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Reproduction in Australian Elapid Snakes
II. Female Reproductive Cycles

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Abstract

Female reproductive cycles were studied in seven species of Australian elapid snakes, and the results compared with published information on snake faunas of other continents. Of the species studied, five are live-bearing (*Austrelaps superbus*, *Hemiaspis signata*, *Notechis scutatus*, *Pseudechis porphyriacus* and *Unechis gouldii*) and two egg-laying (*Pseudonaja nuchalis* and *P. textilis*). The live-bearing species usually produce one clutch per year, a higher reproductive frequency than has been found in most previously studied venomous snakes. All live-bearing species show similar seasonal timing of ovulation and parturition. Gestation occupies about 14 weeks. The egg-laying species ovulate at about the same time as sympatric live-bearers, but oviposit shortly thereafter and may produce a second clutch of eggs in late summer.

P. porphyriacus shows true 'viviparity', including placental transfer of nutrients (ash content of oocytes increases during gestation, energy content decreases only slightly). The live (wet) weight of the oocytes increases up to fourfold during gestation in live-bearing species, but dry weights change very little.

Extra-uterine transfer of oocytes is common. Infertility is rare in *A. superbus* and *P. porphyriacus*, but frequent in *N. scutatus*. Clutch size is correlated with maternal body size in all species. The ratio of clutch weight to body weight decreased slightly with increasing maternal size in *N. scutatus* and *P. porphyriacus*. Published data on reptilian 'reproductive effort' are reviewed.

Introduction

A recent review of female reproductive cycles in squamate reptiles (Fitch 1970) indicates that there is abundant information on some groups and very little on others. The snakes are much less well known than are the lizards, and there are several snake groups for which virtually no detailed data are available. The Elapidae (front-fanged terrestrial snakes) are such a group. The present paper describes female reproductive cycles in seven species of Australian elapid snakes and discusses the evolutionary significance of the patterns observed.

Materials and Methods

Snakes were collected by hand in two study areas in eastern Australia: (1) the New England highlands, within 100 km of Armidale, N.S.W.; (2) the Macquarie Marshes, 400 km west of Armidale and 20 km west of Quambone, N.S.W. The species studied were *Austrelaps superbus*, *Hemiaspis signata*, *Notechis scutatus*, *Pseudechis porphyriacus*, *Pseudonaja nuchalis*, *P. textilis* and *Unechis gouldii*. Study areas, methods, climate, habitats, snake ecology, growth rates, testicular cycles and mating seasons have been described elsewhere (Shine 1975, 1977*a*, 1977*b*, 1977*c*; Shine and Bull 1977).

A few gravid females were maintained in the laboratory until parturition. Other specimens were killed within 48 h of collection, by intracranial injection of sodium pentabarbitone. Records were kept of the size and number of ovarian follicles, corpora lutea, oviducal eggs and ectopic embryos.

Wet weights were measured immediately after dissection. Dry weights were measured after drying to constant weight at 80 C. Ash content was measured after 48 h in a muffle furnace at 350 C. Calorific content was measured with a Gallenkamp Bomb Calorimeter.

Results

Frequency of Reproduction

Most adult-size females reproduce every year (Fig. 1; Table 1). Females of larger species tend to reproduce less often than females of smaller species (Spearman Rank Correlation Coefficient: $n = 5$; $r_s = 0{\cdot}90$; $P = 0{\cdot}05$).

Table 1. Size of adult females, proportion in reproductive condition, and mean ratio of clutch weight to body weight in five species of elapid snakes

N, the number of females in and above the lowest 5-cm snout–vent length interval in which over 50% of females were reproductive. Females were classed as reproductive if they were gravid, had ovarian follicles > 10 mm, or had motile sperm in the oviducts. Sizes and ages at sexual maturity are given elsewhere (Shine 1977*b*). C, clutch weight (mean offspring weight for that species, multiplied by clutch size). B, gravid weight minus embryo weights

Species	*N*	Mean snout–vent length (cm)	Proportion reproductive	C : B
Austrelaps superbus	27	70·6	0·85	0·28
Hemiaspis signata	15	43·3	0·92	—[A]
Notechis scutatus	32	80·8	0·87	0·42
Pseudechis porphyriacus	55	106·1	0·84	0·22
Unechis gouldii	29	30·2	0·93	0·58

[A] Not calculated because of small sample size.

Seasonal Timing

(i) *Live-bearers*

Fig. 1 shows that all of the live-bearing species studied here ovulate in late spring or early summer (October–December). Gestation occupies approximately 14 weeks, with parturition in late summer or autumn (February–April).

Interspecific differences among the elapids in the timing of ovulation and parturition are minor. *Unechis gouldii* show relatively late vitellogenesis, and ovulate later in the season than the other species. *Austrelaps superbus* show early (autumn) vitellogenesis, and ovulate relatively early in spring. This species is found at higher altitudes, and colder climates, than any of the other elapids. The gestation period is consequently longer, and occupies most of the active season.

Most vitellogenesis occurs after emergence from hibernation, and species emerging earlier usually ovulate earlier. The best example of this is the comparison between sympatric *Pseudonaja nuchalis* and *Pseudechis porphyriacus* in the Macquarie Marshes; the latter species is active earlier than the former, and shows earlier follicular development (e.g. three *P. porphyriacus* collected 27 September 1974 had large ovarian follicles of 12, 15 and 16 mm; four *P. nuchalis* from the same area on the same day had follicles of 5, 5, 6 and 7 mm). The onset of spermiogenesis in the males was also earlier in *P. porphyriacus* than in *P. nuchalis* (Shine 1975).

Live-bearing elapids in the Armidale area give birth between February and April, with some annual variation; parturition averaged about 2 weeks earlier in 1975 than in 1974. Parturition dates recorded in the present study were generally similar to earlier records (Waite 1929; Ormsby 1949; McPhee 1959; Cogger 1967), although some authors give December and January as the months of birth (e.g. Kellaway and Eades 1929; Waite 1929; Holmes 1955; Worrell 1963). One exceptional case was described to me by Mr J. Sewell, who found a gravid *P. porphyriacus* in midwinter. Overwintering of gravid vipers has been noted several times (see Saint Girons and Kramer 1963).

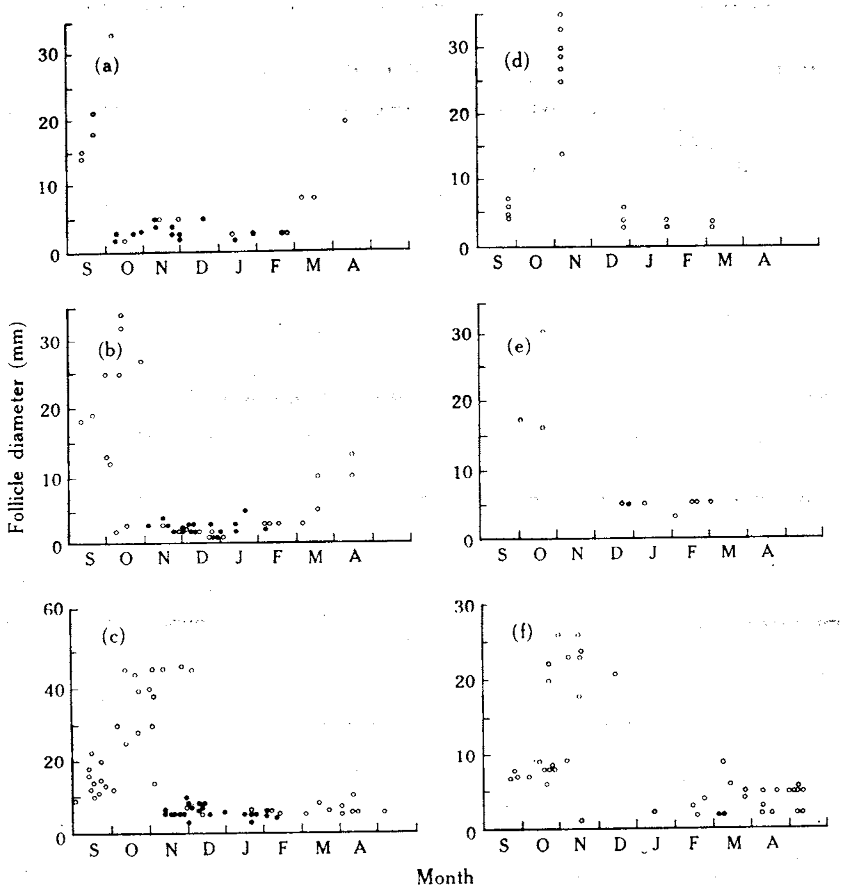

Fig. 1. Seasonal variation in the diameter of the largest developing ovarian follicle in adult female elapid snakes. Points to the right of the April data represent animals collected in winter (May–August). ○ Non-gravid females. ● Gravid females. (*a*) *Austrelaps superbus.* (*b*) *Notechis scutatus.* (*c*) *Pseudechis porphyriacus.* (*d*) *Pseudonaja nuchalis.* (*e*) *Pseudonaja textilis.* (*f*) *Unechis gouldii.*

(ii) *Egg-layers*

The two oviparous species (genus *Pseudonaja*) ovulate at the same time as the live-bearers (October–December), and presumably lay their eggs shortly thereafter. However, one *P. textilis* collected in January contained oviducal eggs without visible embryonic development (Fig. 1*e*). This suggests that oviparous elapids may produce more than one clutch per year. This idea is supported by the following observations:

(1) Although *Pseudonaja nuchalis* in the Macquarie Marshes only produced one clutch in the 1974–75 season, this may have been due to the unusually cool summer. One female collected in April had numerous atretic follicles up to 25 mm diameter. Vitellogenesis had probably occurred in late summer, but ovulation had not taken place.

(2) H. Cogger (personal communication) has recorded the production of two clutches within one summer by a captive *Pseudonaja textilis*.

(3) Peters (1972) described double-clutching in captives of another Australian elapid, *Oxyuranus scutellatus*.

(4) *Pseudonaja guttata* females in reproductive condition (immediately preovulatory to immediately postovulatory) were collected in October (one), February (two) and April (one), in western New South Wales during the unusually favorable (high rainfall) summer of 1973–74.

Newly hatched young of the oviparous species emerge at the same time of year as the young of sympatric live-bearing species are born (late February–March). Occasionally, small specimens are collected in April; these may come from second clutches.

Mechanics of Ovulation

Many more follicles develop in the ovaries than are ovulated that season. Those follicles generally do not exceed 10 mm in diameter, but in occasional specimens (two *Pseudechis porphyriacus*, one *Austrelaps superbus* and one *Pseudonaja nuchalis*) one or two follicles which had attained ovulatory size were not ovulated, became atretic, and had begun to regress.

Table 2. Extra-uterine transfer of oocytes in clutches of live-bearing elapid snakes

Sample sizes smaller than in other Tables, because of difficulty in counting corpora lutea in some specimens

Species	No. of clutches	Mean clutch size	Extra-uterine transfer		Direction of transfer	
			Proportion of clutches	Mean clutch size	R to L	L to R
A. superbus	7	14·0	0·29	13·4	0	2
N. scutatus	17	23·1	0·71	22·6	4	8
P. porphyriacus	19	12·7	0·58	12·8	3	8

Corpora lutea were obvious from the time of ovulation until a week or two after parturition, and were counted to determine the number of oocytes ovulated from each ovary. The percentage of ova which were transferred from one ovary to the contralateral oviduct ('extra-uterine transfer': Tinkle 1959) was calculated from these data. The incidence of such transfer should be reduced by a phenomenon observed in ovulating *P. porphyriacus*, i.e. encapsulation of the ovaries by the oviducts during ovulation (cf. Cuellar 1970). However, extra-uterine transfer was common (Table 2). The estimate of percentage transfer is a conservative one, since reciprocal transfers would not be evident. The incidence of oocyte transfer was apparently independent of clutch size. Transfer from the left ovary to the right oviduct was more common than vice versa. This is part of the reason, though not the complete explanation, for the observation that the right oviduct almost always contained more eggs than the left. The left oviduct (which is shorter than the right) contained, on average, 53% as many eggs as the right oviduct in *Pseudechis porphyriacus*, 58% in *Notechis scutatus*, 60% in *Hemiaspis signata* and 71% in *Austrelaps superbus*.

Occasional dysfunctions occurred at ovulation. These took two major forms: (1) loss of oocytes into the peritoneal cavity (ectopic embryos); (2) non-fertilization of oocytes.

Table 3. Incidence of infertile oocytes in clutches of live-bearing elapid snakes

Species	Total No. of clutches	Clutches with infertile oocytes	Total No. of oocytes	No. of infertile oocytes
A. superbus	13	0	160	0
N. scutatus	18	10	447	41
P. porphyriacus	20	1	253	1

All ectopic embryos seen were in the process of resorption. They often showed considerable embryonic development, and some ectopic implants may have been due to injuries suffered by gravid females, rather than to inadequacies of the ovulatory mechanism. Ectopic embryos were seen in two *Notechis scutatus* (total of four embryos), six *Pseudechis porphyriacus* (nine embryos), and two *Austrelaps superbus* (at least seven embryos). One of the *A. superbus* had at least six, possibly more, ectopic embryos, probably as a result of injury in a previous breeding season. Although most of her body cavity, and oviducts, were taken up with resorbing embryos, she had ovulated one apparently normal and developing oocyte in the year she was collected.

Table 4. The relationship between female snout–vent length and clutch size in six species of elapid snakes

Table gives values to evaluate the equation $y = bx+a$; regression fit by least squares, where y is clutch size and x is snout–vent length in centimetres. Values for clutch size are means, with ranges in parentheses

Species	N	b	a	r^2	Clutch size
A. superbus	19	0·59	−25·10	0·81	16·5 (9–31)
H. signata	8	0·42	−7·74	0·37	10·3 (6–16)
N. scutatus	31	0·44	−12·32	0·28	23·6 (14–37)
P. porphyriacus	35	0·16	−4·75	0·20	12·4 (5–16)
P. nuchalis	6	0·36	−20·38	0·43	27·2 (24–38)
U. gouldii	27	0·21	−2·18	0·31	4·3 (2–7)

The other dysfunction noted was non-fertilization of ova. Infertile eggs were common in *Notechis scutatus*, but rare in *Austrelaps superbus* and *Pseudechis porphyriacus* (Table 3). The infertility rate in *Notechis* was significantly higher than in the two other species. (Proportion of clutches with infertile oocytes (2×2 contingency table): *Notechis–Austrelaps*, $\chi^2 = 6\cdot69$, 1 d.f., $P < 0\cdot01$; *Notechis–Pseudechis*, $\chi^2 = 9\cdot44$, 1 d.f., $P < 0\cdot01$. Proportion of oocytes infertile: *Notechis–Austrelaps*, $\chi^2 = 14\cdot3$, 1 d.f., $P < 0\cdot001$; *Notechis–Pseudechis*, $\chi^2 = 20\cdot5$, 1 d.f., $P < 0\cdot001$.) This suggested that the frequent infertility in *Notechis* might be due to the high clutch size of this species, but analysis with the Spearman Rank Correlation

Coefficient showed that clutch size and the percentage infertility were not significantly related (all *Notechis* clutches: $n = 18, r_s = 0{\cdot}15$, n.s.; clutches with infertile oocytes: $n = 10, r_s = 0{\cdot}35$, n.s.).

Clutch Size

Table 4 shows that clutch size is positively correlated with female body size in all species. Counts of oviducal eggs and of enlarged ovarian follicles gave similar results. The two factors which could reduce this equivalence—follicular resorption, and loss of ova at ovulation—act in opposite directions and tend to cancel each other out. In any case, the effect is minor.

Table 5. Live weight, dry weight, ash content and calorific content of elapid oocytes and embryos

Values are means, with standard errors in parentheses. Calorific content in kilocalories per gram of ash-free dry weight

Species	*N*	Live wt (g)	Dry wt (g)	Ash in dry samples (%)	Calorific content (kcal g^{-1})
A. superbus					
Early oocytes	11	2·420 (0·082)	—	—	—
Full-term embryos	6	5·890 (0·173)	—	—	—
H. signata					
Early oocytes	2	0·85	—	—	—
Full-term embryos	4	1·94	—	—	—
N. scutatus					
Early oocytes	10	2·698 (0·192)	1·380^A	—	—
Full-term embryos	15	5·297 (0·075)	0·900 (0·015)	—	—
P. porphyriacus					
Early oocytes	16	6·593 (0·206)	3·236 (0·138)	8·03 (0·22)	6·62^A
Full-term embryos	14	20·221 (0·750)	3·193 (0·143)	12·53 (0·12)	6·58^A

^{A} Mean of three determinations.

Physiology of Gestation

Table 5 shows that: (1) live weight of embryos increased up to fourfold during gestation; (2) dry weight of embryos did not show any significant change over the period of gestation in *Pseudechis porphyriacus*, but decreased in *Notechis scutatus* ($n = 10$, $P < 0{\cdot}05$, Mann-Whitney 'U' test); (3) energy content of full-term *P. porphyriacus* embryos was only slightly lower than that of recently ovulated oocytes; (4) ash content of *P. porphyriacus* embryos increased during gestation ($n = 12$, $P < 0{\cdot}001$, Mann-Whitney 'U' test).

Reproductive Effort

Ratios of clutch weight to body weight were calculated for all species for which sufficiently large samples were available (Table 1). In the case of the two most common species, regressions of C : B against maternal snout–vent lengths were also computed. In both species, C : B decreased slightly with increasing maternal length (Spearman Rank Correlation Coefficient: *Notechis scutatus*, $n = 29$, $r_s = -0{\cdot}53$, $P < 0{\cdot}01$; *Pseudechis porphyriacus*, $n = 22$, $r_s = -0{\cdot}44$, $P < 0{\cdot}05$).

Discussion

Frequency of Reproduction

Over 80% of adult females of the live-bearing species reproduce every year (Table 2). Yearly reproduction also characterizes most colubrid snakes (Fitch 1970; possible exceptions given by Hebard 1951; Platt 1969). In contrast, the venomous snakes so far studied (crotalids and viperids) have generally been found to show lower frequencies of reproduction; most commonly, females reproduce every second year (Klauber 1956; Saint Girons 1957*a*, 1957*b*; Tinkle 1962; Wharton 1966; Gibbons 1972). These low reproductive frequencies probably reflect a high fecundity-independent cost of reproduction (Bull and Shine 1977) coupled with low food availability. Well fed captive crotalids and vipers will reproduce at much shorter intervals than do wild specimens (Klauber 1956; Naulleau 1970, 1973).

Seasonal Timing

Elapid snakes resemble most other squamates of the temperate zone in the timing of ovulation and parturition. Spring ovulation is presumably adaptive in ensuring that females will be gravid during a season when high and constant temperatures are easiest to attain. This speeds embryonic development, and may reduce the incidence of developmental abnormalities (Vinegar 1974). The only known exceptions to this pattern are a few iguanid lizards, e.g. *Liolaemus multiformis* (Pearson 1954) and the *Sceloporus torquatus* species-group (Fitch 1970), which ovulate in autumn and carry the embryos over winter. Goldberg (1971) has suggested that this adaptation may ensure that the young are born at the season of greatest food abundance, but it is also possible that the climate in these areas is effectively warmer in winter than in summer (e.g. Pearson and Bradford 1976).

Mechanics of Ovulation

Vitellogenesis of many more follicles than will be ovulated in a given season is probably of considerable adaptive value. It delays the time at which clutch size is determined, and may allow adjustment of clutch size to conditions immediately before ovulation. The only likely cost of this provision is the energy wasted in vitellogenesis of non-ovulated follicles, and much of this would be resorbed. Marion and Sexton (1971) and Gibbons (1972) have advance similar arguments. Cohen (1971) offers a different interpretation, suggesting that non-ovulated oocytes are those with genetic defects.

Extra-uterine transfer of ova is probably a simple consequence of space limitations within the female's body; since it does not affect clutch size, it is of doubtful selective importance. Loss of ova at ovulation (ectopic embryos) is potentially a more serious problem, but occurred rarely (less than 2% of embryos).

In contrast, infertility was common in one species, *Notechis scutatus*. There was evidently little resorption of these infertile oocytes, because they did not decrease significantly in live weight from the time of ovulation to parturition ($n = 7$, $r_s = 0{\cdot}39$, n.s.). These cases of infertility may have been due to mechanical difficulties preventing spermatozoa from reaching the eggs, to insufficient spermatozoa in the oviducts, or to some inadequacy of the oocytes. The high rate of infertility comprises an enormous cost to reproducing *N. scutatus* females, and is a very puzzling phenomenon.

Clutch Size

In all species, larger females produced larger clutches (Table 4). This is a general finding in reptiles (Fitch 1970). Mean clutch sizes determined in the present study were generally lower than those previously reported in the literature (Lord 1918; Kellaway and Eades 1929; Waite 1929; Mackay 1949; McPhee 1959; Worrell 1963; Kinghorn 1964; Covacevich 1970; Softly 1971; Garnet 1972). This difference may be attributable in part to a tendency of previous authors to publish the higher counts and disregard the lower, but geographic variation is probably very important (Fitch 1965). All the species studied, with the possible exception of *Pseudonaja textilis*, attain much larger sizes in some other parts of their ranges than they do around Armidale (personal observation). Such larger females may be expected to produce larger clutches.

Physiology of Gestation

Several authors have suggested that true 'euviviparity', including the transfer of nutrients from maternal to foetal circulations, occurs in both snakes and lizards, but the available evidence is weak. Nutrient transfer has been inferred from histology (e.g. Weekes 1935; Parameswaran 1962), radioisotope studies (e.g. Conaway and Fleming 1960; Hoffman 1970; but see Panigel 1956), and from apparent increases in oocyte live weight (Branson and Baker 1974), dry weight (Hall 1969), protein content and ash content (Clark and Sisken 1956) during gestation. The radioisotope work clearly shows that nutrients are transferred across the placenta, but does not reveal the extent of the transfer. Neither do measurements on live weight, because this is a very poor indicator of energy contant (e.g. see Table 5).

Clark and Sisken (1956) and Hall (1969) have suggested that dry weights of snake oocytes increase during gestation, but analysis shows that their data do not reach statistical significance (Spearman Rank Correlation Coefficient for Clark and Sisken (1956): $n = 33$, $r_s = 0{\cdot}01$, n.s.; for Hall (1969): $n = 5$, $r_s = 0{\cdot}60$, n.s.). The trend for increasing ash content during gestation observed by Clark and Sisken (1956) is not significant either ($n = 2$). However, Clark and Sisken's data do show that the protein content of *Thamnophis* embryos increases during development ($n = 17$, $r_s = 0{\cdot}56$, $P < 0{\cdot}05$). To my knowledge, these measurements of protein content are the only published data on the extent of maternal–foetal nutrient transfer in reptiles.

Table 5 shows that the ash content of *Pseudechis porphyriacus* embryos increases significantly during gestation ($P < 0{\cdot}001$). This provides strong evidence for placental nutrient transport. The relative constancy of oocyte dry weights and energy content (Table 5) gives further evidence of nutrient input to the embryo, because otherwise the embryo's metabolism should reduce the energy content of the oocyte by about 50% (Tinkle and Hadley 1973; Vitt 1974). Placental nutrient transfer in *P. porphyriacus* is surprising, since other members of this genus are oviparous in at least part of their ranges (J. Covacevich and C. Tanner, personal communication). However, the increase in ash content in *P. porphyriacus* may not reflect an active mechanism of nutrient transfer. More likely, the ions are carried across passively with the flow of water; a similar increase in ash content during development is shown by the eggs of at least one species of oviparous marine fish (Amoroso 1960).

The degree of embryonic wet weight increase during gestation in *Austrelaps superbus*, *Hemiaspis signata* and *Notechis scutatus* is slightly lower than in *P.*

porphyriacus, and dry weights of *N. scutatus* oocytes decrease during gestation. Placental transfer of nutrients may be less important in these species, despite the existence of a well developed chorio-allantoic placenta in *A. superbus* (Weekes 1935).

The dramatic increase in water content of the developing embryos means that gravid females are heavily burdened physically. This burdening begins at vitellogenesis, when fat is mobilized for follicular development; the act of ovulation does not substantially affect the weight of reproductive materials (Table 6). Thereafter, embryonic weights increase steadily (Shine 1975). This gradual increase in embryonic weights may explain a common observation on live-bearing snakes; gravid females cease feeding midway through gestation [for crotalids see Fitch and Shirer (1971) and Keenlyne and Beer (1973); for *Notechis* and *Pseudechis* see Shine (1975)]. This cessation of feeding midway through gestation, rather than at ovulation, may be due to the gravid snake becoming increasingly burdened and finally reaching a critical clutch weight : body weight ratio at which feeding ability is greatly impaired.

Table 6. Water content of body fat, enlarging ovarian follicles, and oocytes in *Pseudechis porphyriacus*

Values are means, with standard error in parentheses

Tissue	*N*	Water content (%)
Abdominal fat body	10	14·4(1·4)
Ovarian follicles	4	54·9(47·3–63·8)[A]
Newly ovulated oviducal oocytes	16	50·9(14)
Near full-term oviducal oocytes	14	84·2(1·0)

[A] Range.

Reproductive Effort

Williams (1966*a*) suggested that an organism's total seasonal investment in reproduction be designated 'reproductive effort' (RE). All activities which reduce the 'residual reproductive value' of the reproducing organism (Williams 1966*b*) are part of RE; thus, it involves risk (e.g. defence against predators) as well as energy costs (energy directly expended on reproduction, plus the reduction in feeding rate due to involvement in reproductive activities). Because of its complex nature, RE has proved very difficult to measure in field populations. Tinkle (1969) used a host of morphological and behavioural criteria [suggested by Williams (1966*a*)] to examine RE levels in lizards. Most other workers have used some sort of ratio of clutch weight to body weight (C : B) or, more recently, the ratio of clutch energy content to body energy content (e.g. Tinkle 1969; Gadgil and Solbrig 1972; Ballinger and Clark 1973; Vitt 1974; Pianka and Parker 1975).

(i) *Changes in RE with age*

There is a general prediction that RE should increase with age within a species (Williams 1966*a*; Gadgil and Bossert 1970), although this may not always be true (Fagen 1972; Schaffer 1974; Hirshfield and Tinkle 1975). Attempts to test this hypothesis for reptiles have shown:

(1) In one species of lizard, *Lacerta vivipara*, females devote an increasing proportion of their annual food intake to reproduction as they grow larger, and C : B remains constant (Avery 1975).
(2) In two other lizards, *Sceloporus malachiticus* (Marion and Sexton 1971) and *S. jarrovi* (Tinkle and Hadley 1975), and in a snake, *Carphophis vermis* (Clark 1970) C : B increases with increasing body size.
(3) In most other reptiles studied, C : B remains constant with increasing body size (e.g. Vitt 1974; Tinkle and Hadley 1975; Fitch 1975; Vinegar 1975; Pianka and Parker 1975).

Thus, the trend for decreasing C : B with increasing maternal length in *N. scutatus* and *P. porphyriacus* is unusual. The many inadequacies of the available RE measures make it difficult to draw any definite conclusions. The general reptilian pattern seems to be that C : B remains rather constant with age and, hence, that old specimens tend to devote more of their available energy to reproduction than do young ones, since food intake per gram body weight is lower in larger animals. This is certainly true in *Lacerta vivipara*.

(ii) *Interspecific differences in RE*

Williams (1966*a*) predicted that short-lived species should expend a higher reproductive effort per season than long-lived species. He also suggested that species body size should give a rough index of longevity. Table 1 shows that the smaller species tend to show relatively high 'frequency of reproduction' (i.e. proportion of reproductive to non-reproductive 'adult' females) and high C : B ratios, in agreement with Williams' hypothesis.

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