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## The Evolution of Viviparity: Ecological Correlates of Reproductive Mode within a Genus of Australian Snakes (*Pseudechis*: Elapidae)

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Five species of large venomous snakes of the genus *Pseudechis* are oviparous, whereas one (*Pseudechis porphyriacus*) is viviparous. Data were gathered on body sizes, food habits, activity patterns and reproductive biology of all the *Pseudechis* species, based on dissection of 996 museum specimens and maintenance of animals in captivity. These data revealed that oviparous and viviparous congeners do not differ in most of the factors predicted to favor the evolution of viviparity, or to evolve in response to viviparity. Specifically, all of the *Pseudechis* species are similar in average adult body size (100-130 cm), sexual size dimorphism (adult males approx. 15% longer than females), seasonal timing of reproduction (ovulation in spring, at least in the temperate zone), fecundity (averages of 8-12 offspring), and sizes of eggs and offspring (hatchlings of 200-300 mm snout-vent length [SVL] except in *P. colletti*, 280-370 mm SVL). Interspecific differences were evident in activity patterns (diurnal to nocturnal) and food habits (catholic, eating mainly reptiles, frogs and mammals), but geographic variation in these characteristics in wide-ranging species suggests that such differences reflect phenotypic plasticity rather than fixed interspecific differences. The only unique characteristic of the viviparous species is its occupancy of cold climates, and possibly its restriction to riparian habitats. These data strongly falsify several hypotheses on morphological and ecological consequences of the evolution of viviparity. Hypotheses on selective forces for the origin of viviparity are much more difficult to test. Of the many alternative hypotheses on this question, the "cold climate" hypothesis is the only one which successfully predicts ecological correlates of reproductive mode in *Pseudechis*.

VIVIPARITY has evolved independently at least 90 times in squamate reptiles (Shine, 1985), and the selective forces favoring the evolution of viviparity have been a subject of vigorous debate for more than 50 yr (Packard et al., 1977; Blackburn, 1982; Shine, 1985). Many squamate genera (and more rarely, species) are reproductively bimodal, providing ideal material for comparisons of closely related oviparous and viviparous taxa. Such comparisons may shed light on the selective forces that favored viviparity, or on subsequent adaptations to the shift in reproductive mode (Tinkle and Gibbons, 1977). Distinguishing between these two alternatives is difficult: any interpretation that a particular factor was a selective pressure for vivi-

parity rather than a subsequent adaptation is essentially a hypothesis about the sequence of events (for example, that the taxon inhabited cold climates before rather than after it evolved viviparity). Such assertions are likely to be untestable unless there is an excellent fossil record, although the chances of error are reduced if attention is focussed on closely related oviparous and viviparous taxa among which phylogenetic relationships are well understood. Hence, comparisons of this type should yield strong tests of ideas about the evolutionary and ecological consequences of viviparity, and weaker (but still useful) information on the selective advantages important in the origin of the trait. Although there have been broad-scale analyses

comparing characteristics of oviparous and viviparous congeners (Shine and Bull, 1979; Shine, 1985), the only detailed studies to date have dealt with iguanid lizards of the genus *Sceloporus* (Guillette et al., 1980; Guillette, 1982). In the present paper, I consider ecological correlates of oviparity and viviparity in a genus of large venomous Australian snakes (*Pseudechis*).

There are many hypotheses about factors important in the evolution of viviparity, and on the ecological consequences of a shift in reproductive mode. Indeed, there seem to be few ecological variables that have not been suggested to play some role! These hypotheses yield a considerable array of predictions on ecological characteristics of oviparous vs viviparous congeners. These predictions include the following:

- 1) If viviparity is an adaptation to increase survivorship of embryos under harsh conditions, viviparous taxa should occur under different climatic conditions than oviparous taxa: either colder (Mell, 1929), hotter (Shine and Bull, 1979), wetter (Sowerby, 1930), drier (Neill, 1964) or less predictable (Tinkle and Gibbons, 1977), or some combination of the above.
- 2) Body sizes of viviparous taxa should be larger than in oviparous taxa because females of large species should be less vulnerable to predation while gravid (Neill, 1964).
- 3) Female body size relative to male body size should be larger in viviparous taxa because the relatively infrequent reproduction of females in viviparous taxa favors larger body size (and hence fecundity) at each reproduction (Fitch, 1981).
- 4) Viviparous taxa should be less reliant on mobility for feeding or for escape from predators because the costs of prolonged oviductal retention of eggs to the female are thereby reduced (Fitch, 1970).
- 5) Viviparous taxa should be heliothermic rather than thigmothermic, so that oviductal retention of eggs in cold areas accelerates embryonic development (Shine, 1985).
- 6) Relative clutch mass should be lower in viviparous than in oviparous taxa because viviparous females are burdened with the developing offspring for a longer time (Seigel and Fitch, 1984).
- 7) Offspring should be larger in viviparous taxa because higher survivorship of eggs in utero than in the nest may favor an evolutionary increase in size of neonates according to the safe harbor hypothesis (Shine, 1978a).
- 8) The seasonal timing of reproduction may shift, resulting in earlier ovulation in the viviparous taxon because of the advantages of maternal thermoregulation (Guillette, 1982).
- 9) The number of clutches produced per female per year should be lower in a viviparous species because of the longer duration of burdening of the female (Fitch, 1970).

This list is not exhaustive; other factors which have been suggested to play a role in the evolution of viviparity (for example, arboreal, aquatic or fossorial habits, and maternal care of eggs; Neill, 1964; Fitch, 1970; Shine and Bull, 1979) have not been considered in the present study, as no *Pseudechis* species shows these characteristics.

The genus *Pseudechis* contains six species of large proteroglyphous snakes: *Pseudechis papuanus* of southeastern New Guinea; *P. australis*, widely distributed throughout mainland Australia and also known from southeastern New Guinea; *P. butleri* of southern Western Australia; *P. colletti* of central Queensland; *P. guttatus* of central New South Wales and eastern Queensland; and *P. porphyriacus* of southeastern Australia, extending into central eastern regions of Queensland (Fig. 1). All six species of *Pseudechis* are similar in general body form, scalation, and external morphology (see Mengden et al., 1986 for data and photographs). Recent studies provide extensive information on phylogenetic relationships within the genus (Mengden et al., 1986), and on thermoregulation, movement patterns, behavior, habitat use and general biology of one species, *P. porphyriacus* (Shine, 1977a, 1977b, 1977c, 1978b, 1987a; Shine et al., 1981). Determinants of geographic distributions of oviparous and viviparous species of *Pseudechis* are analyzed in another paper (Shine, 1987b).

#### MATERIALS AND METHODS

Most data were obtained from examination of preserved specimens in collections of the Australian Museum, Western Australian Museum, Northern Territory Museum, Queensland Museum, South Australian Museum, Museum of Victoria, Australian National Wildlife Collection, and Museum of Comparative Zoology (Harvard). My extensive collections of *P. porphyriacus* used in previous studies (Shine,

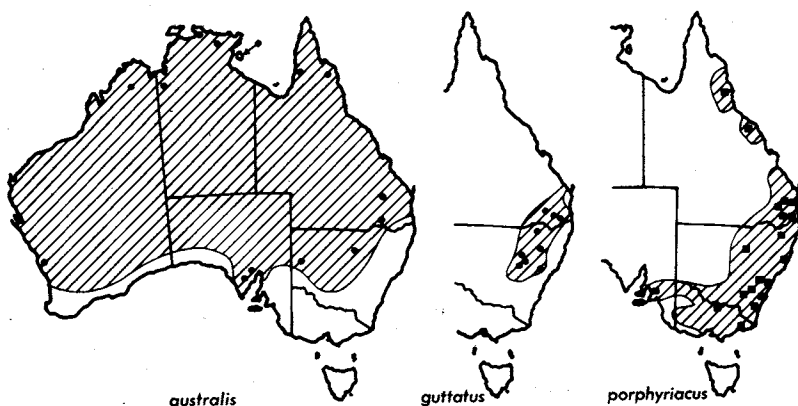


Fig. 1. Distributions and reproductive modes of the three wide-ranging *Pseudechis* species. Squares indicate a record of viviparous reproduction (in captivity, or dissection of a gravid specimen); dots indicate oviparous reproduction.

1977a, 1977b, 1977c, 1978b, 1979) were not included in the present analysis. All museum specimens were measured (SVL) and a midventral incision was made to determine: 1) sex; 2) reproductive status (males were considered mature if they had enlarged testes or opaque, thickened vasa deferentia; females were considered mature if they had ovarian follicles >5 mm diameter, or thickened oviducts); 3) fecundity in reproductive females (based on counts of enlarged follicles or oviductal eggs or embryos); 4) reproductive mode (presence or absence of thick eggshell around oviductal eggs); 5) sizes of oviductal eggs; and 6) identity of any prey items in the gut. Mammalian hairs were identified by examining microscopic sections and whole mounts (Brunner and Coman, 1974).

In addition to the 996 specimens available from these sources (see Table 1 for sample sizes for each species), I also obtained information from field work, and from observations of captive specimens of all of the Australian *Pseudechis* species (maintained at the University of Sydney). Available published data on *Pseudechis* also were reviewed, and are discussed where relevant to the predictions listed above.

#### RESULTS

*Reproductive mode.*—Published information is contradictory with respect to *Pseudechis* reproductive modes. It has long been recognized that *P. porphyriacus* is viviparous, and my data confirm that this is true throughout the geographic range of the species (Fig. 1). However, sugges-

tions that other *Pseudechis* species are also viviparous (Kellaway, 1932; Worrell, 1970; McPhee, 1979) are not supported by data. Oviparity has now been firmly established for all of the other *Pseudechis* species by breeding records in captivity (*P. guttatus*—Charles et al., 1980; *P. colletti*—Charles et al., 1983; *P. australis*—Fitzgerald and Pollitt, 1981; *P. butleri*—Fitzgerald and Mengden, 1987; *P. papuanus*—E. Worrell, pers. comm., Mengden et al., 1986), and the only remaining question is whether any of these taxa are themselves reproductively bimodal. A tentative report of viviparity in a population of *P. guttatus* (Charles et al., 1980) seems unlikely to be valid, as captive specimens of the same color phase from the same area have produced eggs in captivity (N. Charles, pers. comm.). There is only one specific record of viviparity in an oviparous *Pseudechis*: McPhee's (1979) account of a 188 cm adult *P. australis* giving birth to 22 young, each 11–14 cm long. McPhee (pers. comm.) based this account on information from W. Hosmer, who (pers. comm.) based his account on information from Mr. Berkeley Cook (now deceased). The clutch size and offspring size in the record are far outside the ranges reported in the present study, and I doubt that much reliance can be placed on the report. My own data show that oviparity characterizes *P. australis* in every mainland state in which it occurs (Fig. 1). Unfortunately, no data are available for central Australian specimens. All of the *Pseudechis* species appear to be oviparous throughout their ranges, except for the viviparous *P. porphyriacus*.

TABLE 1. SAMPLE SIZES, ADULT BODY SIZES, ADULT SEX RATIOS AND SEXUAL SIZE DIMORPHISM IN *Pseudechis* SPECIES. "Sample size" includes juveniles as well as adults. Criteria for "adult" (sexually mature), based on dissection, are described in text. SVL = snout-vent length (cm). N.T. = Northern Territory, Qld = Queensland, W.A. = Western Australia, S.A. = South Australia, N.S.W. = New South Wales.

	<i>P. australis</i>				
	W.A.	S.A.	N.S.W.	N.T.	Qld
Sample size	180	50	23	152	52
Adult males					
N	77	24	16	83	33
$\bar{x}$ SVL $\pm$ SE	120.1 $\pm$ 2.9	115.4 $\pm$ 4.0	129.7 $\pm$ 6.5	132.0 $\pm$ 4.0	131.8 $\pm$ 4.4
SVL extremes	73.0-194.0	85.5-156.0	85.0-169.0	76.3-231.0	93.5-177.3
Adult females					
N	39	9	3	22	10
$\bar{x}$ SVL $\pm$ SE	100.2 $\pm$ 1.8	96.2 $\pm$ 3.7	105.7	108.7 $\pm$ 4.0	103.4 $\pm$ 4.1
SVL extremes	76.5-131.0	79.2-111.5	91.8-118.0	71.0-148.9	86.5-129.0
Adult sex ratio ( $\delta/\varnothing$ )	1.97	2.67	5.33	3.77	3.30
Sexual dimorphism ( $\bar{x}$ SVL $\delta/\varnothing$ )	1.20	1.20	1.23	1.21	1.27

There is considerable variability in the duration of uterine retention of eggs in oviparous squamates, with some species on the threshold of viviparity (see Shine, 1983, for a review). Data are available for two oviparous *Pseudechis* species in this respect, and both are typical of oviparous snakes in retaining eggs only about halfway through the total duration of embryonic development (as judged by embryonic stage at oviposition—Dufaure and Hubert stage 33: Shine, 1983 and unpubl. data on *P. australis*). Similarities among all of the oviparous *Pseudechis* in hatchling sizes and incubation periods (see below) suggest that none of the oviparous *Pseudechis* has unusually prolonged oviductal retention of eggs.

**Body sizes.**—Data in Table 1 reveal both intraspecific (geographic) and interspecific variation in mean and maximum adult body sizes in *Pseudechis*, but the observed differences are small. Average body lengths of adult males range from 103 cm (*P. guttatus*) to 132 cm (*P. colletti*), and females from 93 cm (*P. butleri*) to 124 cm (*P. colletti*). Geographic variation in body lengths is evident in the wide-ranging *P. australis* and *P. porphyriacus*, but the technique of combining samples from throughout each state may obscure small-scale geographic variation in body sizes. Local populations of *P. porphyriacus* vary greatly in average body lengths (Shine, 1987a).

**Sexual differences in body size.**—Adult males average larger than adult females in all of the samples (Table 1), but the difference is significant ( $P < 0.05$ ) only in *P. australis*, *P. butleri*, *P. colletti* and *P. porphyriacus*. Sexual size dimorphism is highly correlated with reproductive mode (Fitch, 1981), but also with the occurrence of male-male combat (Shine, 1978c). Hence, it is worth enquiring whether combat occurs in *Pseudechis* species. Wrestling matches between rival males have been reported in *P. porphyriacus* (Fleay, 1937; Baker, 1969; Shine et al., 1981), *P. australis* (R. Pengilly, pers. comm.; D. Stammer, pers. comm.; C. Tanner, pers. comm.; P. Smyrk, pers. comm., with photographs), and *P. guttatus* (R. Williams, pers. comm.). The absence of records of male combat in the remaining taxa (*P. butleri*, *P. colletti*, *P. papuanus*) means little, because virtually no field observations are available on these species.

**Activity patterns and thermoregulation.**—*Pseudechis porphyriacus* is a diurnal heliotherm, with occasional records of nocturnal activity (Shine, 1979, 1987a). Both diurnal and nocturnal activity have been reported in the other *Pseudechis* species (Slater, 1956; McPhee, 1979; Worrell, 1970), with an apparent dependence on weather conditions: *P. australis* is "often diurnal in southern parts of its range . . . [and] . . . more often nocturnal in the north or in hot weather"

TABLE 1. EXTENDED.

<i>P. butleri</i>	<i>P. colletti</i>	<i>P. guttatus</i>	<i>P. papuanus</i>	<i>P. porphyriacus</i>		
				S.A.	N.S.W.	Qld
20	49	124	11	25	182	128
11	20	42	3	14	80	37
103.6 ± 5.9	131.7 ± 6.4	103.1 ± 2.6	119.5	106.5 ± 6.3	106.0 ± 1.9	105.6 ± 2.2
82.0–135.0	96.2–177.5	78.2–163.0	72.0–143.5	72.5–143.0	72.7–144.0	84.0–129.5
2	11	16	4	7	39	20
92.5	124.2 ± 5.4	101.9 ± 2.2	115.9 ± 9.4	91.1 ± 3.2	94.9 ± 1.5	92.8 ± 2.4
92.0–93.0	98.0–144.5	88.6–119.5	90.0–131.0	78.0–100.0	76.2–111.7	73.4–111.5
5.50	1.82	2.63	0.75	2.00	2.05	1.85
1.12	1.06	1.01	1.03	1.17	1.12	1.14

(Cogger, 1983:448). Collection data for Northern Territory specimens of *P. australis* confirm that most activity in these warm regions occurs in the evening or soon after nightfall, but with another peak of activity in the morning (Fig. 2).

Extensive field radiotelemetric studies show that *P. porphyriacus* maintains diurnal body temperatures in the range 28–31 C (Shine, 1987a), and *P. australis* temperatures may be similar (Heatwole, 1976). Thermal preferences of *P. australis*, *P. guttatus* and *P. porphyriacus* in thermal gradients in the laboratory all are close to 30 C (Heatwole, 1976; Lillywhite, 1980; Shine, unpubl.). No data on thermoregulation are available for the other species in the genus, but observations of captive *P. colletti* and *P. butleri* suggest that they are similar to the taxa which have been studied.

**Food habits.**—All of the *Pseudechis* species for which large samples are available have very generalized diets, composed mainly of frogs, reptiles and small mammals (Tables 2 and 3). Chi-square analysis, omitting *P. colletti* and *P. papuanus* because of insufficient data, showed significant dietary differences among species overall ( $\chi^2 = 60.5$ , 9 df,  $P < 0.001$ ), and in all interspecific comparisons except for that between *P. australis* and *P. butleri* ( $P = 0.05$ ; for all other comparisons, using Orders of prey as categories,  $P < 0.02$ ). The proportion of the

diet composed of mammals was higher in *P. guttatus* (32%) and *P. australis* (24%) than in either *P. butleri* or *P. porphyriacus* (8%), whereas frogs were more important in *P. porphyriacus* (60%) and *P. guttatus* (45%) than in *P. australis* (20%) or *P. butleri* (0%). The other common prey type, reptiles, was most important in *P. butleri* (92%) and *P. australis* (51%), and less so in *P. porphyriacus* (31%) or *P. guttatus* (23%). Chi-square analysis showed significant variation among species in the proportions of each of these major prey types ( $2 \times 4$  contingency table, 3 df: mammals— $\chi^2 = 11.96$ ,  $P < 0.01$ ; frogs—

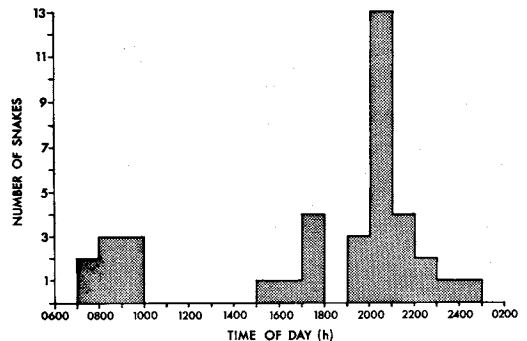


Fig. 2. Numbers of active king brown snakes (*Pseudechis australis*), collected at various times of day. All data from the Northern Territory (from Northern Territory Museum records, and pers. obs.).

TABLE 2. PREY ITEMS IDENTIFIED FROM STOMACHS OF *Pseudechis australis*, BASED ON 162 PREY ITEMS FROM 135 SNAKES.

	Western Australia	South Australia	New South Wales	Northern Territory	Queensland
Invertebrates					
Grasshopper			1		
Amphibians					
Frog sp.	4		5		1
Hylidae sp.					
<i>Cyclorana</i> sp.			1		
<i>C. australis</i>				1	
<i>Litoria caerulea</i>	1				
<i>L. rothii</i>	3				
Myobatrachidae sp.	2		1	1	4
<i>Limnodynastes convexiusculus</i>				4	
<i>L. dorsalis</i>	1				
<i>L. salmini</i>					1
<i>L. tasmaniensis</i>			1		
<i>Neobatrachus pictus</i>			1		
<i>Pseudophryne</i> sp.	1				
Lizards					
Agamidae sp.					
<i>Chlamydosaurus kingii</i>	1	3	1		1
<i>Ctenophorus inermis</i>	2				1
<i>C. isolepis</i>	1				
<i>C. reticulatus</i>	2				
<i>Pogona</i> sp.	1				
<i>P. vitticeps</i>		1	1	1	
<i>Tympanocryptis lineatus</i>	2				
<i>T. parviceps</i>	1				
Gekkonidae					
<i>Diplodactylus intermedius</i>		1			
<i>Nephurus levis</i>		1			
<i>Phyllurus milii</i>		2			
Pygopodidae					
<i>Delma</i> sp.	1				
<i>Pygopus lepidopodus</i>	1				1
Scincidae sp.					
<i>Ctenotus</i> sp.	3			3	1
<i>C. c. brooksi</i>	3			4	
<i>Lerista</i> sp.	1	1			
<i>Sphenomorphus</i> sp.				2	
<i>S. douglasi</i>				1	
<i>S. isolepis</i>	3				
<i>Tiliqua branchialis</i>	1				
<i>T. rugosa</i>	1		1		
<i>T. scincoides</i>					1
Varanidae sp.					
<i>Varanus acanthurus</i>	1	1		1	
<i>V. breviceaudus</i>	2			1	
<i>V. caudolineatus</i>	1				
<i>V. gouldii</i>		1			
<i>V. mertensi</i>	2				

TABLE 2. CONTINUED.

	Western Australia	South Australia	New South Wales	Northern Territory	Queensland
Snakes					
Colubridae					
<i>Boiga irregularis</i>				1	
Elapidae sp.	2	4		2	
<i>Demansia</i> sp.	1				
<i>D. psammophis</i>		1			
<i>D. reticulata</i>				1	
<i>Drysdalia coronata</i>		1			
<i>Pseudonaja modesta</i>	1				
<i>P. guttata</i>					1
<i>P. nuchalis</i>	1				
<i>P. textilis</i>		2			
<i>Simoselaps semifasciatus</i>	1				
<i>Unechis gouldii</i>			1		
Squamate eggs	4				
Birds					
sp.	1	4			1
Acanthizidae eggs	1	1			
Mammals					
sp.	6				
<i>Mus musculus</i>	17	4	1	7	1
<i>Rattus</i> sp.				2	
Dasyuridae				1	
<i>Sminthopsis</i> sp.				1	
<i>S. oldea</i>	1				

$\chi^2 = 48.1$ ,  $P < 0.001$ ; reptiles— $\chi^2 = 23.62$ ,  $P < 0.001$ ). Intraspecific (geographic) variation in diets was significant in *P. australis* (comparisons among states,  $\chi^2 = 50.34$ , 12 df,  $P < 0.001$ ) but not in *P. porphyriacus* ( $\chi^2 = 4.68$ , 4 df,  $P = 0.32$ ). Geographic variation in diets has previously been recorded in *P. australis* (Jones, 1980).

The prey types recorded for *Pseudechis* include most of the common small vertebrates in Australian habitats (Tables 2, 3). One group which was poorly represented was tree-frogs (*Litoria*: N = 7 specimens) compared to terrestrial frogs (Myobatrachidae and *Cyclorana*: N = 41 specimens). The lizards consumed included both diurnal and nocturnal taxa, and ranged in size from small geckoes to large varanids. The most commonly eaten mammals were introduced European house-mice, which are abundant throughout Australia. However, native rodents and marsupials also were consumed.

*Seasonal timing of reproduction.*—Ovaries of adult female *Pseudechis* contain small (<10 mm) follicles for most of the year, with rapid vitellogenesis in spring (Sept.–Nov.) in both the oviparous *P. australis* and the viviparous *P. porphyriacus* (Fig. 3). Gravid females of the latter species were found only in summer, whereas there was no obvious seasonal pattern in the occurrence of gravid *P. australis* (Fig. 3). Limited data on the other *Pseudechis* species suggest a seasonal timing of reproduction similar to that of *P. porphyriacus*. Captive specimens of *P. butleri* (N = 2), *P. colletti* (N = 7), and *P. guttatus* (N = 10) all oviposited in Dec. (Charles et al., 1980, 1983; N. Charles, pers. comm.). A gravid *P. papuanus* was recorded in Nov. and three gravid *P. guttatus* in Dec. (present study). Females with enlarged ovarian follicles (>20 mm) were observed in Oct. and Nov. in *P. butleri* (present study).

TABLE 3. PREY ITEMS IDENTIFIED FROM STOMACHS OF *Pseudechis* SPECIES, BASED ON 114 PREY ITEMS FROM 103 SNAKES.

	<i>Pseudechis</i>						
	<i>butleri</i>	<i>colletti</i>	<i>guttatus</i>	<i>papuanus</i>	<i>porphyriacus</i>		
					NSW	Qld	S.A.
Invertebrates							
Insect sp.			1				
Beetle			1				
Grasshopper			1				
Amphibians							
Frog sp.		1	5		24	5	1
Hylidae							
<i>Litoria</i> sp.			1			2	
Myobatrachidae							
<i>Adelotus brevis</i>					1		
<i>Helioporus</i> sp.							1
<i>Lymnodynastes</i> sp.			1		3		
<i>L. dumerilii</i>							2
<i>L. fletcheri</i>						1	
<i>L. ornatus</i>							1
<i>L. peronii</i>					2		
<i>L. tasmaniensis</i>			3		4		
<i>Mixophyes</i> sp.					1		
<i>Pseudophryne bibronii</i>					1		
<i>Ranidella signifera</i>							1
Lizards							
Agamidae sp.						1	
<i>Ctenophorus caudicinctus</i>	2						
<i>C. inermis</i>	1						
Pygopodidae							
<i>Pygopus lepidopodus</i>	1						
Scincidae sp.	1		2		4	2	
<i>Egernia cunninghami</i>					2		
<i>E. major</i>						1	
<i>Eremiascincus richardsoni</i>			1				
<i>Lampropholis delicata</i>						1	
<i>L. guichenoti</i>					2		
<i>L. mustelina</i>					1		
<i>Saiphos equalis</i>					1		
<i>Sphenomorphus murrayi</i>					1		
<i>S. quoyi</i>					2		
<i>Tiliqua branchialis</i>	3						
<i>T. casuarinae</i>					2	1	
<i>T. scincoides</i>					2		
Varanidae							
<i>Varanus caudolineatus</i>	1						
Snakes sp.			2				
Colubridae							
<i>Boiga irregularis</i>						1	
Elapidae							
<i>Demansia reticulata</i>	1						
<i>Hemiaspis signata</i>					1		
<i>Pseudechis porphyriacus</i>						1	
<i>Pseudonaja modesta</i>	1						



TABLE 3. CONTINUED.

	<i>Pseudechis</i>						
	<i>butleri</i>	<i>colletti</i>	<i>guttatus</i>	<i>papuanus</i>	<i>porphyriacus</i>		
					NSW	Qld	S.A.
Mammals sp.	1	2	5	3	4	2	1
Muridae							
<i>Mus musculus</i>			2				
Dasyuridae							
<i>Planigale gilesi</i>		1					

**Reproductive biology.**—Clutch sizes of *Pseudechis* ranged from 4–19, with all species averaging between 8 and 12 offspring (Table 4). These minor interspecific differences were not statistically significant ( $P > 0.05$ ). Analysis of the two largest samples revealed a significant correlation between maternal SVL and clutch size in *P. australis* ( $N = 19$ ,  $r = 0.67$ ,  $P < 0.01$ ) but not *P. porphyriacus* ( $N = 21$ ,  $r = 0.19$ , n.s.). The result for *P. porphyriacus* may be an artifact from combining samples from different areas: a previous study of a single population found a significant correlation between maternal SVL and litter size (Shine, 1977b).

Relative clutch mass (female's mass loss at parturition, divided by her post-parturient mass) was measured as 0.33, 0.57 and 0.60 in three captive *Pseudechis guttatus* (♀ masses 338, 255 and 484 gm), and 0.53 and 0.77 in two *P. porphyriacus* (♀ masses 507 and 342 gm).

Based on reproduction in captivity, and dissections of museum specimens, egg sizes are similar among most of the *Pseudechis* species: approx.  $45 \times 27$  mm, 13–19 gm for *P. australis*;  $52 \times 24$  mm for *P. butleri*;  $45 \times 26$  mm, 10–

20 gm for *P. guttatus*;  $40 \times 25$  mm for *P. papuanus* (Fitzgerald and Pollitt, 1981; Fitzgerald and Mengden, 1987; present study). Eggs of *P. colletti* are larger than in the other species ( $55 \times 32$  mm; 36 gm; Charles et al., 1983). Hatchling sizes also show relatively little variation, with ranges of 198–298 mm SVL (5.3–18.7 gm) for *P. australis*, 212–286 mm SVL (9.0 gm) for *P. butleri*, 194–250 mm SVL (8.2–12.0 gm) for *P.*

TABLE 4. CLUTCH SIZES OF *Pseudechis* SPECIES, BASED ON COUNTS OF OVIDUCTAL EGGS AND ENLARGED OVARIAN FOLLICLES IN PRESERVED SPECIMENS, AND CLUTCHES LAID IN CAPTIVITY. SVL = snout-vent length.

	N	Mean maternal SVL (cm)	Clutch size	
			Mean	Extremes
<i>P. australis</i>	19	96.2	8.6	4–19
<i>P. butleri</i>	4	92.5	9.5	7–12
<i>P. colletti</i>	7	98.0	11.7	7–14
<i>P. guttatus</i>	6	103.5	11.8	6–15
<i>P. papuanus</i>	3	111.7	8.7	7–11
<i>P. porphyriacus</i>	21	91.5	11.6	5–18

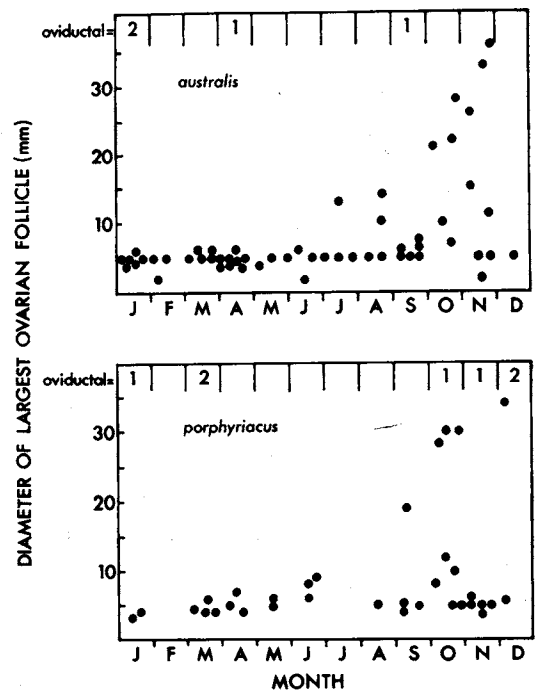


Fig. 3. Seasonal reproductive cycles in female *Pseudechis*. Dots show diameter of the largest ovarian follicle in adult females; figures at top of graphs show numbers of females with oviductal eggs collected at various times of year.

*guttatus*, and 176–267 mm SVL (10.5–13.6 gm) for *P. porphyriacus*. Again, the young of *P. colletti* are larger (280–370 mm SVL, 19.0–29.0 gm) (see above references). Data on incubation periods for 20 clutches of *Pseudechis* eggs are available from published studies and my own laboratory. Combining data for all species, incubation period is accurately predicted by mean incubation temperature (over the range 24–31 C;  $r = 0.86$ ; mean observed incubation period is 79.3 d at 28.4 C; predicted incubation period at 25 C is 104 d). Actual records of incubation periods ranged from 56 d at 31 C (*P. colletti*, Charles et al., 1983) to 120 d at 25 C (*P. guttatus*, present study).

#### DISCUSSION

A consistent feature of the data presented above is the similarity among all of the *Pseudechis* species in most of the variables studied. This conservatism is also reflected in external morphology (Mengden et al., 1986). Remarkably little variation is evident in adult body sizes, sexual size dimorphism, fecundity, reproductive seasonality, incubation periods and sizes of eggs and hatchlings. The significant interspecific differences which do exist (e.g., in diets and activity patterns) may simply be phenotypic responses to different environments, rather than genetically-based characters. For example, although tropical *P. australis* are primarily nocturnal (Fig. 2), their southern conspecifics tend to be diurnal (Cogger, 1983). Analogously, the normally diurnal *P. porphyriacus* may show nocturnal activity in the hottest parts of its range (Shine, 1979). A similar situation exists with food habits, where interspecific differences may reflect prey availability in different areas, rather than species-specific adaptations for foraging. Thus, for example, the diet of *P. australis* in hot dry regions of Western Australia is similar to that of *P. butleri* in the same area (mainly reptiles: Tables 2 and 3), whereas *P. australis* in more mesic areas of New South Wales feeds mainly on frogs, as does *P. porphyriacus* in the same region (Tables 2 and 3). Indeed, ecological flexibility seems to be a major reason for the success of *Pseudechis* in diverse habitats throughout the Australian continent. The snakes are very generalized foragers, consuming any small vertebrate that they can capture, and apparently foraging whenever ambient temperatures are suitable. Certainly, *P. porphyriacus* shows extensive geographic and temporal variation in

habitat use, movement patterns and times of activity (Shine, 1987a). The broad interspecific similarities in morphology, behavior, diets and reproductive biology hence give little or no support to most predictions of differences between oviparous and viviparous congeners:

*Climates.*—The viviparous *P. porphyriacus* inhabits areas in southeastern Australia much colder than those inhabited by any oviparous *Pseudechis* (Fig. 1: mean midsummer temperature over the range of *P. porphyriacus* approx. 12–28 C, vs 20–32 C for oviparous taxa—Shine, 1987b). The range of annual precipitation in areas occupied by the live-bearers (390–1800 mm) is similar to that for the egg-layers (130–2200 mm: data from CSIRO “Bioclim” climatic estimation program). The preference of *P. porphyriacus* for riparian habitats (Cogger, 1983) may restrict it to wetter substrate conditions, on average, than would be true for any of its oviparous congeners. However, this bias is likely to be slight: even the arid-zone oviparous *Pseudechis* prefer moist microhabitats (pers. obs.), and telemetered *P. porphyriacus* spend most of their time more than 50 m from water (Shine, 1987a). The prediction that viviparous species should be in unpredictable habitats (Tinkle and Gibbons, 1977) is untestable unless one identifies the variables for which predictability is to be assessed. Temperatures and precipitation are the obvious variables to consider, and these may be less predictable at lower elevations than at higher elevations (Zammuto and Millar, 1985). The viviparous *P. porphyriacus* occurs at higher elevations than any of its oviparous congeners, so may not conform to the predictability hypothesis in this respect. However, this is a very weak test of the hypothesis because of the difficulty in defining the relevant type of predictability.

*Body sizes.*—Contrary to prediction, females of the viviparous *P. porphyriacus* tend to be smaller than females of most of their oviparous congeners, although the differences are minor (Table 1).

*Sexual size dimorphism.*—This variable is difficult to interpret in terms of selective forces, as it may reflect both differential growth rates and survivorship rates between the sexes. Such differences might be due to proximate environmental effects rather than adaptation. Detailed analysis is unnecessary in the present case, as the

viviparous *P. porphyriacus* shows a direction and degree of sexual size dimorphism similar to those of the oviparous taxa (Table 1).

*Reliance on mobility.*—Data on diets (Tables 2 and 3) reveal significant interspecific differences, but these seem to reflect geographic variation in prey availability rather than species-specific adaptations for foraging. Field studies on the behavior of *P. porphyriacus* (Shine, 1979, 1987a) show that this species is an active "searching" forager, with home range sizes among the largest recorded for snakes. Although no comparable data are available for the oviparous *Pseudechis*, it would be surprising if they were markedly less sedentary than *P. porphyriacus* (as would be predicted by the hypothesis).

*Thermoregulation.*—*Pseudechis porphyriacus* is more consistently diurnal than the other *Pseudechis*, and maintains high and relatively constant body temperatures (Shine, 1987a). However, body temperatures of other *Pseudechis*, which inhabit warmer areas, are probably equally high (Heatwole, 1976).

*Reproductive investment.*—Limited data on relative clutch mass do not reveal any difference between *P. porphyriacus* and *P. guttatus*. More extensive data on fecundity and offspring size suggest that *P. porphyriacus* is similar in these respects to the oviparous taxa (Table 4).

*Offspring size.*—Neonates of *P. porphyriacus* are similar in size to hatchlings of all the oviparous species except *P. colletti*, which has unusually large offspring.

*Reproductive seasonality.*—Data from oviposition of captive animals, and dissection of museum specimens, suggest that all of the *Pseudechis* species show vitellogenesis and ovulation in spring or early summer. Tropical *P. australis* may be the exception to this rule, with gravid females being recorded in April and Aug. as well as Jan. (Fig. 3). Within another genus of Australian elapid snakes (*Demansia*), the strongly seasonal reproduction of temperate-zone taxa changes to aseasonal reproduction in tropical forms (Shine, 1980), and the same phenomenon may occur in *Pseudechis*.

*Frequency of reproduction.*—Based on ovaries of dissected specimens, and many records of

breeding in captivity, none of the *Pseudechis* species seems likely to produce eggs or offspring more than once per annum.

The overall result from this analysis is clear: the viviparous *P. porphyriacus* is remarkably similar to its oviparous congeners in virtually all of the characteristics which have been suggested as stimulating the evolution of viviparity. One hypothesis (environmental predictability) seems impossible to test at present. Hence, this study offers no support for the role of most of these factors. The only exceptions are the variables associated with climate and perhaps with habitat: *P. porphyriacus* certainly inhabits cooler areas, and perhaps moister substrates, than do its oviparous congeners. Whether these ecological differences between *P. porphyriacus* and its congeners played an important role in the evolution of viviparity in this genus, or reflect modifications subsequent to the development of viviparity, remains unclear. A broad comparative analysis has revealed that occupancy of cold climates is the most consistent correlate of viviparity within reproductively bimodal reptilian genera (Shine, 1985). This could mean either that viviparity has usually evolved in cold climates, or that species in which viviparity has evolved are then likely to invade cold climates. Broad correlational analyses cannot resolve this ambiguity, but the present study offers further support for the association of viviparity with low environmental temperatures. At present, there is very little empirical support for any alternative hypothesis on selective forces favoring viviparity, or on subsequent adaptations to (or consequences of) the evolution of the live-bearing habit.

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