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Ecology of Eastern Australian Whipsnakes of the Genus *Demansia*

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ABSTRACT—Body sizes, food habits and reproduction in eastern Australian elapid whipsnakes are described, based on dissection of 537 specimens. The four species studied are *Demansia atra, D. olivacea, D. psammophis* and *D. torquata.* Males attain larger body sizes than females in all species, and male-male combat is recorded in *D. atra.* The diet consists mainly of lizards, especially skinks. Female reproductive cycles are strongly seasonal in the two southernmost *Demansia (D. psammophis* and *D. torquata),* with ovulation in spring. In contrast, the tropical *D. atra* and *D. olivacea* apparently reproduce year-round. All four species are oviparous, with mean clutch sizes between 3 and 8 eggs. Inferred rates of bodily growth in Queensland *D. psammophis* are high, with sexual maturation at ≈ 20 months of age in both sexes.

Several colubrid snake taxa in other continents are remarkably similar to *Demansia* in morphology (slender body, long tail, large eyes) behavior (rapid movement, diurniality, terrestriality) and ecology (saurophagy and oviparity). These whipsnake characteristics are interpreted as adaptations to facilitate the chase and capture of fast-moving diurnal prey items, especially lizards.

* * *

INTRODUCTION

"Whipsnakes" of various taxa are conspicuous elements of the terrestrial snake fauna in most parts of the world. Despite their different phyletic origins all of these whipsnakes are similar in morphology and behavior: they all have slender bodies, long tails, large eyes, alertness, diurniality and great speed of movement. Obvious examples of whipsnakes include *Masticophis* in America, *Coluber* in Europe and Asia, and *Psammophis* in Africa. The Australian representatives of this "type" are elapids, not colubrids, and belong to the genus *Demansia.* They are strikingly convergent with colubrid whipsnakes in appearance and habits.

Despite its conspicuousness and virtually Australia-wide distribution, the genus *Demansia* has never been the subject of detailed ecological study. The present paper, based on dissection of museum specimens, provides data on body sizes, feeding, reproduction and inferred growth rates in eastern Australian populations of four *Demansia* species.

Until recently, only four species of whipsnakes *(D. atra, D. olivacea, D. psammophis, D. torquata)* have been generally recognized as occurring in Australia (Cogger 1978). However, a recent revision by Storr (1978) has added three more species *(D. papuensis, D. reticulata, D. simplex).* The two latter forms are western, and are not considered in the present paper. *D. papuensis* was recorded by Storr (1978) from Western Australia and the Northern Territory, and at least one Queensland Museum specimen which I examined (J 8122, from Cape York Peninsula) is referable to this species (G. Czechura, pers. comm.). However, this paper primarily is concerned with the other four eastern species recognized by Cogger (1978). As noted above, these four species morphologically are similar to each other and to unrelated colubrid whipsnakes (Fig. 1). The species differ, however, in body size *(D. atra* is by far the largest species, *D. olivacea* the smallest) and in geographic distribution. *D. atra* and *D. olivacea* are most common in tropical northern

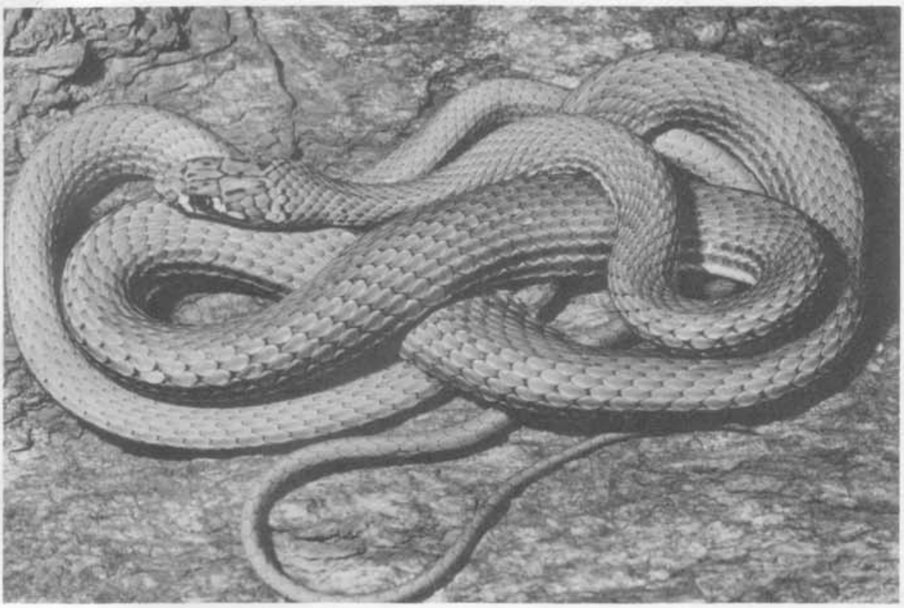

FIGURE 1. *Demansia olivacea.* Note typical "whipsnake" morphology (slender body, long tail, large eyes). Photo by H. Cogger.

Australia. The range of *D. torquata* extends from the north down into the central eastern part of the continent. The remaining species, *D. psammophis,* is distributed over most of mainland Australia, and is absent only from the central northern region (Cogger 1978).

All four *Demansia* species may be encountered in a wide range of habitats, from monsoon forests to arid regions. *D. atra* is most common in drier areas (Cogger 1978). The whipsnakes are primarily diurnal, although crepuscular or nocturnal behaviour may be observed in very warm weather (Gow 1976, 1977, Cogger 1978, McPhee 1979). All the *Demansia* are venomous, but are not regarded as highly dangerous to man.

METHODS

I examined all whipsnakes (n = 537) in the collections of the Australian Museum (Sydney) and the Queensland Museum (Brisbane). The following data were taken from each specimen: (i) snout-vent length (SVL); (ii) identity of any prey items in stomach; (iii) sex; (iv) reproductive maturity or immaturity (see Shine 1977a, b for criteria); and (v) clutch sizes and ovarian follicle diameters in adult females. Growth rates of Queensland *D. psammophis* were inferred from a plot of SVL against date of collection (see Shine 1978a for discussion and examples of this method).

RESULTS

(1) *Body Sizes.* Sample sizes, SVLs and sexual size dimorphism are described in Table 1. Mean body size varies greatly between species, but Table 1 reveals no obvious geographic differences in body size within the wide-ranging *D. psammophis.* Although males usually mature at smaller body sizes than do females (compare minimum adult SVLs for each sex in Table 1) males eventually attain much larger body sizes. This is true for both mean SVL and maximum SVL, for all taxa in Table 1. The degree of male size superiority is similar in all species.

TABLE 1. Body sizes, sample sizes and sexual size dimorphism in *Demansia* species.

			psammophis		
	atra	*olivacea*	N.S.W.	Qld.	*torquata*
Total sample size (N)	113	27	116	179	101
Adult ♂♂					
N	62	10	34	75	24
$\bar{x}$ SVL (S.E.)	78.5(2.2)	45.9(1.5)	58.4(1.9)	55.6(1.1)	53.9(1.9)
range	41.0–145.5	41.6–55.1	40.0–83.5	31.8–81.2	34.1–69.0
Adult ♀♀					
N	35	9	39	40	31
$\bar{x}$ SVL (S.E.)	73.0(3.2)	42.9(1.4)	52.0(1.2)	52.9(1.2)	51.0(1.5)
range	47.0–130.4	36.4–48.0	40.9–67.2	42.0–75.3	37.8–64.8
$\bar{x}$ SVL $\frac{♂}{♀}$	1.08	1.07	1.12	1.05	1.06

(2) *Food Habits.* Lizards are by far the most common prey type taken (73% of prey items were lizards in *D. atra,* 86% in *D. olivacea,* 90% in *D. psammophis,* 100% in *D. torquata*). Lizards of at least four families were found in *Demansia* stomachs, but skinks comprised the majority of records (Table 2). Most species consumed by whipsnakes were active diurnal lizards (e.g. *Carlia, Ctenotus, Lampropholis*), but a few nocturnal forms were also taken (e.g. geckoes, *Lerista,* frogs). These latter records suggest that *Demansia* may sometimes forage nocturnally, or else can locate nocturnal prey items in their daytime retreats. Feeding apparently continues year-round in all four species.

(3) *Reproduction.* Figure 2 presents data on the seasonal timing of vitellogenesis and ovulation. Ovaries of adult female *D. psammophis* and *D. torquata* are inactive for much of the year, with vitelllogenesis in spring (September–November), and ovulation in late spring or summer.

In contrast, no clear seasonal pattern is evident in *D. atra*

TABLE 2. Prey items from *Demansia* stomachs.

		Demansia species				
				psammophis		
	Prey type	*atra*	*olivacea*	N.S.W.	Qld.	*torquata*
(1)	Lizards					
	Unidentified spp.	—	—	—	—	2
	Agamids—spp.	1	—	—	—	—
	Amphibolurus spp.	1	—	—	—	—
	A. muricatus	1	—	1	—	—
	Geckoes—spp.	—	—	—	—	—
	Gehyra variegata	—	—	—	2	2
	Oedura sp.	—	—	—	—	1
	O. leseurii	—	—	2	—	—
	Phyllurus cornutus	—	—	—	—	—
	Skinks—spp.	3	—	3	9	—
	Carlia spp.	6	2	—	3	3
	Ctenotus spp.	2	2	—	1	—
	C. taeniolatus	—	—	2	1	—
	Cryptoblepharus sp.	—	—	1	2	—
	Lampropholis sp.	—	—	7	5	—
	L. delicata	—	—	4	—	—
	L. guichenenoti	—	—	4	8	—
	Leiolopisma sp.	2	—	5	—	—
	L. mustelina	—	—	1	—	—
	Lerista spp.	—	—	—	5	—
	L. stylis	—	1	—	—	—
	Sphenomorphus sp.	—	—	—	—	1
	S. quoyii	—	—	—	1	—
	Pygopodids—spp.	—	—	—	—	—
	Pygopus nigriceps	—	1	—	—	—
(2)	Frogs					
	Unidentified spp.	3	—	—	1	—
	Myobatrachid spp.	2	—	2	—	—
	Adelotus brevis	—	—	—	1	—
	Litoria rothi	1	—	—	—	—
	L. verreauxi	—	—	1	—	—
(3)	Reptile eggs	—	1	—	2	—
	Total =	22	7	34	41	9

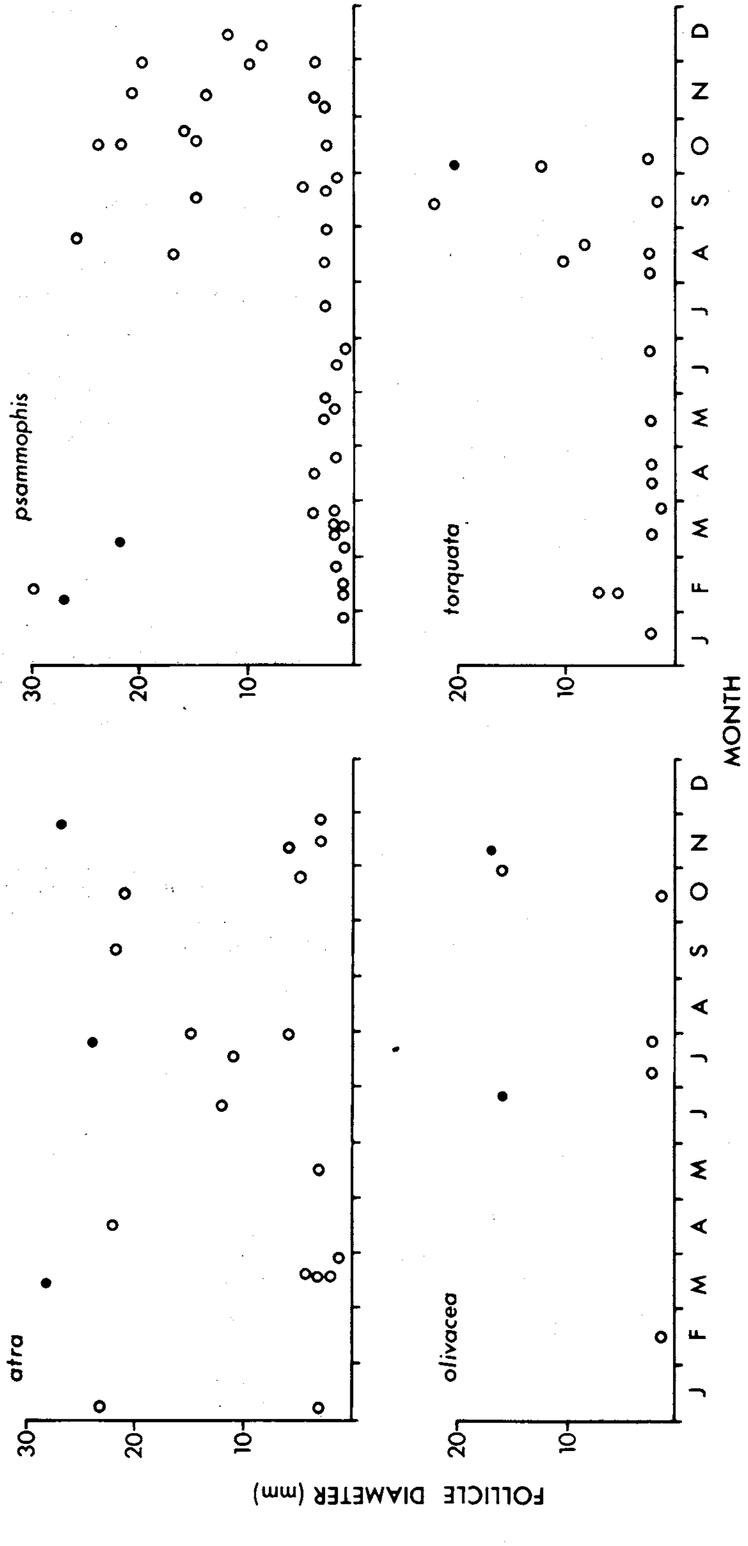

FIGURE 2. Seasonal variation in diameter of the largest ovarian follicle in adult females of four *Demansia* species. Circles show ovarian follicles, solid dots show oviducal eggs.

TABLE 3. Fecundity of *Demansia* species. Table gives values to solve the least-squares linear regression equation y = bx + a, where y = clutch size, x = SVL (cm). p = probability level (* = $p < .05$, n.s. = not significant). N = sample size.

Species		N	b	a	r^2	p	$\bar{x}$ clutch (S.E.)	Range of clutch sizes
atra		12	.16	−2.99	.32	*	7.5 (0.7)	4–13
olivacea		4	.00	3.68	.00	n.s.	3.5 (0.3)	3–4
psammophis	(N.S.W.)	8	.11	.42	.26	n.s.	6.0 (0.7)	4–9
	(Qld.)	12	.18	−3.72	.34	n.s.	5.8 (0.5)	3–9
	(combined)	20	.14	−1.34	.29	*	5.9 (0.4)	3–9
torquata		8	.19	−4.90	.76	*	4.0 (0.7)	2–8

or *D. olivacea*. Enlarged follicles and oviducal eggs are present throughout the year in these species (Fig. 2).

Females containing oviducal eggs were examined in all four *Demansia* species, and a single gravid *D. papuensis* was also dissected. In each case, oviducal eggs were enclosed in thick shells. These observations confirm oviparity as the mode of reproduction in *Demansia*.

Clutch sizes in the whipsnakes showed relatively little variation, both within and between species (Table 3). In the three species for which sufficient sample sizes were obtained, clutch size was significantly correlated with maternal SVL (Table 3). Mean clutch size varies in concert with mean adult SVL in an interspecific comparison: fecundity is lowest in the species with the smallest body size *(D. olivacea)*, and highest in the large *D. atra*.

(4) *Growth Rates.* Size at hatching is known with certainty only for *D. psammophis:* two clutches of newly-hatched young averaged 17.2 cm SVL (n = 4) and 17.3 cm (n = 3). Size at hatching may be similar for other *Demansia* species. The smallest available *D. atra* measured 18.1 cm SVL, the smallest *D. olivacea* 16.6 cm SVL, and the smallest *D. torquata* 16.7 cm SVL. Hatchlings of the larger species *D. papuensis* may, however, be of much greater size. A single gravid female *D. papuensis* from Cape York (Queensland) was examined: fecundity was low (n = 9) in relation to the snake's size (SVL = 115.8 cm), and the oviducal eggs were very large (diameter 48 mm, as opposed to a maximum of 28 mm seen in eggs of *D. atra*).

Figure 3 depicts the seasonal distribution of body sizes (SVLs) in the Queensland *D. psammophis* sample. I infer that juvenile *D. psammophis* attain ≃ 40 cm SVL at the end of their first year of life. Hence, both sexes probably mate for the first time at ≃ 20 months of age, and females produce their first clutch of eggs when 24 months old. These estimates are based on SVLs of the smallest mature specimens, combined with inferred growth rates from Figure 3.

DISCUSSION

(1) *Body Sizes.* Males attain larger body sizes than do females in all the eastern *Demansia* species (Table 1). A review of published literature reveals a strong correlation between male size superiority and the existence of male-male combat (Shine 1978b). Hence, it seems likely that male combat occurs in all of the *Demansia*. No published data are available to confirm this, but male-male combat in *D. atra* has been observed by N. Charles (pers. comm.). Mr. Charles witnessed this behaviour in northeast Queensland (near Cooktown) on 22 September. The two males were plaited together in typical ritualized combat (Bogert and Roth 1966). The specimens were captured and their sex confirmed.

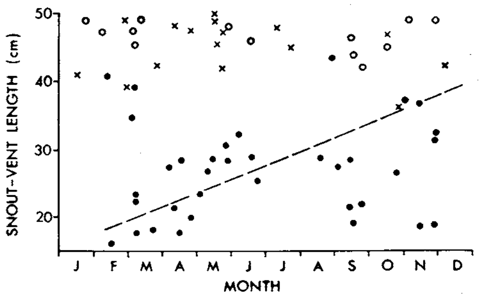

FIGURE 3. Seasonal distribution of body size, and inferred juvenile growth rate, in Queensland *Demansia psammophis*. Solid dots = juveniles; circles = mature ♀♀; crosses = mature ♂♂; Dashed line shows inferred growth pattern.

(2) *Food Habits.* Most previous authors have correctly suggested that lizards are the main prey type of *Demansia* (Table 4). Early records of predation on invertebrates seem to be in error; *Demansia,* like other Australian elapids, feeds mainly or exclusively on vertebrate prey (Shine 1977c). *D. atra* takes more frogs in its diet (27%) than the other *Demansia* (0%, in *olivacea* and *torquata,* 7% in *psammophis*); this difference is surprising in view of the preference of *D. atra* for drier habitats (Cogger 1978).

Many other Australian elapid snakes feed on lizards: the proportion of saurophagous (lizard-eating) snake species is higher in Australia than in other continents for which data are available (see Table 4 in Shine 1977c). However, lizards comprise only a small proportion of the diet in many of these snakes (e.g. Shine 1977c). Apart from *Demansia,* the only Australian elapids that definitely are known to feed *primarily* on lizards (> 70% of the diet) are small fossorial nocturnal species (*Cacophis harriettae, C. krefftii, C. squamulosus, Drysdalia coronoides, D. mastersi, Furina diadema, Simoselaps bertholdi, Unechis gouldii:* Shine 1977c, 1980a, b and unpublished).

TABLE 4. Published data on *Demansia* diet and fecundity.

	SPECIES			
AUTHOR	*atra*	*olivacea*	*psammophis*	*torquata*
(1) DIET				
Krefft 1869	—	—	insects, frogs, lizards	—
Lucas & Le Souef 1909	—	—	insects, frogs, lizards	—
Mackay 1949	—	—	skinks	—
Worrell 1963	lizards, mammals	—	skinks	—
Werler & Keegan 1963	—	—	mammals, birds, lizards, frogs, insects	—
Kinghorn 1964	—	—	mammals, birds, lizards, frogs, insects	—
Gow 1976	skinks, mammals, frogs	geckoes, skinks	skinks, snakes, frogs	skinks, snakes
Gow 1977	frogs, lizards	lizards, frogs	—	—
Cogger 1978	small vertebrates, esp. lizards	—	small diurnal lizards	lizards, esp. skinks
McPhee 1979	—	—	mainly skinks	—
Present study	lizards, frogs	lizards, esp. skinks	lizards, esp. skinks	geckoes & skinks
(2) FECUNDITY				
Krefft 1869	—	—	15–20	—
Lucas & Le Souef 1909	—	—	15–20	—
Worrell 1963	8	3–4	6	—
Werler & Keegan 1963	—	—	15–20	—
Kinghorn 1964	—	-	15–20	—
Gow 1976	8–20	3–4	6	—
Gow 1977	8–20	5	—	—
McPhee 1979	—	—	5–20	—
Present study (range)	4–13	3–4	3–9	2–8

All of these fossorial saurophagous snakes capture their prey at night when the lizards are inactive (an African elapid, *Walterinnesia aegyptia,* forages in the same way: Zinner 1971). Prey items probably are located by scent (Zinner 1971). This foraging strategy is fundamentally different from that of the whipsnakes, which locate their prey items visually, during the day, and capture them by direct chasing (Shine, pers. obs.). The Australian species most similar to *Demansia* in this regard are the large *Pseudonaja (P. textilis, P. nuchalis):* although slightly heavier-bodied than *Demansia* they forage actively during the day, and lizards are an important component of their diet (Shine 1977c). An analogous situation occurs with colubrid whipsnakes: many are congeneric with large heavier-bodied species which forage actively and diurnally, but take a higher proportion of mammalian prey (at least when adult) than do the true whipsnakes. Examples of these heavier-bodied larger species include *Psammophis sibilans, Masticophis flagellum,* and *Coluber viridiflavus* (references in Table 5).

(3) *Reproduction.* The seasonal timing of reproduction is of particular interest in *Demansia.* The two southernmost, relatively cool-climate species *(D. psammophis* and *D. torquata)* show similar synchronized cycles with ovulation in spring. This pattern is almost universal among the other Australian elapid snakes studied to date (Shine 1977b, 1980a, b, c, d). However, the tropical *D. atra* and *D. olivacea* appear to reproduce throughout the year (Fig. 2). Cogger (1967) previously has suggested that reproduction is aseasonal in northern Australian elapids, but the present paper offers the first definite data in support of Cogger's statement.

Most published estimates of *Demansia* clutch sizes are too high (Table 4), as is often the case with anecdotal reports of snake fecundity (Fitch 1970). The dependence of fecundity on maternal body size (Table 3) is common in reptiles (Fitch 1970). Hatchling sizes and oviposition seasons in *D. psammophis* are consistent with published data of Covacevich and Limpus (1972). These authors also record communal oviposition sites in *D. psammophis.*

(4) *Growth Rates.* The inferred rates of bodily growth in Queensland *D. psammophis* are similar to, but higher than, growth rates of several other elapid species (Shine 1978a and subsequent papers). This rapid growth may be a function both of the favorable climate, and of the

TABLE 5. Ecological data on slender-bodied colubrid "whipsnakes".

Species	Distribution	Oviparous ?	Diurnal ?	Terrestrial?	Diet	Authority
Masticophis bilineatus	North America	√	√	√	birds?	Wright & Wright 1957
M. lateralis	North America	√	√	√	reptiles, mammals	Wright & Wright 1957
M. taeniatus	North America	√	√	√	mainly lizards	Parker 1974
Drymobius margaretiferus	Central America	√	√	√	frogs	Hardy & McDiarmid 1969, Conant 1975
Leimadophis almadensis	South America	√	?	√	rodents, lizards	do Amaral 1977
L. melanostigma	South America	√	?	√	rodents, lizards	do Amaral 1977
Liophis genimaculatus	South America	√	?	√	lizards, frogs, rodents	do Amaral 1977
Coluber najadum	Europe	√	√	√	lizards	Steward 1971
C. spinalis	China	√	√	√	lizards	Pope 1935
Psammophis lineolatus	Asia	?	?	√	lizards	Pope 1935
P. angolensis	Africa	√	√	√	lizards	Broadley & Cock 1975
P. jallae	Africa	√	√	√	lizards	Broadley & Cock 1975
P. leightoni	Africa	√	√	√	lizards	Fitzsimons 1974
P. notostictus	Africa	√	√	√	lizards	Fitzsimons 1974
P. subtaeniatus	Africa	√	√	√	lizards	Fitzsimons 1974

slender body shape of *D. psammophis.* The slender form means that a slight increase in biomass (or energy content) translates into a large increase in body length. The age at sexual maturity in *D. psammophis* is similar to that in other small Australian elapids (Shine 1978a and subsequent papers).

(5) *Comparison of* Demansia *with other Whipsnakes.* Distantly-related colubrid snakes in America, Asia, Europe and Africa have evolved typical "whipsnake" morphology and behavior (see Table 5 for a partial list). The degree of morphological convergence between these species and *Demansia* is remarkable. This similarity extends to ecology and behavior as well. In addition to being slender-bodied, long-tailed and large-eyed, all the whipsnakes typically are terrestrial, oviparous, active, diurnal, and feed mainly on lizards (Table 5). In keeping with their diurnal active foraging, the whipsnakes studied to date have all shown high preferred body temperatures (Brattstrom 1965, Heatwole 1976, Hammerson 1979).

Why have these unrelated snakes evolved such extreme similarities? I suggest that all the major whipsnake characteristics are adaptations to facilitate the chase and capture of fast-moving diurnal prey, usually lizards. This hypothesis is consistent with the common saurophagy of whipsnakes, and offers possible explanations for the other whipsnake characteristics noted above: (i) *diurniality and terrestriality* clearly are related to this type of saurophagy; (ii) *slender bodily form* enables rapid movement, essential for capturing agile lizards; (iii) *large eyes* provide the visual acuity required for active chasing (in contrast to most other snakes, which rely heavily on chemoreception during foraging); and (iv) *oviparity* is advantageous because it minimizes the time period for which gravid females are physically burdened by eggs. In species which rely on speed for foraging, viviparity is unlikely to be favoured because it would too greatly restrict the gravid snake's foraging ability (Fitch 1970).

Tests of these ideas will come only from further ecological studies on whipsnakes. The abundance and ease of observation of many whipsnake species make them ideal subjects for such studies; Parker's (1974) work is perhaps the best example of what can be achieved. In the absence of detailed ecological data on other whipsnake taxa, the available information still is sufficient to reveal an interesting example of convergent evolution.

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