PARKER, F. 1982. The Snakes of Western Province. Division of Wildlife, Konedobu, Papua New Guinea.

SCHWANER, T. D., P. R. BAVERSTOCK, H. C. DESSAUER, AND G. A. MENGDEN. 1985. Immunological evidence for the phylogenetic relationships of Australian elapid snakes. Pp. 177–184. *In* G. C. Grigg, R. Shine, and H. Ehmann (Eds.), The Biology of Australasian Frogs and Reptiles. Royal Zoological Society of New South Wales, Sydney.

SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology. Pp. 210–252. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), Snakes: Ecology and Evolutionary Biology. Macmillan, New York.

SHINE, R. 1980. Ecology of the Australian death adder, *Acanthophis antarcticus* (Elapidae): Evidence for convergence with the Viperidae. Herpetologica 36:281–289.

———. 1985. Reproductive biology of Australian reptiles: A search for general patterns. Pp. 297–303. *In* G. C. Grigg, R. Shine, and H. Ehmann (Eds.), Biology of Australasian Frogs and Reptiles. Royal Zoological Society of New South Wales, Sydney.

———. 1988. Parental care in reptiles. Pp. 275–330. *In* C. Gans and R. B. Huey (Eds.), Biology of the Reptilia, Vol. 16. Alan R. Liss, New York.

———. 1989. Constraints, allometry and adaptation: Food habits and reproductive biology of Australian brownsnakes (*Pseudonaja*, Elapidae). Herpetologica 45:195–207.

SLIP, D. J., AND R. SHINE. 1988*a*. Feeding habit of the diamond python, *Morelia s. spilota*: Ambush predation by a boid snake. J. Herpetol. 22:323–330

———. 1988*b*. Reptilian endothermy: A field stud of thermoregulation by brooding diamond python J. Zool. (Lond.) 216:367–378.

———. 1988*c*. The reproductive biology and mating system of diamond pythons, *Morelia spilot* (Serpentes, Boidae). Herpetologica 44:396–404.

SMITH, L. A. 1981. A revision of the python gener *Aspidites* and *Python* (Serpentes: Boidae) in Western Australia. Rec. West. Aust. Mus. 9:211–226.

SMITH, M., AND M. PLANE. 1985. Pythonine snake (Boidae) from the Miocene of Australia. Burea Mineral Resources J. Geol. Geophys. 9:191–195.

*Accepted:* 19 November 1989
*Associate Editor:* Daniel Formanowicz, J