Sexual dimorphism, diet and aspects of reproduction of the western keeled snake, *Pythonodipsas carinata* (Serpentes: Colubridae)

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Examination and dissection of museum specimens provided original data on morphology, sexual dimorphism, feeding habits and reproductive biology of the rare western keeled snake (Pythonodipsas carinata) *from Namibia and Angola. This small, slender snake is nocturnal. Females mature at a larger size (47-51 cm snout-vent length, SVL) than males (29-31 cm SVL), and attain considerably larger maximum sizes (to 77 cm SVL). At the same body length, males have significantly longer tails than females. Relative to SVL, analysis of covariance detected no significant differences between the sexes in head length, head width, body width, or head shape (i.e., width relative to length, or relative eye size). All prey items were vertebrates, with lizards comprising 67 % of the diet, rodents 25 %, birds 4 %, and unidentified vertebrate bones 4 %. Among lizard prey, geckos (39 % of all prey) and skinks (18 %) predominated. Nocturnal geckos* (Afroedura, Chondrodactylus, Palmatogecko *and* Pachydactylus) *as well as diurnal ones* (Rhoptropus *and* Narudasia) *were eaten. All skink prey were* Mabuya *sp. Mammalian prey were eaten primarily by larger snakes. The unusual fragmented head shields and enlarged palatine teeth of* Pythonodipsas carinata *may be adaptations that permit sleeping diurnal prey to be extracted from retreats.*

Introduction

The western keeled snake, *Pythonodipsas carinata*, is a rare back-fanged snake restricted to gravel plains and arid savannah from the Bethanie District in southern Namibia to extreme south-western Angola (Broadley 1990). The genus is monotypic and of uncertain taxonomic affinities. It is unusual among colubrids (sensu lato) in possessing greatly fragmented head shields, a peculiar maxillary dentition (3rd to 6th largest, posteriormost tooth large and grooved), a reduced number of palatine teeth (including a greatly enlarged "fang"), and hypapophyses developed throughout the vertebral column (Marx et al. 1982; Schätti & McCarthy 1987). These features have stimulated investigations into its possible status as a "protoviper" (i.e., resembling a putative transitional form between colubrids and early vipers; Marx et al. 1982). Except in phylogenetic investigations and in national (eg., Mertens 1955, 1971; FitzSimons 1962;

Branch 1988; Broadley 1990) or regional surveys of herpetofauna (Bauer et al. 1993), there are few references to this species in the literature.

Günther's (1868) type specimen of *Pythonodipsas carinata* was allegedly "found by Mr J. Chapman on the Zambeze", but Boulenger (1888) noted a second specimen from Damaraland. The species is now known to be restricted to the western arid region of southern Africa, and to be absent from the Zambezi drainage area (Broadley 1990). As Chapman travelled from Walvis Bay on his journey to the Zambezi, Broadley (1971) restricted the type locality to Damaraland. Little is known of the biology of *Pythonodipsas carinata* except for anecdotal observations (Lankes 1914; Falk 1921; Stuart 1976). Perhaps confused by the original type locality, and influenced by the unusual large, upwardly-directed nostrils of the species, Sternfeld (1910) mistakenly suggested that the species lives near water.

Previous sources of information on the habits of *Pythonodipsas carinata* have come primarily from observations of captive specimens. Lankes (1914) noted that a captive specimen of *Pythonodipsas carinata* was nocturnal and that during daylight hours it often hid under bark or stones on sand in the terrarium. Another captive snake was fed a small, sympatric skink, namely *Mabuya acutilabris*, which it bit two or three times and shook before releasing (Falk 1921). The prey was subsequently ingested, leading Falk (1921) to infer that the snake possess a weak venom. However, Marx et al. (1982) recorded that these small snakes constrict lizard prey, which continues to struggle for some time after being seized. These observations suggest that envenomation plays little part in prey immobilization. Other observations (Branch pers. obs., Haacke pers. comm., May 1996) on feeding in captive specimens confirm those of Marx et al. (1982). The only recent report on the biology of wild specimens is that of Stuart (1976), for three snakes from the Namib Desert Park. Two of these came from sparsely vegetated, arid areas, whilst the third was found in riverine vegetation near semi-permanent pools in the Kuiseb River. Two specimens had eaten, one containing an adult gecko (*Pachydactylus bibronii* = *P. laevigatus*) and the other two unidentified small rodents.

Marx et al. (1982) drew attention to the striking morphological convergence between *Pythonodipsas*, *Spalerosophis* (a North African colubrid also having fragmented head shields) and vipers. These authors conjectured that the unusual fragmentation of head shields in vipers, boids and the colubrid genera *Spalerosophis* and *Pythonodipsas* may promote the wide gape required to engulf large prey. They also suggested that the enlarged palatine fangs in *Pythonodipsas* might function to restrain geckos that are prone to escape capture by tearing their skin. Marx et al. (1982) made a plea for more ecological information on *Pythonodipsas* to address these problems. Subsequently, Schätti & McCarthy (1987) demonstrated that the various morphological similarities between *Spalerosophis* and *Pythonodipsas* represent convergence. Werner (1985) also proposed an alternative hypothesis for head shield fragmentation in *Spalerosophis* and *Pythonodipsas*, suggesting that, along with dorsal colouration and other features, they formed a suite of adaptations for Batesian mimicry of sympatric vipers. Resolution of these conflicting hypotheses is hampered by the dearth of information on the species' biology. In this context, we present here biological data for *Pythonodipsas carinata* derived from detailed analysis of preserved museum material.

Materials and methods

Information on the distribution, morphology, diet and reproductive biology of *Pythonodipsas* was based on examination of preserved specimens in the collections of the Transvaal Museum (Pretoria), Port Elizabeth Museum, South African Museum (Cape Town), Namib Desert Research Station (Gobabeb), State Museum of Namibia (Windhoek) and California Academy of Sciences (San Francisco, USA).

Preserved specimens were measured and dissected as follows. We recorded snout-vent length (SVL), tail length, head length (from posterior margin of the lower jaw to the tip of the snout), head width (at the widest point), eye diameter, body width (diameter at midbody) and body mass. The specimens were opened with a midventral incision, and any prey items in the alimentary canal (including the hindgut) were removed for later identification and measurement. Sizes of relatively undigested prey (length, width, mass) were determined directly, and reconstituted sizes of more fully digested prey items were determined by comparison with similar-sized, intact specimens in the collection of the Port Elizabeth Museum. Relative prey mass (RPM) of a gut item was calculated by expressing its mass as a percentage of the snake's mass (minus the prey item).

Sex and reproductive status of the snakes were determined by visual inspection of the gonads. Males were considered mature if they had enlarged, turgid testes and/or white, thickened efferent ducts (indicating the presence of sperm). Females were classified as mature if they had thick, muscular oviducts, vitellogenic ovarian follicles and/or oviductal eggs. Some mature snakes with regressed gonads may be mistakenly classed as immature. Additional data on diet and reproduction were obtained from the literature, and from personal communication.

Statistical analysis follows that outlined in Shine et al. (1996a - c), and involved two-tailed unpaired t-tests to assess the significance of sex differences in mean trait values. Measurements of mass were log-transformed prior to analysis to achieve normality of distributions and equality of variances. To examine differences in body proportions between the sexes, we used analysis of covariance and heterogeneity of slopes tests. Contingency-table (chi-square) analyses were used to test the significance of observed sex differences in dietary composition. An alpha level of 0.05 was used throughout.

Results

Sexual dimorphism: We examined 55 specimens of *Pythonodipsas carinata* in museum collections. Of these, 13 were juveniles too small or poorly preserved to sex accurately. The remainder comprised 15 adult males, 3 juvenile males, 15 adult females, and 9 juvenile females.

This species displays considerable sexual dimorphism in body size and proportions. Adult females attain significantly larger sizes than adult males. For most of the traits we measured (snout-vent length, head length, head width, body width, body mass), the difference in mean values between adult males and adult females was statistically significant despite our relatively low sample

Table 1. Body sizes and sexual size dimorphism in adult *Pythonodipsas carinata*. Mean values for each trait, with standard deviation in brackets, are shown. The two right columns show results of unpaired two-tailed t-tests and statistical significance of the differences between the sexes. For mass, untransformed data given in table, but tests are based on ln-transformed values.

Trait	Males	Females	t (28 df)	P
Sample size	15	15		
Snout-vent length (cm)	38.49 (6.99)	54.51 (10.48)	16.03	< 0.0001
Range of SVLs (cm)	29.0 - 51.5	38.5 - 77.0		
Tail length (cm)	6.60 (0.99)	6.40 (1.15)	0.20	0.62
Range of tail lengths	5.0 - 9.2	4.9 - 8.4		
Head length (mm)	18.84 (2.57)	25.09 (2.88)	6.25	< 0.0001
Range of head lengths	15.0 - 23.0	19.6 - 29.4		
Head width (mm)	10.32 (2.03)	14.64 (2.77)	4.32	< 0.0001
Range in head widths	0 - 10	0 - 5		
Mass (g)	24.6 (19.3)	55.1 (29.3)	3.46	< 0.003
Range in mass (g)	8 - 65	19 - 110		
Body width (mm)	10.25 (2.80)	13.48 (2.61)	3.23	< 0.007
Range in body widths	0 - 10	0 - 5		

Table 2. Diet in *Pythonodipsas carinata*. Percentage occurrence of identified prey shown in brackets. N = 28.

| Prey type	No.	No. stomachs	Reference
Vertebrate bone (3.6 %)	1	1	
Reptilia			
Lizard bone (3.6 %)	1	1	
Gekkonidae (39.3 %)			
Afroedura africana	2	1	Boulenger, 1888
Chondrodactylus angulifer	1	1	
Narudasia festiva	1	1	
Pachydactylus sp.	1	1	
Pachydactylus bibronii (= P. laevigatus)	1	1	Stuart, 1976
Palmatogecko rangei	1	1	
Rhoptropus afer	1	1	
Rhoptropus biporosus	1	1	
gecko	2	1	
Scincidae (17.9 %)			
Mabuya acutilabris	1*	1	Falk, 1921
Mabuya striata wahlbergi	1	1	
Mabuya striata punctatissima	2*	1	
Mabuya sp.	1	1	
Lacertidae (3.6 %)			
Pedioplanis gaerdesi	1	1	
Agamidae (3.6 %)			
Agama anchietae	1	1	Stuart, 1980
Aves (3.6 %)			
downy feather	1	1	
Mammalia (25.0 %)			
rodent fur	6	5	
rodent fur (*Tatera leucogaster*)	1	1	
Insecta - Secondary	5		
Indeterminate	7		
Empty	19		

* = captive feeding
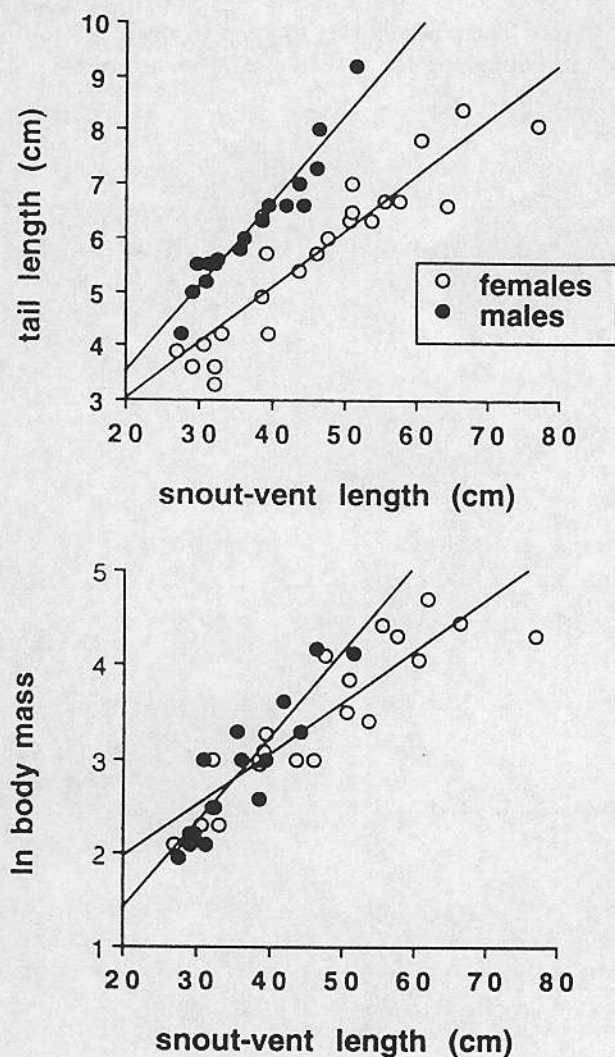
Figure 1. Scatterplot of sexual dimorphism in the western keeled snake, *Pythonodipsas carinata*. Males (dots) have relatively longer tails (a, upper graph) and higher increase on body mass with increasing SVL (b, lower graph) than do females (circles). See text for statistical tests.

sizes (Table 1). This result reflects the magnitude of the difference; e.g. adult females weighed, on average, more than twice as much as adult males (Table 1). Tail length provides a notable exception to this general pattern, being very similar in absolute length in adult males and females (Table 1). This apparent anomaly is due to a sex difference in proportions; males have longer tails than females of the same snout-vent length (Figure 1a). A heterogeneity of slopes test confirms the statistical significance of this difference (with sex as the factor, SVL as the covariate, and tail length as the dependent variable: $F_{1,28} = 9.17$, P < 0.006). Analysis of covariance detected no significant differences between the sexes in head length relative to SVL (slopes $F_{1,28} = 2.26$, P = 0.14; intercepts $F_{1,29} = 3.49$, P = 0.07), head width relative to SVL (slopes $F_{1,28} = 3.05$, P =

0.09; intercepts $F_{1,29} = 0.82$, P = 0.37), or body width relative to SVL (slopes $F_{1,28} = 2.48$, P = 0.13; intercepts $F_{1,29} = 0.41$, P = 0.53). The rate of increase in body mass with increasing SVL was higher in males than in females (slopes $F_{1,28} = 7.03$, P < 0.015) but this pattern is difficult to interpret, as the two regression lines cross at intermediate SVLs (Figure 1b).

We also examined possible sex differences in head dimensions in *Pythonodipsas carinata*, by carrying out analyses of covariance with head length (rather than SVL) as the covariate. These analyses revealed no significant sex differences in head shape (width relative to length: slopes $F_{1,28} = 0.03$, P = 0.87; intercepts $F_{1,29} = 0.02$, P = 0.89) or in relative eye size (eye diameter versus head length: slopes $F_{1,28} = 0.75$, P = 0.39; intercepts $F_{1,29} = 1.16$, P = 0.29).

One of the specimens that we examined considerably extends the maximum body size known for *Pythonodipsas carinata*. The previous record was from FitzSimons (1962), who gave a maximum size of 550 SVL + 75 tail = 625 mm total for a female specimen. This is increased considerably by a female from Goanikontes, Swakop River, Swakopmund (TM 41632) with measurements of 770 + 81 = 851 mm. The largest male (TM 69260; unknown locality) measures 515 + 92 = 607 mm.

Diet: Of 58 snakes examined, 33 (56.9 %) had gut contents, of which 20 had identifiable prey items. Five contained small insect fragments (presumably secondarily ingested with vertebrate prey), and nine had ingested fangs and/or unidentifiable material. Two prey items (*Mabuya striata punctatissima*) in the same gut must have been accepted in captivity, because this subspecies of skink does not occur in sympatry with *Pythonodipsas carinata*. The Gobabeb collection yielded an additional record, although the snake itself was not available for examination. The snake, which contained a very large *Palmatogecko rangei* in its gut, was collected at the Homeb silts in 1991, and found freshly dead on the ground during the day. Details of a further five prey items were available from other sources (Boulenger 1888; Stuart 1976, 1980; Falk 1921).

Combining these records with the information that we obtained from our dissections, it is apparent that *Pythonodipsas carinata* takes a taxonomically diverse array of prey items. Table 2 lists the items that have been identified from alimentary tracts of this species; the number of guts involved is shown in brackets. With the exception of insects, which were probably secondarily ingested (5), all prey items in the guts examined were vertebrates (20). With the inclusion of additional records (8, including those taken in captivity), lizards comprised 67 % of the diet, with geckos (11.39 % of all prey) and skinks (5.18 %) predominating (Figure 2). The former included both nocturnal (*Afroedura, Chondrodactylus, Palmatogecko* and *Pachydactylus*) and diurnal (*Rhoptropus* and *Narudasia*) genera. All skinks were referable to *Mabuya*, although three of these items had been accepted in captivity. Rodents comprised 25 % of the dietary items (7), but presumably comprised a larger proportion of the total diet in terms of biomass and energy
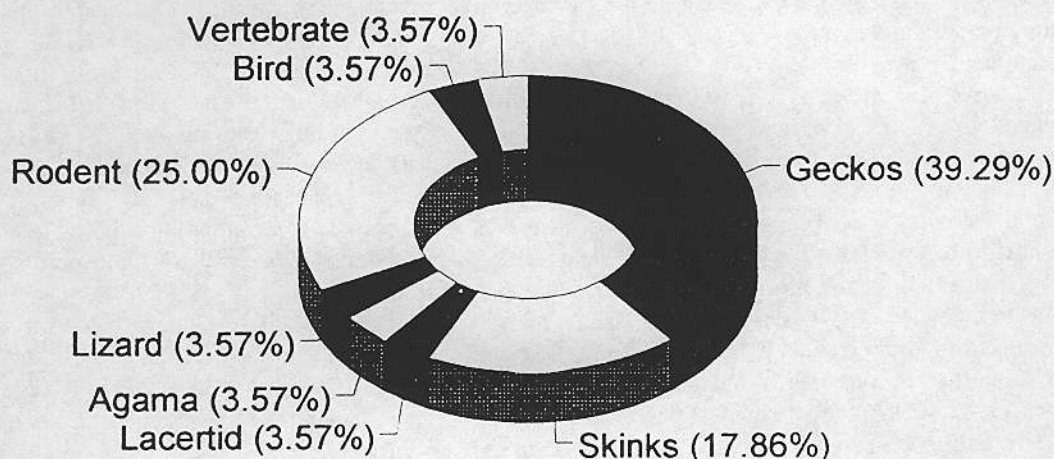
Figure 2. Diet of the western keeled snake, *Pythonodipsas carinata*.. Pie chart indicating the percentage composition of prey classes of all recorded food items is shown (n = 28). Guts containing secondarily ingested insects and unidentifiable matter are not included. Geckos comprise the largest proportion of the diet

consumption (because they tend to be much larger than the lizards that are consumed). The only mammalian prey item that could be specifically identified was a bushveld gerbil (*Tatera leucogaster;* 1). Other prey items included a diurnal lacertid lizard *(Pedioplanis gaerdesi;* 1), a diurnal agamid lizard (*Agama anchietae;* 1), lizard bones and claws (1), a down feather from an unidentified bird (1), and vertebrate bones (1). Nine additional hindguts contained dirt, shed fangs and/or other unidentifiable material.

Relative Prey Mass (RPM) could be determined for seven intact prey items (all lizards), and ranged from 0.5 - 42.8 %. Excluding the unusual record of a hatchling *Narudasia festiva* (SVL 13 mm, mass 0.1 g) in an adult (370 mm SVL, mass 19.8 g) male snake (RPM 0.5 %), the average RPM was 28.8 %. Four of the six snakes containing rodent remains were females. Snakes eating rodents had an average SVL of 497 mm (range 310 - 770; n = 6). The snakes containing gecko remains (details of the Gobabeb snake containing a *Palmatogecko rangei* are unknown) included six males, two females and an unsexed juvenile, and had an average SVL of 330 mm (range 176 - 394 mm; n = 9). Analysis of all wild *Pythonodipsas carinata* that consumed lizards increases the average SVL to 371 mm (range 176 - 617 mm; n = 15), with eight males, six females and a juvenile. There was no significant difference between the sexes in the frequency of ectothermic versus endothermic prey taken (chi-square with 1 df = 0.60 after continuity correction, P = 0.44), but there was a significant difference in mean SVL between snakes eating lizards and those eating rodents (unpaired two-tailed t-test (t with 19 df = 2.272, P = 0.0349).

Reproduction: The smallest female with thick muscular oviducts (TM 69260), indicating reproductive maturity, had a SVL of 477 mm. Other females with SVLs of 460 mm (TM 56973) and 510 mm (TM 46117) still had thin-walled oviducts indicating they may not have yet bred. Females

therefore probably mature between 475 - 510 mm SVL. Non-breeding mature females were collected in January (3), April (1), May (5), July (1) and August (1). These females contained no ovarian follicles larger than 3 mm in diameter.

The smallest sexually mature male (thick efferent ducts and/or sperm present) had a SVL of 292 mm (SMW 2310). A male of SVL 310 mm (TM 55700) had thin walled efferent ducts and tiny testes and may have still been immature. These observations indicate that male sexual maturity is reached at SVL 290 - 310 mm. Mature males with sperm in the efferent ducts were collected in May (1), June (1), and October (1).

The smallest specimens measured (PEM R8325 and SMW 2309) both had SVLs of 160 mm. One of these snakes was collected on 1 June 1965; the date for the other was not recorded. Other small juveniles (165 - 180 mm SVL), all bearing prominent umbilical scars, were collected in March (1), April (1), May (1) and July (1).

Discussion

Pythonodipsas carinata appears to be a genuinely rare snake, and knowledge of its biology and distribution has been infrequently reviewed (FitzSimons 1962; Broadley 1990). Certainly, it is very rarely encountered by humans, with less than 80 specimens collected for museums during the last 130 years. The extreme scarcity of *Pythonodipsas carinata* specimens in museum collections emphasises the usefulness of these collections as repositories of ecological data, and not just taxonomic information. Given the amount of time it would take to locate even a single specimen of *Pythonodipsas carinata* in the wild, "conventional" ecological methods (e.g., detailed autecological studies of marked animals) clearly cannot be applied to such rare species for logistical reasons. Nonetheless, our examination of museum specimens collected from a wide area, over a

long time period, and by many different people, provides an opportunity to document some aspects of the basic biology of this enigmatic serpent.

Pythonodipsas carinata is now known to be widely distributed in Namibia, with a small extension into the coastal desert of southern Angola. An updated distribution map is shown in Figure 3. There are few records from dune seas, and the species has been mainly collected on gravel plains and in rocky outcrops in the Desert and Nama-Karoo biomes (Irish 1994). It also has a limited extension into arid savanna in the western regions of the Etosha Game Reserve. The scattered southern records indicate that it may be more common in the region, which remains poorly collected (Branch 1994). There are few details of microhabitat. Stuart (1976) records specimens from sparsely vegetated, rocky areas, from derelict buildings, and from near semi-permanent pools in dry river beds. The prey of *Pythonodipsas carinata* is found in a variety of habitats, indicating that the snake itself may also be a habitat generalist.
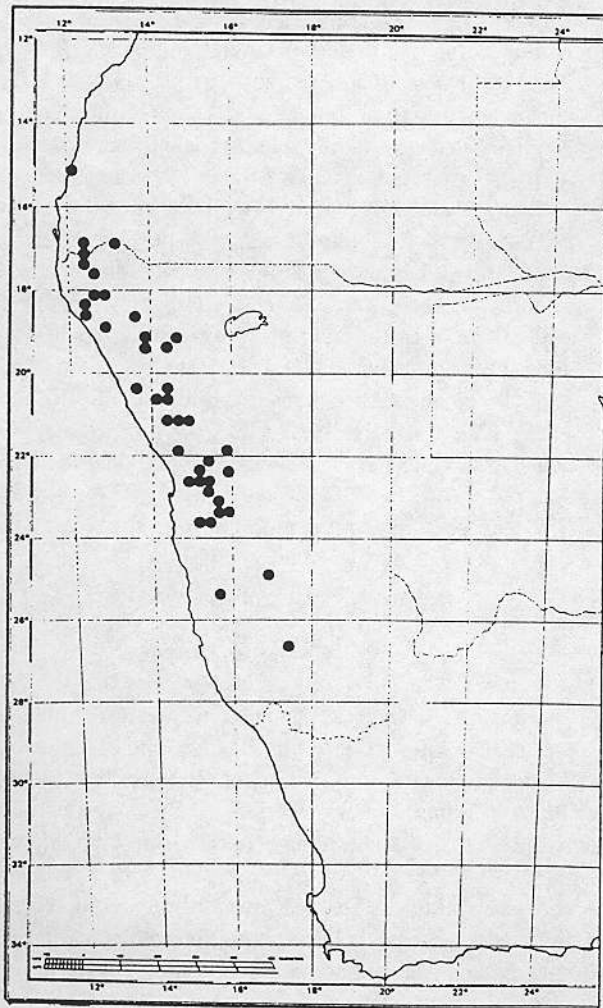

Figure 3. Distribution map of the western keeled snake, *Pythonodipsas carinata.*. Dots represent quarter-degree squares from which specimens have been recorded.

Sexual dimorphism: The ratio of mean SVL of adult female to adult male *Pythonodipsas carinata* is 1.416. A recent compilation of data on this trait among snakes in general (Shine 1994) revealed that this value was exceeded by only 4 other colubrid species (of 229 species for which data are available) and by only nine other snake species studied to date (of a total of 375 species). Hence, the degree of sexual size dimorphism in *Pythonodipsas carinata* represents an extreme case compared to the usual situation in snakes.

The probable evolutionary pressures involved in such cases have attracted considerable speculation from biologists (King 1989; Shine 1993, 1994). Madsen & Shine (1995) have demonstrated that female European adders (*Vipera berus*) experience high costs associated with reproduction, including: lower survival and lower growth rates of reproductive females; and reduced reproductive rates consequent on the postponement of subsequent reproduction due to the high energy demands of ovulation and gestation. Due to these costs, female growth after maturation slows dramatically and there is thus selective pressure for a female to delay maturation until she reaches a size where her first (perhaps, only) clutch is large. Such a scenario may explain the large body size in female *Pythonodipsas carinata.*

The huge difference in mean adult body sizes might also have been affected by, or have consequences for, ecological differences between the sexes. In several highly dimorphic snake species, the sexes have been reported to feed upon different prey types and/or forage in different habitats (e.g., Zinner 1985; Shine 1993). Our dietary data suggest that the same kind of phenomenon may occur in *Pythonodipsas carinata* also, with the larger sex (females) taking a disproportionate number of large mammalian prey. However, our sample sizes are too small to enable a quantitative test of this proposition.

The extreme female-biased dimorphism in *Pythonodipsas carinata* also allows us to make some inferences about mating systems in this taxon. Comparative analyses have identified the evolution or loss of male-male combat as a major influence on the degree of sexual size dimorphism in snakes, and no species known to engage in male-male combat displays as extreme a female-biased dimorphism as that seen in *Pythonodipsas carinata* (Shine 1994). Hence, we doubt that male *Pythonodipsas carinata* engage in combat behaviour during the mating season.

In contrast to their extreme disparity in absolute body size, male and female *Pythonodipsas carinata* are similar in body proportions (relative head length, etc.). The only morphological variable that showed different allometric trajectories in males and females was tail length relative to SVL (Figure 1a). Sex differences of this kind are widespread (but not ubiquitous) among snakes, and might result either from selection for longer tails in males (to accommodate the hemipenes or to enhance male success in courtship) or for shorter tails in females (posterior displacement of the vent may provide more abdominal space for eggs) (King 1989; Shine 1993). The significant divergence in relative tail lengths in *Pythonodipsas carinata*

is consistent with a general trend documented by King (1989) and Shine (1994), namely that sex divergence in tail length relative to SVL is most pronounced in snake taxa with strong sexual size dimorphism in body size.

Diet: The prey of *Pythonodipsas carinata* includes both diurnal and nocturnal species, that may also be terrestrial or rupicolous. Of the latter, *Afroedura africana*, *Narudasia festiva* and *Rhoptropus biporosus* are strictly rupicolous, whilst *R. afer* is rupicolous, but prefers sheet bedrock and often retreats under low rock slabs at night. Among the terrestrial species, the geckos *Chondrodactylus angulifer* and *Palmatogecko rangei* are restricted to sandy habitats, whilst the lacertid *Pedioplanis gaerdesi* prefers gravel plains. The gecko *Pachydactylus bibronii* (= *P. laevigatus*) and the skink *Mabuya striata wahlbergi* have wider habitat preferences, and are often commensal (Branch 1988). The bushveld gerbil is nocturnal and occurs in open savanna on sandy soils (De Graaff 1981).

What does this tell us about the foraging tactics adopted by *Pythonodipsas*, or the adaptive significance of the unusual cranial features, namely fragmented head-shields and enlarged palatine teeth? Experience with captive specimens confirms the nocturnal habits of *Pythonodipsas carinata* (Mertens 1955; Werner 1985). Hence, the numerous prey items belonging to diurnally-active lizard genera (*Rhoptropus*, *Narudasia*, *Mabuya*, *Pedioplanis*, *Agama*) are unlikely to have been captured from ambush during daylight hours. They were probably located by the snake in their retreats at night. This infers active searching by the snake.

Discussions of snake diet often stress foraging theory and predator-prey size optimization (see Arnold 1993 for recent review). However, in such discussions on the costs and benefits of prey selection, little attention has been paid as to how snakes locate cryptically hidden prey, and what behavioural and morphological adaptations they may use to extract prey items from their retreats. This, despite the fact that many snakes are known to feed on prey that have different temporal activity patterns. Besides *Pythonodipsas carinata*, a number of other snakes have nocturnal habits and yet feed almost exclusively on diurnal lizards. These include African wolf snakes (*Lycophidion* sp.; Branch 1976), and North American lyre snakes (*Trimorphodon* sp.; Tennant 1985). Members of both genera have greatly enlarged anterior maxillary teeth and, like *Pythonodipsas carinata*, also have dorsoventrally flattened heads. We thus suggest that in all three genera, enlarged anterior teeth (on any of the dentigerous bones), function in extracting sleeping diurnal prey from their retreats in burrows and rock crevices. The flattened heads of these snakes may also permit easier manipulation of prey in restricted spaces. After extraction, prey may be subdued either by constriction (*Lycophidion* and *Pythonodipsas carinata*) or by venom introduced via grooved posterior fangs (*Trimorphodon* and possibly *Pythonodipsas carinata*). Current phylogenetic hypotheses (e.g., Schätti & McCarthy 1987; Cadle 1988) place these three genera in different subfamiles or tribes

within the Colubridae, and the unusual cranial features must therefore be convergent.

Of the three species of *Lycophidion* recorded from Namibia (Broadley 1991), only the Namib wolf snake (*L. namibianum*) significantly overlaps the range of *Pythonodipsas carinata*. These two species occur in wide sympatry in northern Namibia (Figure 3; Broadley 1991) and appear to inhabit similar rocky situations. Among wolf snakes, *L. namibianum* is of average size (maximum SVL 460 mm), and females grow larger than males (Broadley 1991). It is possible that the unusual extreme size sexual dimorphism in *Pythonodipsas carinata*, and the increased frequency of mammalian prey eaten by larger specimens, helps to reduce dietary overlap between the two species.

Marx et al. (1982) suggested that the enlarged palatine fangs of *Pythonodipsas carinata* are used to overcome a specific defensive strategy employed by some geckos (i.e., "self-mutilation" by skin loss when seized). Although geckos do form the major component of the diet of *Pythonodipsas carinata* (39 % of all prey), we discount the hypothesis of Marx et al. (1982) as such a defensive strategy is used by only a few southern African geckos, none of which have been recorded in the diet of *Pythonodipsas carinata*. This defense mechanism is most conspicuous in the *Pachydactylus namaquensis* complex (Branch et al. 1996), but none of these species occur significantly within the range of *Pythonodipsas carinata*. Moreover, the high proportion of geckos within the diet may not reflect dietary specialisation on this group as the western arid region of southern Africa is a radiation centre of geckos, particularly of *Pachydactylus* and its relatives (Bauer 1990). They form the dominant component of the nocturnal vertebrate fauna in the range of *Pythonodipsas carinata*, and can be expected to form a significant proportion of the diet of even non-specialist predators.

Marx et al. (1982) also suggested that the unusual fragmentation of head shields in vipers, boids and *Pythonodipsas carinata* may promote the wide gape required to engulf large prey. The RPM of *Pythonodipsas carinata* ranges from 0.5 % to 42.8 %, although the average is 28.8 % and most records range from 18 - 25 %. However, only lizard prey was sufficiently intact for RPMs to be calculated, and it is likely that rodent prey would comprise larger RPMs. RPM has been documented for very few other southern African snakes (examples in Shine et al. 1996a - c, 1997), but it does not seem likely that *Pythonodipsas carinata* is exceptional in this respect. Instead, we propose that the fragmented head shields of *Pythonodipsas carinata* may permit greater distortion of the head and allow easier prey manipulation within the confines of a lizard's retreat.

Reproduction: Due to the lack of sexually-active females, our investigations resolve only certain aspects of reproduction in *Pythonodipsas carinata*. Although few detailed studies on reproduction in southern African snakes have been undertaken (*Duberria lutrix*, Kofron 1990; *Psammophis* sp., Flemming 1994; *Mehelya* sp., Shine et al. 1996a; *Aspidelaps scutatus*, Shine et al. 1996b; and

Thelotornis capensis, Shine et al. 1996c), it is evident from the general literature (Broadley & Cock 1975; Branch 1988; Broadley 1990) that a common reproductive strategy for oviparous species in the temperate regions of southern Africa involves maturation of eggs and mating in early spring (August - October), egg laying in late spring (September - November), with emergence of hatchlings in late summer (January - March). That *Pythonodipsas carinata* conforms to this reproductive seasonality is supported by: (i) the fact that several of the females we examined showed clear evidence of sexual maturity (i.e., had large muscular oviducts) over this spring - summer period; and (ii) the occurrence of recently-hatched young in the March to July period.

Females of viviparous species are usually still gravid with late-term embryos in late summer (January - March), with birth occurring in the February - April period. No details of reproduction in *Pythonodipsas carinata* occur in the literature except for Marais' (1992) claim that it is oviparous. We are unaware of any data to support this statement. All southern African museum collections lack mature females from the critical period, September to December. However, our data do not conflict with a typical oviparous seasonal breeding cycle for *Pythonodipsas carinata*. The absence of embryos in three mature females collected in January also mitigates against viviparity, but more data are required.

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