

Venomous Snakes in Cold Climates: Ecology of the Australian Genus *Drysdalia* (Serpentes: Elapidae)

RICHARD SHINE

The southern Australian elapid snake genus *Drysdalia* comprises four species, living under a wide variety of climatic conditions. One species (*D. coronoides*) covers the entire range from relatively warm through to extremely cold areas. Dissection of >650 *Drysdalia* specimens provided data on reproductive cycles, food habits and general ecology. Attention is focussed on those aspects of *D. coronoides* ecology that reflect the harsh environment occupied by southern populations of this species.

Body sizes of all four *Drysdalia* species are similar, and sexual size dimorphism is negligible. About 90% of the diet of *D. coronoides*, *D. mastersi* and *D. rhodogaster* consists of scincid lizards, but *D. coronata* takes anurans and lizards in equal numbers. Reproduction does not reduce food intake in *D. coronoides*. All four species are live-bearers, with ovulation in spring and parturition in late summer. Adults reproduce every year except in the coldest climate (Tasmanian) *D. coronoides*, where females reproduce only once in every 2-3 years. Sex ratio at birth is 1:1 in *D. coronoides* and *D. rhodogaster*. Neonatal body size is negatively correlated with maternal size in *D. coronoides*. Clutch sizes generally fall within the range of 3-5 offspring. Inferred growth rates are low in *D. coronoides* (maturity at 2½ years of age) but rapid in *D. coronata* (maturity at 1½ years).

I suggest that the following aspects of *D. coronoides* ecology are effects of, or adaptations to, occupancy of cold climates: i) cessation of activity and feeding in winter; ii) low growth rate and delayed sexual maturation; iii) viviparity; iv) continued feeding by females when gravid and v) lowered frequency of reproduction in females.

ENVIRONMENTAL factors may shape a species' life history "strategies" and general ecology in many ways, and much recent theoretical work has focussed on this interaction (Stearns, 1976). Some of the data most relevant to this topic have come from studies of populations at the limits of distribution, because it is under these conditions that the effects of the physical environment often are most apparent. Several studies on Northern Hemisphere snake species suggest that snakes may be an excellent group in which to examine life history adaptations to cold climates. For example, snakes in extremely cold regions have been found to exhibit lowered frequencies of reproduction (Saint Girons, 1957; Hebard, 1951; Smith and Hall, 1974; Bull and Shine, 1979), and extensive migrations to and from communal "hibernacula" (Viitanen, 1967; Gregory, 1977).

The venomous terrestrial snakes of the Elapidae have undergone an extensive radiation in Australia, and provide excellent material for a comparative analysis of this question. *Drysdalia*

is of particular interest, as its component species are distributed over an unusually wide range of climatic conditions. One species, *D. coronoides*, occurs in severely cold highland areas of extreme southeastern Australia, but also ranges into warmer central eastern areas. As is true for most venomous snakes, almost nothing is known of the ecology of *Drysdalia* species. The present paper provides data on this topic, with emphasis on ecological adaptations to cold climates. Attention is focussed on life-history variables (e.g. clutch size, offspring size, age at maturity, frequency of reproduction), but food habits and general ecology are also described.

Drysdalia consists of four species, rather similar to each other in body size and morphology (Fig. 1). The whitelipped snake, *D. coronoides*, has the most extensive geographic distribution. It is common over much of southeastern Australia, extending into alpine regions in Tasmania (Lord, 1918) and mainland Australia (Cogger, 1975). Throughout this alpine area, monthly temperatures average less than 0 C for



Fig. 1. Adult female whitelipped snake, *Drysdalia coronoides*.

6–8 months each year. *D. coronoides* has been collected near the summit of Mt. Kosciuszko, the highest Australian mountain (Copland, 1947). The related species *D. mastersi* (in Victoria) and *D. rhodogaster* (in NSW) are superficially similar to each other, and were regarded as conspecific until a recent revision (Coventry and Rawlinson, 1980). Both forms inhabit mountainous country, but at lower elevations than *D. coronoides*. The other member of the genus is the crowned snake (*D. coronata*), an endemic southwestern Australian species separated by several hundred kilometers from its congeners in southeastern Australia. Based on head musculature and hemipenial morphology, McDowell (1967) has suggested that *D. coronata* is an evolutionary intermediate between true *Drysdalia* and the larger snakes of the genera *Notechis*, *Tropidechis* and *Oxyuranus*; he indicated that *D. coronata* may merit separate generic distinction.

MATERIALS AND METHODS

Most data for the present study were gathered by dissection of preserved specimens in the Australian Museum, National Museum of Victoria, Queen Victoria Museum and Western Australian Museum. Over 650 snakes were examined, and the following data recorded for each specimen: i) snout-vent length (SVL); ii)

reproductive maturity or immaturity (criteria in Shine, 1977b, c); iii) diameters of largest ovarian follicles; and iv) gut contents. Growth rates were inferred from seasonal distributions of body sizes (Shine, 1978a). Further reproductive data were obtained from captive *D. coronoides*. Geographic variation in *D. coronoides* was examined by separate analysis of populations in each state, except that data for South Australian specimens were combined with Victorian data, and Australian Capital Territory records combined with New South Wales records. Nonparametric statistical tests are from Siegel (1956).

RESULTS

Body sizes and sexual size dimorphism.—Adults of all four species attain similar body sizes (Table 1). Within the wide-ranging *D. coronoides*, southern (Tasmania) snakes grow larger than their mainland (Victoria and New South Wales) conspecifics (median test, 1 df, $P < .05$). There is little difference between males and females in mean adult size, maximum size or minimum SVL at maturity (Table 1). However, the trend for mean body size to be larger in females than males is consistent enough (6 out of 6 samples) to attain statistical significance ($0.5^5 = .03$).

TABLE 1. BODY SIZES AND SEXUAL SIZE DIMORPHISM IN *Drysdalia* SPECIES. SVL = snout-vent length (cm).

	<i>coronoides</i>			<i>mastersi</i>	<i>rhodogaster</i>	<i>coronata</i>
	NSW	Vict.	Tas.			
Sample size	98	165	119	25	71	177
Adult ♂♂:						
N	18	34	44	7	15	76
\bar{x} SVL (SE)	27.1 (.6)	27.2 (.6)	32.3 (.6)	22.1 (.6)	30.4 (.8)	31.8 (.6)
SVL range	21.5–31.5	22.5–34.3	24.3–39.6	20.9–25.3	26.9–36.0	22.8–43.1
Adult ♀♀:						
N	28	52	35	4	30	57
\bar{x} SVL (SE)	30.1 (.9)	28.5 (.5)	32.6 (.7)	22.7 (.4)	30.9 (.5)	32.1 (.6)
SVL range	22.2–37.5	22.7–35.7	25.2–41.4	21.8–23.4	23.6–36.3	24.5–52.3
Ratio \bar{x} SVL ♂/♀	.90	.95	.99	.97	.98	.99

Seasonal abundance.—Not surprisingly for a cold climate snake, most specimens of *D. coronoides* were collected in the warmer months of the year (Fig. 2b, c). The scarcity of winter records is clear from this figure, and is confirmed by analysis against a null hypothesis of random monthly distribution of captures (mainland populations: $N = 161$, $\chi^2 = 76.8$, 11 df, $P < .01$; Tasmania: $N = 101$, $\chi^2 = 99.9$, 11 df, $P < .01$). The greater seasonality of the Tasmanian collection is evidenced by a higher coefficient of variation (1.04 versus 0.72) and by a significant difference between the seasonal distributions of captures of mainland and Tasmanian snakes ($N = 262$, 4×2 contingency table, $\chi^2 = 27.9$, 3 df, $P < .01$). Seasonal distributions of adult males, adult females and juveniles did not differ significantly from each other (all data combined, 4×3 contingency table, χ^2 with 6 df, n.s.). Other species tended to show the same seasonal trends in numbers as *D. coronoides*, but with a less pronounced decline in winter (Fig. 2a).

Adult females outnumber males in collections of *D. rhodogaster* and mainland populations of *D. coronoides* (Table 1). However, males were more numerous than females in Tasmanian *D. coronoides*, and the observed adult sex ratio in this sample is significantly different from that shown by mainland conspecifics ($N = 211$, 2×2 contingency table, $\chi^2 = 4.7$, 1 df, $P < .05$). Males also tended to be more numerous than females in *D. coronata* (Table 1; $\chi^2 = 1.36$, 1 df, n.s.). Among 54 oviducal embryos of NSW *D. coronoides*, the observed sex ratio (28 ♂♂:26 ♀♀) did not differ significantly from 1:1 ($N = 54$, $\chi^2 = 0.0$, 1 df, n.s.). Similarly, the

sex ratio was close to 1:1 (7 ♂♂:9 ♀♀) in 16 oviducal embryos of *D. rhodogaster*.

Food habits.—Small scincid lizards are the main prey type of *Drysdalia* (Table 2). Among the eastern Australian species (*D. coronoides*, *D. mastersi*, *D. rhodogaster*), skinks comprised 61 of the 71 recorded food items (86%). Another 6 items were scincid eggs. Hence, skinks and their eggs constitute over 90% of the eastern *Drysdalia* diet. A wide range of scincid species is taken, ranging from small secretive burrowers (e.g. *Anotis maccoyi*) to large robust diurnal forms

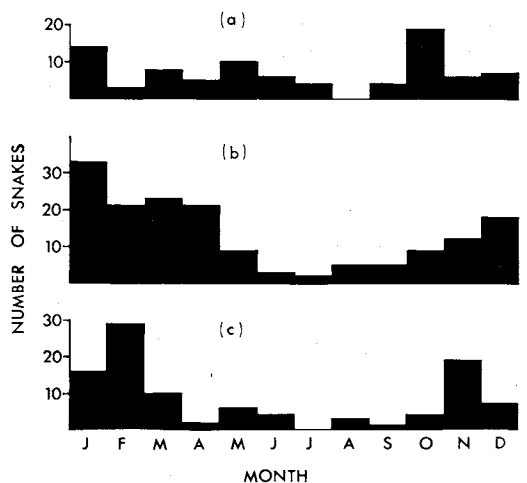


Fig. 2. Seasonal abundances of *Drysdalia* species, based on collection data from museum specimens. (a) *D. coronata*, (b) Mainland *D. coronoides*, (c) Tasmanian *D. coronoides*.

TABLE 2. PREY ITEMS FROM STOMACHS OF *Drysdalia* SPECIES. FOR *D. coronoides*, "NSW" data include Australian Capital Territory records, and "Victorian" data include South Australian records.

Prey type	<i>D. coronoides</i>			<i>D. mastersi</i>	<i>D. rhodogaster</i>	<i>D. coronata</i>
	NSW	Vict.	Tas.			
(1) Lizards						
Unidentified skinks	2	6	8	1	3	8
<i>Anotis maccoyi</i>	1	—	—	—	—	—
<i>Ctenotus</i> sp.	—	—	—	—	—	2
<i>Lampropholis delicata</i>	1	2	—	—	1	—
<i>L. guichenoti</i>	3	2	—	—	—	—
<i>Leiopisma</i> sp.	1	4	9	—	3	2
<i>L. entrecasteauxii</i>	2	—	—	—	—	—
<i>L. trilineata</i>	4	—	—	—	—	—
<i>Morethia lineocellata</i>	—	—	—	—	—	1
<i>Pseudemöia spenceri</i>	1	2	—	—	—	—
<i>Sphenomorphus</i> sp.	—	1	—	—	1	—
<i>S. tympanum</i>	2	1	—	—	—	—
Gecko— <i>Gehyra variegata</i>	—	—	—	—	—	1
(2) Skink eggs	—	6	—	—	—	—
(3) Frogs	—	—	—	—	—	6
<i>Litoria</i> sp.	—	—	2	—	—	2
Leptodactylid sp.	—	—	—	—	—	8
<i>Pseudophryne</i> sp.	—	—	—	—	—	1
<i>Ranidella</i> sp.	1	—	—	—	—	—
(4) Small mammals	—	1	—	—	—	—
(5) Insects—Cicada	—	—	—	—	—	1
Totals	18	25	19	1	8	32

(e.g. *Sphenomorphus tympanum*). Observations on captive *D. coronoides* indicate that foraging occurs both by day and by night, with most activity in the evening.

The Western Australian form, *D. coronata*, has more varied diet than its eastern congeners (Table 2). The percentage of frogs in the *D. coronata* diet (17 of 32 items, or 53%) is much higher than in the eastern species ($\bar{x} = 4\%$; $N = 103$, $\chi^2 = 11.2$, 1 df, $P < .01$). The proportion of specimens containing food tends to be similar in the two sexes (e.g. *D. coronoides*: 19% of adult males and 21% of adult females), but is higher in these adults than in conspecific juveniles (9%; $N = 267$, $\chi^2 = 9.0$, 1 df, $P < .01$). Gravid female *D. coronoides* show no decrease in feeding rate; indeed, the proportion of specimens containing food is higher in gravid snakes (33%) than in non-gravid snakes (19%). However, sample sizes are too small for significance ($N = 66$, $\chi^2 = .8$, 1 df, n.s.). In *D. coronata*, the proportion of snakes with prey is lower in gravid (9%) than non-gravid (18%)

specimens, but again the differences are not significant ($N = 45$, $\chi^2 = .04$, 1 df, n.s.).

Feeding is concentrated in the warmer months of the year, and no feeding records during winter were obtained for *D. coronoides* or *D. coronata* (Fig. 3). However, one of only three feeding records for *D. rhodogaster* was from a specimen collected in June (midwinter).

Mode of reproduction.—All four *Drysdalia* species are live-bearing, as evidenced by large embryos (and lack of eggshells) in gravid females (*D. coronoides*, $N = 41$ ♀♀; *D. mastersi*, $N = 2$; *D. rhodogaster*, $N = 19$; *D. coronata*, $N = 10$). Also, birth in captivity was observed in 7 *D. coronoides* ♀♀, and observed by J. Scanlon (pers. comm.) in 2 *D. rhodogaster* ♀♀.

Reproductive timing.—Vitellogenesis of ovarian follicles commences in autumn, and follicles are already large before "hibernation" (Fig. 4). This trend is most obvious in NSW populations of *D. coronoides*, and least obvious in *D. coronata*.

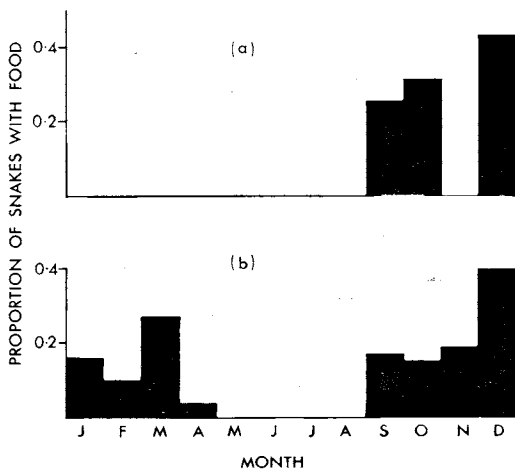


Fig. 3. Seasonal variation in the proportion of (a) *Drysdalia coronata* and (b) *D. coronoides*, containing food items in the stomach.

Ovulation occurs in late spring to early summer (September–December), and females are gravid until March or April. Hence, gestation oc-

cupies about 4 months. Parturition in two field-fresh captive *D. coronoides* ♀♀ (NSW population) occurred on 5 and 10 March. Snakes collected from the same area, but kept in captivity in Sydney (a warmer climate) from 1 Nov., produced young about a month earlier (29 Jan., 7 Feb., 10 Feb., 12 Feb.). J. Scanlon (pers. comm.) recorded parturition of captive *D. rhodogaster* ♀♀ on 28 Feb. and 13 March.

Reproductive frequency.—All adult-size males dissected had opaque efferent ducts, indicating the presence of sperm (Shine, 1977b). Hence, I infer that males reproduce each year. The situation is different in females. Data on ovarian follicle diameters (Fig. 4) enable females to be classed as “reproductive” (follicles ≥ 5 mm) or “nonreproductive” (follicles < 5 mm) for that year. I exclude data from March, as it may be difficult to distinguish recently parturient females from nonreproductive specimens. Almost all adult-size females are reproductive in *D. coronata*, *D. rhodogaster* and mainland populations of *D. coronoides*. However, only about half of the “adult” female *D. coronoides* from

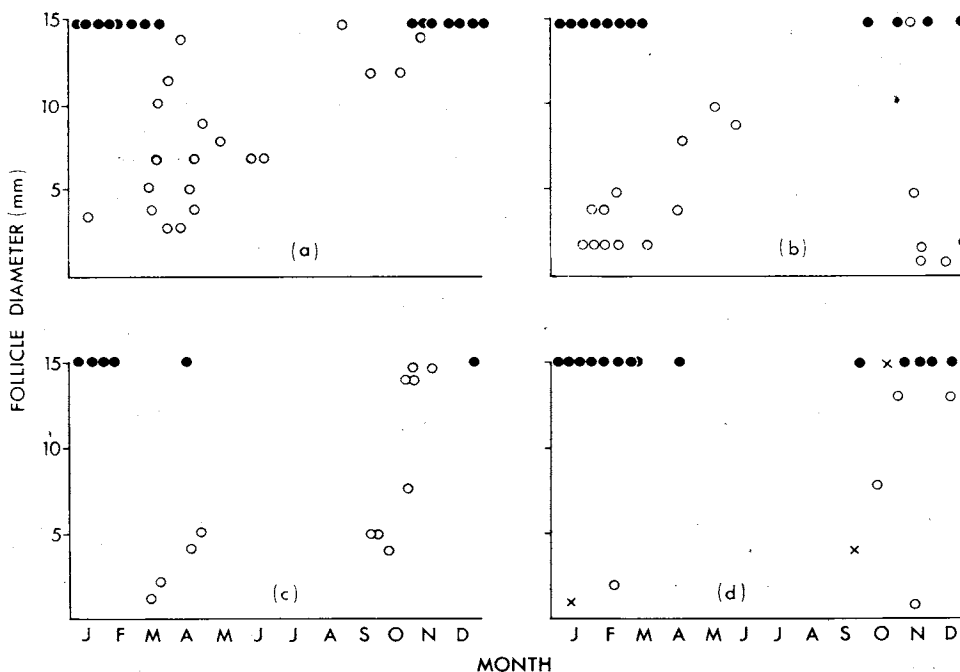


Fig. 4. Seasonal variation in diameter of the largest ovarian follicle in *Drysdalia* species. (a) Mainland *D. coronoides*, (b) Tasmanian *D. coronoides*, (c) *D. coronata*, and (d) *D. mastersi* (crosses) and *D. rhodogaster* (circles). Ovarian follicles = open circles; oviducal embryos = solid circles. Follicles or embryos > 15 mm shown at 15 mm.

TABLE 3. REPRODUCTIVE FREQUENCY IN FEMALE *Drysdalia*.

Species	Reproductive	Non-reproductive	Proportion of ♀♀ reproductive
<i>D. coronoides</i> NSW	10	1	.91
Victoria	27	2	.93
Tasmania	16	13	.55
<i>D. rhodogaster</i>	14	2	.88
<i>D. coronata</i>	15	2	.88

Tasmania are reproductive (Table 3). The difference between mainland and Tasmanian *D. coronoides* populations in the proportion of reproductive females is highly significant ($N = 30$, 2×2 contingency table, $\chi^2 = 11.1$, 1 df, $P < .01$).

Size at birth.—Mean SVL at birth was 9.8 cm ($SE = .1$) in 39 *D. coronoides* from NSW. Size at birth is probably similar in other *D. coronoides* populations. Table 4 summarizes available data. Size at birth in *Drysdalia* ranges from ≈ 8 cm (*D. mastersi*) to ≈ 12 cm (*D. coronata*). Interestingly, neonatal SVL of *D. coronoides* is negatively correlated with maternal body size (Fig. 5; $P < .01$).

Fecundity.—Clutch sizes of the four *Drysdalia* species are described in Fig. 6 and Table 5. Mean clutch sizes vary from 2.8 (*D. mastersi*) to 5.4 (Tasmanian *D. coronoides*). Geographic variation in clutch size within *D. coronoides* is low. Overall mean clutch size shows a significant correlation with mean adult female SVL in a comparison between populations of *Drysdalia* ($N = 6$, $r = .85$, $P < .05$). However, the correlation between clutch size and maternal SVL within a population is significant in only 2 of 5 cases, and only just significant in one of these (Table 5). Covariance analysis revealed no significant interspecific differences in the slopes of the relationship between maternal body size and fecundity (Fig. 6; df = 114,5; $F = 0.4$, n.s.). However, interspecific differences in the intercepts of this relationship were highly significant (df = 119,5; $F = 3.1$, $P < .001$).

In 7 broods of NSW *D. coronoides* born in the laboratory, relative clutch mass (ratio of weight loss at parturition to female's post-parturition weight) averaged 0.49 (range .29–.61).

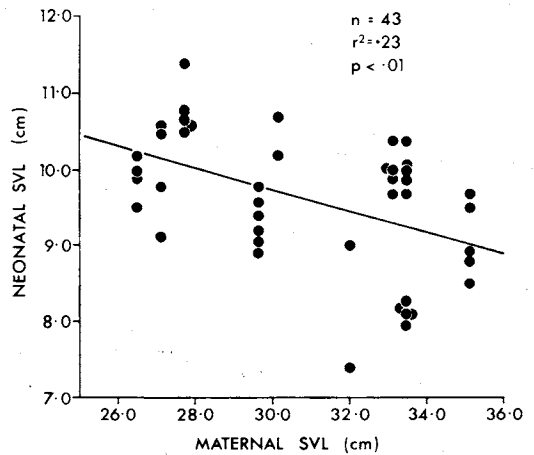


Fig. 5. Relationship between body sizes of adult female *Drysdalia coronoides* and sizes of their young at birth. Calculated regression line has slope -0.15 , intercept 14.1.

Growth rates.—Seasonal distributions of body size allow estimation of growth rates in *D. coronata* and *D. coronoides* (Fig. 7). High variability makes interpretation difficult, but clear differences between the two species are evident (note particularly the absence of small individuals in midsummer in *D. coronata*, and their abundance in *D. coronoides*). I infer that *D. coronoides* has slow growth, especially in the first year of life. Both sexes attain mature size at about 3 years of age, with females first ovulating when ≈ 32 months old. In contrast, the Western Australian species *D. coronata* has more rapid growth, maturing at ≈ 20 months in both sexes.

TABLE 4. SIZE AT BIRTH IN *Drysdalia* SPECIES. SVL = snout-vent length.

Species	SVL largest oviducal embryo (cm)	SVL smallest field-collected specimen (cm)
<i>D. coronoides</i> NSW	11.4	9.6
Vict.	8.1	10.2
Tas.	10.7	8.2
<i>D. mastersi</i>	—	8.2
<i>D. rhodogaster</i>	11.0	10.3
<i>D. coronata</i>	13.5	12.2

TABLE 5. RELATIONSHIP BETWEEN MATERNAL BODY SIZE AND CLUTCH SIZE IN *Drysdalia* SPECIES. Table gives values to solve the equation $y = ax + b$, where y = clutch size and x = snout-vent length (cm). Regression fit by least squares. Probability levels are: * = $P < .01$, n.s. = not significant ($P > .05$).

Species	N	a	b	r^2	P	Clutch size	
						Mean (SE)	Range
<i>D. coronoides</i>							
NSW	25	.12	1.45	.10	n.s.	5.0 (.3)	2-8
Victoria	36	.24	-1.97	.20	*	4.9 (.3)	3-10
Tasmania	18	.18	-.69	.10	n.s.	5.4 (.4)	2-8
<i>D. mastersi</i>	4		—	—	—	2.8 (—)	2-3
<i>D. rhodogaster</i>	21	.15	.41	.10	n.s.	4.9 (.3)	2-6
<i>D. coronata</i>	22	.20	-2.2	.62	*	4.3 (.9)	3-9

DISCUSSION

The most striking aspect of *Drysdalia* ecology is the great similarity between species—particularly with respect to body sizes, sexual size dimorphism (Table 1), food habits (Table 2) and clutch sizes (Table 5). Exceptions to this general uniformity include i) the more varied diet of *D. coronata*, ii) the smaller body sizes and clutch sizes of *D. mastersi*, iii) the inferred higher growth rates of *D. coronata* than of *D. coronoides* and iv) the differing reproductive frequencies in different populations of *D. coronoides*. Below, I compare the ecological data gathered on *Drysdalia* with published information.

Sexual dimorphism.—The virtual absence of sexual dimorphism in body length in *Drysdalia* (Table 1) is characteristic of many Australian elapid species (Shine, 1978b). This equality of body sizes between the sexes offers good circumstantial evidence for the existence of physical combat between adult males (Shine, 1978b). However, no behavioral data are available to test this hypothesis.

Food habits.—The preponderance of small scincid lizards in the *Drysdalia* diet is consistent with data on other small Australian elapid snakes (*Uroechis gouldii*, Shine, 1977a; three species of *Cacophis*, Shine, 1980a). The foraging behavior of *D. coronoides*, active both diurnally and nocturnally, is more similar to that of *Hemiaspis signata* than of other elapids I have studied (Shine, 1979). Laboratory studies (Shine, 1980b) show that *D. coronoides* prey more heavily on gravid female skinks than on conspecific male skinks, a difference that is probably due to the lowered mobility of the gravid lizards.

The more varied diet of *D. coronata* than of its eastern congeners may be attributable to habitat differences: little is known on the general biology of the Western Australian form. Most previous studies have considered insects to be an important prey type of all the *Drysdalia* (Table 6), but the results of the present study contradict this suggestion. In fact, Australian snakes only rarely prey on invertebrates (Shine, 1977a).

The high proportion of feeding records obtained from gravid female *D. coronoides* is of particular interest, since feeding ceases during gestation in many other snakes (Shine, 1979, 1980b). The continued feeding of gravid *D. coronoides* occurs despite their being heavily burdened with developing embryos (comprising about half of the female's post-parturition body weight). I suggest the hypothesis that natural selection has favored continued feeding during gestation as an adaptation to the cold climate inhabited by *D. coronoides*. In these areas, feeding can only occur during warm months of the year (Fig. 3). The cold weather also slows embryogenesis, resulting in prolonged gestation. (Note the reduced gestation period of *D. coronoides* kept in a warmer climate.) These two factors in combination mean that unless females feed while gravid, they will have little chance to feed at all. In milder climates, females may have ample time to feed in the spring (prior to ovulation) and in the autumn (after parturition), so that they can "afford" not to feed while gravid. One major problem with this hypothesis is the observation of Gregory and Stewart (1975) that feeding ceases during gestation in gartersnakes inhabiting a severely cold area (Manitoba). Further compar-

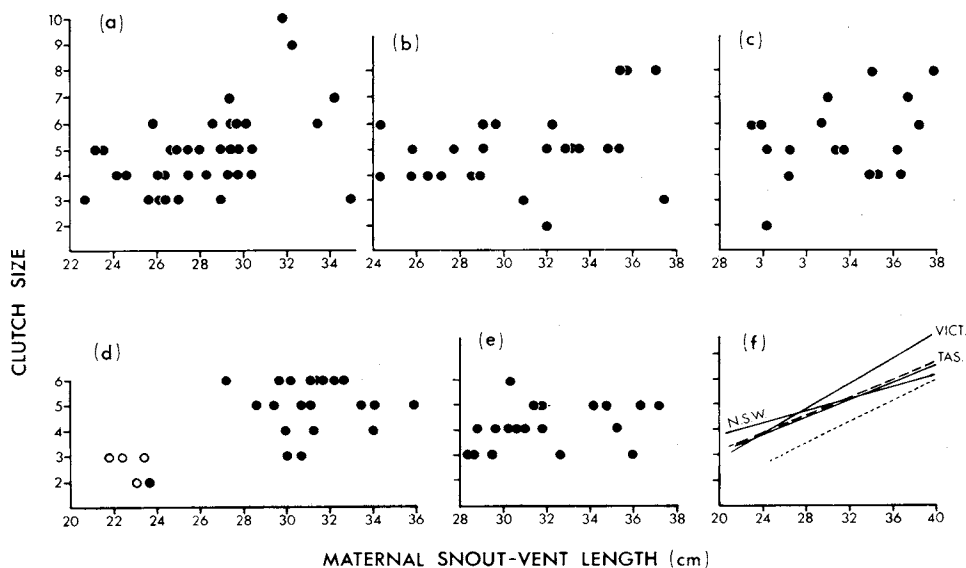


Fig. 6. Fecundity in *Drysdalia* species. Upper three graphs show data for *D. coronoides* in (a) Victoria, (b) New South Wales, and (c) Tasmania. Lower three graphs show data for (d) *D. rhodogaster* (solid circles) and *D. mastersi* (open circles), (e) *D. coronata*, and (f) a comparison of calculated regression lines. Unbroken line shows *D. coronoides*, dashed shows *D. rhodogaster*, dotted shows *D. coronata*. Two records for *D. coronata* omitted because of lack of space (clutch sizes 3, 9).

ative data on a wide range of snake species are needed to clarify this situation. Possible selective advantages of the cessation of feeding in reproducing snakes have been discussed elsewhere (Shine, 1979, 1980b).

Reproductive frequency.—The low proportion of “reproductive” adult females in the sample of Tasmanian *D. coronoides* (55%; Table 3) suggests that individual females in this population may breed only in alternate years. Other possible explanations for the low frequency of reproductive females could be: i) mistakes in assigning females as “reproductive” or “nonreproductive.” This could occur if Tasmanian females gave birth much earlier than mainland specimens, leading me to classify post-parturient animals as nonreproductive. On the contrary, the observed apparent dependence of gestation period on temperature, and the seasonal distribution of gravid females in the collection, indicate that parturition occurs quite late in Tasmania. ii) Alternatively, one could attribute the low reproductive frequency to delayed maturation in the Tasmanian snakes. Unfortunately for this hypothesis, reproductive and nonreproductive Tasmanian

females do not differ significantly in body sizes (\bar{x} SVL = 33.8 [SE 0.7] and 31.5 [SE 1.3], respectively). I conclude that adult female *D. coronoides* in Tasmania reproduce less often than annually.

The exact frequency of reproduction is difficult to assess. Based on the proportion of females reproductive (55%), snakes may reproduce every second year (on average). However, this estimate relies on equal catchability of reproductive and nonreproductive snakes. Since gravid snakes may bask more often than non-gravid specimens and hence be more easily collected (Shine, 1979), this procedure may overestimate the proportion of reproductive females. The highly skewed sex ratio of the Tasmanian collection (Table 1), indicates that females are collected less often than expected from mainland samples (see Results section; $P < .05$). This bias could be due to many females being nonreproductive, and hence less easily collected.

An alternative system to calculate female reproductive frequency is to use the observed adult sex ratio. In the mainland samples, the ratio of males to reproductive females is about 1:1.5. In the Tasmanian sample this ratio is

TABLE 6. PUBLISHED DATA ON *Drysdalia* DIET AND FECUNDITY.

Author	Species		
	<i>coronoides</i>	<i>mastersi-rhodogaster</i>	<i>coronata</i>
Diet			
Fleay, 1952	—	frogs	—
Glauert, 1957	—	—	insects, lizards, frogs
Mitchell, 1961	—	insects	—
Worrell, 1963	skinks, frogs	lizards	lizards, frogs
Kinghorn, 1964	insects	insects	insects, lizards, frogs
Rawlinson, 1965	lizards, insects	—	—
Cogger, 1975	skinks, frogs, insects	—	lizards, frogs, insects
Gow, 1976	skinks, frogs	frogs, lizards	insects, lizards, frogs
Present study	84% skinks	100% skinks	50% frogs, 50% lizards
Fecundity			
Krefft, 1869	—	—	10–15
Glauert, 1957	—	—	10–15
Worrell, 1963	6–12	5	10–15
Kinghorn, 1964	10	10	10
Cogger, 1975	6–12	5–10	10–15
Gow, 1976	6–12	3–5	10–15
Present study*	5.0 (2–10)	4.6 (2–6)	4.3 (3–9)

* Mean and range of clutch sizes.

1:0.5. Since males reproduce annually in both populations (and hence should have similar "catchabilities"), these ratios imply that reproductive females are only about one-third as common in Tasmanian collections as one would expect from the mainland data. Hence, this suggests that females may only breed every third year (on average), rather than every second year. I see no way of judging between these two estimates, but suggest that they offer a reasonable approximation of the frequency of reproduction in female Tasmanian *D. coronoides*. A test of this hypothesis will only come from field mark-recapture studies (Fitch, 1970: *Agkistrodon contortrix*).

Low reproductive frequencies occur in a variety of venomous snake species (Bull and Shine, 1979). The case in *D. coronoides*, where only the coldest-climate population shows a low reproductive frequency, resembles the trend in European vipers (Saint Girons, 1957). In contrast, reproductive frequencies in North American pit vipers are less clearly associated with climatic conditions (Wharton, 1966; Keenlyne, 1978). Bull and Shine (1979) argue on theoretical grounds that low reproductive frequencies will not evolve without high "costs" of reproducing (e.g. mortality, or reduction in food in-

take) that are independent of fecundity. Clearly, food intake is not reduced in gravid *D. coronoides* (above). However, predation by seabirds on basking snakes may be heavy on Tasmanian populations of this species (Rawlinson, 1974). If gravid snakes spend most of their time basking (as is true in some other Australian elapids, Shine, 1979), then seabird predation might be enough of a fecundity-independent reproductive "cost" to favor the evolution of low reproductive frequencies.

Size at birth.—The strong negative correlation between maternal SVL and neonatal SVL in *D. coronoides* (Fig. 5) is puzzling. It is not due to offspring being smaller in larger clutches ($N = 10$, $r = .06$, n.s.), and I can offer no reasonable hypothesis to explain the data. A positive correlation between maternal SVL and neonatal SVL has been observed in several reptiles (Pimentel, 1959), while a lack of correlation has been found in others (e.g., *Nerodia sipedon* J. M. McKinley, pers. comm.). To my knowledge, *D. coronoides* is the only species known to show a negative correlation between these parameters.

Fecundity.—Clutch sizes of all four *Drysdalia* species are low and remarkably constant.

Eighty-seven of the 126 clutch sizes recorded in the present study (69%) ranged between 3 and 5 offspring. Most snakes show a much greater range of fecundities (Shine, 1977c; Fitch, 1970). Since clutch sizes in mainland *D. coronoides* do not differ from those of Tasmanian conspecifics (\bar{x} 's = 4.9, 5.4), the lower reproductive frequency of the Tasmanian females means that overall average survivorship must be higher in the island population. Previous authors have generally attributed higher clutch sizes to *Drysdalia* than those I have recorded (Table 6). The example of *D. coronata* is particularly illuminating; almost all authors have repeated Krefft's (1869) original overestimate of 10–15 offspring as the average clutch size. The correct figure is close to 4 (Table 5).

Growth rates.—The apparently slow rates of bodily growth in *D. coronoides* (Fig. 7) are consistent with the cold climates occupied by this species. These conditions restrict feeding to warmer months of the year (Fig. 3). Also, the small size of newborn *D. coronoides* (Table 4) means that they have only a limited range of possible prey items. This range is further limited by the lack of invertebrates in the diet (Table 2). Although neonatal *D. coronoides* in the laboratory feed voraciously on young skinks, analysis of gut contents from field-collected specimens indicated that juveniles contained food less often than adults (see Results; $P < .01$). This low feeding rate may be an important determinant of the observed low growth rates. The inferred high growth rates of *D. coronata* are consistent with the much warmer climates occupied by this species.

Overview.—As well as providing basic ecological data on a poorly-known snake genus, the information presented above can shed light on some of the ways in which ecological characteristics are shaped by climatic conditions. In particular, the ecology of cold-climate Tasmanian populations of *D. coronoides* may be compared to warmer-climate (mainland) conspecifics, to congeneric species, and to other elapids. In the last category, perhaps the best comparison is with three *Cacophis* species; they resemble *Drysdalia* in body sizes and food habits, but occur in warmer coastal regions of eastern Australia (Shine, 1980a). The data on *Drysdalia* presented above suggest that the following ecological characteristics of Tasmanian *D. coronoides* reflect the harsh climate of that area.

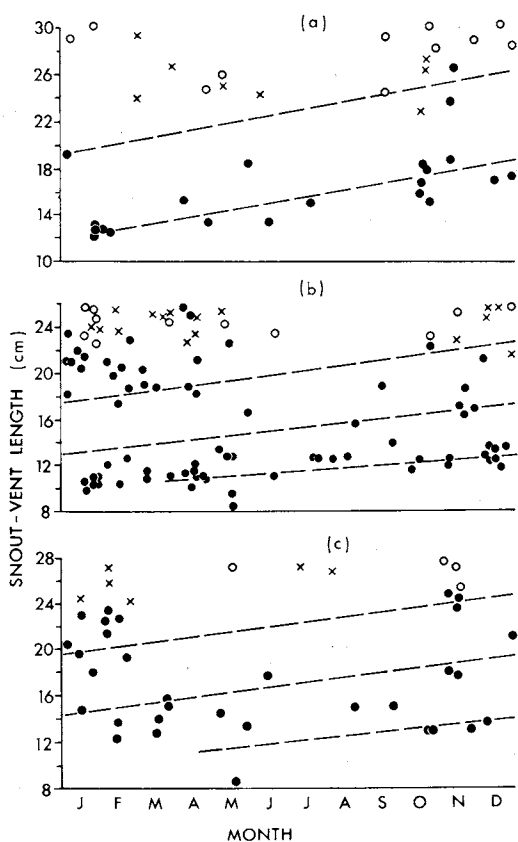


Fig. 7. Inferred growth rates and seasonal size distributions of (a) *Drysdalia coronata*, (b) mainland *D. coronoides* and (c) Tasmanian *D. coronoides*. Solid circles show juveniles, open circles show adult females, and crosses show adult males.

Seasonality.—Southern populations of *D. coronoides* show a more pronounced winter decline in activity and feeding than do elapids in warmer areas (Figs. 2, 3; Shine, 1980a).

Growth rates.—Growth is slower in *D. coronoides* than in most other small elapids studied, including *D. coronata* (Fig. 7; Shine, 1978a). Concurrently, sexual maturity is delayed.

Mode of reproduction.—All *Drysdalia* species are live-bearing (viviparous). Recent studies suggest that live-bearing has evolved from egg-laying primarily as an adaptation to cold climates (Shine and Bull, 1979). This conclusion is supported by the observed increase in proportions of live-bearing species at lower latitudes (colder climates) in both Australia and North America

(Tinkle and Gibbons, 1977; Shine and Berry, 1978).

Feeding by gravid females.—*D. coronoides* females continue feeding during gestation, in contrast to many other snake species (Shine, 1979, 1980b). I have interpreted this continued feeding as an adaptation to prolonged gestation and a highly seasonal food supply, both of these factors resulting from the cold climate (discussed above).

Reproductive frequency.—Adult female Tasmanian *D. coronoides* reproduce only once every two to three years, while mainland conspecifics and other warmer-climate elapids reproduce yearly (Shine, 1977b). As in the previous characteristic, prolonged gestation and a short period of food availability are the probable selective factors favoring this low frequency of reproduction.

Some of the factors listed above are simple effects of cold climates (e.g. seasonality), while others are adaptations (e.g. viviparity), and still others may be either or both (e.g. growth rates, reproductive frequency). However, the basic point seems clear: the general ecology of southern populations of *D. coronoides* is profoundly affected by the severe climate of the region.

ACKNOWLEDGMENTS

My sincere thanks to the following Curators, who allowed me to examine specimens in their care: J. Coventry (National Museum), R. Green (Queen Victoria Museum), A. Greer (Australian Museum) and G. Storr (Western Australian Museum). J. Scanlon provided data on captive snakes. I am grateful also to S. Warren for typing, and to T. Shine for assistance in collecting snakes. The work was supported financially by a University of Sydney Postdoctoral Fellowship.

LITERATURE CITED

- BULL, J. J., AND R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. *Amer. Natur.* 114:296-303.
- COGGER, H. G. 1975. Reptiles and amphibians of Australia. A. H. and A. W. Reed, Sydney.
- COPLAND, S. J. 1947. Reptiles occurring above the winter snowline at Mt. Kosciusko. *Proc. Linn. Soc. N.S.W.* 72:69-72.
- COVENTRY, A. J., AND P. A. RAWLINSON. 1980. Taxonomic revision of the elapid snake genus *Drysdalia* Worrell 1961. *Memo Nat. Mus. Vic.* 41:65-78.
- FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 52.
- FLEAY, D. 1952. The crowned or coronated snake. *Vict. Nat.* 68:146-150.
- GLAUERT, L. 1957. A hand-book of the snakes of Western Australia. W.A. Naturalists' Club, Perth.
- GOW, G. F. 1976. Snakes of Australia. Angus & Robertson, Sydney.
- GREGORY, P. T. 1977. Life-history parameters of the red-sided gartersnake (*Thamnophis sirtalis parietalis*) in an extreme environment, the interlake region of Manitoba. *Nat. Mus. Canada, Publ. Zool.* 13:1-44.
- , AND K. W. STEWART. 1975. Long-distance dispersal and feeding strategy of the red-sided gartersnake (*Thamnophis sirtalis parietalis*) in the interlake of Manitoba. *Canad. J. Zool.* 53:238-245.
- HEBARD, B. 1951. Notes on the life history of the Puget Sound garter snake, *Thamnophis ordinoides*. *Herpetologica* 7:117-119.
- KEENLYNE, K. D. 1978. Reproductive cycles in two species of rattlesnakes. *Amer. Midl. Nat.* 100:368-375.
- KINGHORN, J. R. 1964. The snakes of Australia. Angus & Robertson, Sydney.
- KREFFT, G. 1869. The snakes of Australia. Govt. Printer, Sydney.
- LORD, C. E. 1918. Notes on the snakes of Tasmania. *Pap. Proc. R. Soc. Tasm.* 1918:76-81.
- MCDOWELL, S. B. 1967. *Aspidomorphus*, a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *J. Zool., Lond.* 151:497-543.
- MITCHELL, F. J. 1961. Harmless or harmful? South Australian Museum, Adelaide.
- PIMENTEL, R. A. 1959. Positive embryo-maternal size correlation in the northern alligator lizard, *Gerrhonotus coeruleus principis*. *Herpetologica* 15:6-8.
- RAWLINSON, P. A. 1965. Snakes of the Melbourne area. *Vict. Nat.* 81:245-254.
- . 1974. Natural history of Curtis Island. 4. The reptiles of Curtis and Rodondo islands. *Pap. Proc. Roy. Soc. Tasm.* 107:153-163.
- SAINT GIRONS, H. 1957. Le cycle sexuel chez *Vipera aspis* (L.) dans l'ouest de la France. *Bull. Biol.* 91:284-350.
- SHINE, R. 1977a. Habitats, diet and sympatry in snakes: a study from Australia. *Canad. J. Zool.* 55:1118-1128.
- . 1977b. Reproduction in Australian elapid snakes. I. Testicular cycles and mating seasons. *Aust. J. Zool.* 25:647-653.
- . 1977c. Reproduction in Australian elapid snakes. II. Female reproductive cycles. *Ibid.* 25:655-666.
- . 1978a. Growth rates and sexual maturation in six species of Australian elapid snakes. *Herpetologica* 34:73-79.
- . 1978b. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269-278.
- . 1979. Activity patterns in Australian elapid

- snakes (Squamata: Serpentes: Elapidae). *Herpetologica* 35:1-11.
- . 1980a. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes: Elapidae). *Copeia* 1980:831-838.
- . 1980b. "Costs" of reproduction in reptiles. *Oecologia* 46:92-100.
- , AND J. F. BERRY. 1978. Climatic correlates of live-bearing in squamate reptiles. *Ibid.* 33:261-268.
- , AND J. J. BULL. 1979. The evolution of live-bearing in lizards and snakes. *Amer. Natur.* 113:905-923.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioural sciences*. McGraw-Hill, Sydney.
- SMITH, H. M., AND W. P. HALL. 1974. Contributions to the concepts of reproductive cycles and the systematics of the *scalaris* group of the lizard genus *Sceloporus*. *Great Basin Nat.* 34:97-104.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3-47.
- TINKLE, D. W., AND J. W. GIBBONS. 1978. The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool., Univ. Michigan* 154.
- VIITANEN, P. 1967. Hibernation and seasonal movements of the viper, *Vipera berus berus* (L.), in southern Finland. *Ann. Zool. Fenn.* 4:472-546.
- WHARTON, C. H. 1966. Reproduction in the cottonmouths, *Aghkistrodon piscivorus* Lacépède, of Cedar Keys, Florida. *Copeia* 1966:149-161.
- WORRELL, E. 1963. *Reptiles of Australia*. Angus & Robertson, Sydney.
- SCHOOL OF BIOLOGICAL SCIENCES, UNIVERSITY OF SYDNEY, NSW 2006, AUSTRALIA. Accepted 31 Dec. 1979.