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"Costs" of Reproduction in Reptiles

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Summary. Many theoretical models of life-history evolution rely on the existence of trade-offs between current fecundity and probable *future* fecundity and survival. Such "costs" of reproduction have been demonstrated only rarely. Field and laboratory studies on six species of Australian scincid lizards show that gravid females are more vulnerable to predation than are non-gravid females, primarily because (i) they are physically burdened (running speeds are reduced by 20 to 30%), and (ii) they bask more often (in some species). However, food intake is not reduced in gravid animals. A review of published literature suggests that reproductive trade-offs are widespread among reptiles, but the nature of the reproductive "costs" may vary widely among related species. Within the range of annual survivorship rates of most lizard species, trade-offs between fecundity and survival are likely to be the main evolutionary determinants of optimal levels of "reproductive effort". Trade-offs between fecundity and bodily growth are less likely to be significant.

Introduction

Many recent models of life-history evolution rely on hypothetical "trade-offs" between expenditure on current reproduction on the one hand, and future probable reproductive success on the other (e.g. Tinkle 1969, Tinkle and Hadley 1975, Gadgil and Bossert 1970, Fagen 1972, Schaffer 1974, Hirschfield and Tinkle 1975, Pianka and Parker 1975, Pianka 1976, Stearns 1976). This approach derives from Williams (1966), who suggested that life-history "tactics" (e.g. age at first reproduction, clutch size) should evolve to maximize the sum of present reproductive success plus probable future reproductive success. The key to maximizing this sum is the postulated trade-off between "present" and "future" components. For example, a low current expenditure on reproduction might be favoured if a high expenditure would greatly reduce the organism's chance of survival to next breeding. The same result holds if current reproductive expenditure greatly reduces subsequent growth rate (and hence, fecundity at later reproductions). Life-history theory predicts that the form of this trade-off between current "profits" and future "losses" is a prime evolutionary determinant of such parameters as clutch size, reproductive effort, mode of reproduction, reproductive frequency and iteroparity *versus* semelparity (Stearns 1976). Nonetheless, there are few field studies of these trade-offs in any animal population. The present paper provides data on the "costs" of reproduction in females of several species of montane Australian scincid lizards, and reviews published data on reproductive trade-offs in reptiles.

Reproductive "costs" could take several forms in reptiles, but two major categories may be distinguished.

(1) *Survival* of females might be reduced by behavioural changes associated with reproduction. For example, gravid females might spend more time basking than do non-gravid females, for at least three reasons: (i) increased body mass would mean that heating rates are slower in gravid females and it would therefore take longer to attain preferred body temperatures; (ii) females may select higher temperatures so as to speed embryonic development; and (iii) females may select higher temperatures to compensate for their lowered mobility when gravid (data below). Basking lizards may be particularly vulnerable to avian predators (pers. obs.). Other potential survival costs include (i) reduced ability to evade predators, because of lowered mobility, and (ii) total depletion of energy reserves during reproduction, leading to starvation. This latter factor is unlikely to be significant, given the low maintenance energy requirements of reptiles (e.g. Turner et al. 1976).

(2) The other major category of reproductive "costs" involves *energy allocation*. Since fecundity depends on body size in most reptiles (e.g. Fitch 1970), energy allocation to reproduction rather than growth is expected to depress fecundity at later reproductions. Reproduction may be even more expensive in energetic terms if reproducing females reduce their food intake.

Materials and Methods

The hypothetical reproductive "costs" described above were investigated in five species of montane eastern Australian scincid lizards. Most specimens were collected at Corree Flats (elevation 1,200 m) in the Brindabella Range 40 km west of Canberra, A.C.T. The study area consists of extensive swamps among sclerophyll eucalypt forest, and has been described previously by Pengilley (1971, 1972). Pengilley (1972) studied the ecology and reproduction of the Corree Flats scincid fauna, and his work provided an invaluable background to the present study. I collected all five scincid species (from leaf litter and under fallen logs) during four three-day visits to Corree Flats from November through February. Females were gravid during most of this period (Fig. 1).

Immediately after capture, lizards were placed individually in numbered plastic bags. After three days, the animals were removed, weighed, measured and maintained individually in boxes at constant 25° C and under natural photoperiod. Food was not provided, but water was available *ad libitum*. Faeces produced in the plastic bags during the initial three-day period were removed, dried to constant weight in a 50° C oven, and dry faeces weights used as an index of food consumption rates (Avery 1971).

Following the faeces collection period, lizards were left undisturbed for 24 h in boxes, and then running speeds at 25° C were

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Fig. 1. Gravid and non-gravid adult female *Leiolopisma entrecasteauxii*. Note general body shape, and great physical distension of gravid female (RCM = 0.5)

measured in trials at 24-h intervals. Speeds were measured by filming the lizards with an 8 mm movie camera as they ran along a horizontal runway one m long and 3.5 cm wide (two m long and 10 cm wide for *Sphenomorphus*). Each lizard was run at least twice in every trial. Films were analysed frame-by-frame, and lizard positions at successive 1/18 s intervals recorded. Stoppages (no lizard movement between successive frames) were omitted from the analysis, and distances moved in other frames were combined to yield an average running speed for each lizard. To control for stress or thermal acclimation, the mean score for each female lizard was computed as a proportion of the mean speed of all male lizards in the same trial. A more valuable comparative "standard" would have been non-gravid female lizards in every trial, but insufficient non-gravid specimens were obtained. This use of male lizards as controls assumes only that stress and thermal acclimation affect both sexes in the same way: it does not require that the sexes are identical in any other respect. Results from two or three successive daily trials were combined to give a mean mobility score (relative to male speeds) for each female lizard.

Vulnerability to predation was studied in laboratory trials with *Drysdalia coronoides*, the White-lipped Snake. This small venomous elapid is the main predator of Corree Flats skinks (Pengilley 1972, Shine 1980). Two adult female *D. coronoides* were housed individually in aquaria (50 × 30 × 30 cm) at 25° C, and *Leiolopisma coventryi* were introduced in pairs of approximately equal body size (one male and one gravid female). The more direct comparison between a gravid and a non-gravid female was impossible because of the scarcity of non-gravid specimens. Whenever a lizard was taken by a snake, its sex was recorded and it was replaced by another skink of the same sex.

Effects of reproduction on thermoregulatory behaviour were studied with *Leiolopisma entrecasteauxii* and *Sphenomorphus tympanum* in a large (4 × 4 m) outdoor enclosure. These two species were chosen because both commonly bask in the field. Ten individuals (5♂♂, 5♀♀) were released into the enclosure, and behavioural observations commenced 24 h later. The number of lizards of each sex basking in sunlight was recorded at 15-minute intervals over a full day. Studies were conducted in late January (when females were gravid) and repeated with recently-collected lizards in early February (soon after parturition).

On completion of basking and mobility trials (≦8 days after collection), lizards were killed by freezing, and dissected. Clutch weights and carcass weights were recorded to permit calculation of Relative Clutch Mass (RCM). I defined RCM as the ratio of (wet) clutch weight to carcass weight, rather than clutch weight to total (clutch plus carcass) weight, as has been used by Vitt and Congdon (1978). I suggest that the former ratio better reflects the degree of physical burdening of the gravid female, and avoids statistical problems caused by non-ovigerous weight appearing both in the numerator and denominator of Vitt and Congdon's (1978) ratio. Relative Clutch Mass was calculated on an age-specific basis for the common species, using growth data from Pengilley's (1972) mark-recapture studies of Corree Flats lizards. I estimated mean body sizes of each reproductive year class from Pengilley's (1972) formulae, and calculated RCM from offspring weights, adult female weights, and fecundities at each body size (Pengilley 1972, Shine unpubl.).

Results

(1) Mobility Trials. These tests yielded consistent estimates of relative speed (Table 1), and hence should show whether or not gravid females are physically slowed by the weight of the clutch. In all 6 species, running speeds of gravid females averaged slower than those of conspecific males (median test, 1 d.f., $p < 0.01$ in all cases). In the 4 most common species, running speeds declined markedly with higher RCM's (Fig. 2; using natural-log-transformed data to correct for the use of ratios, all regressions remain significant at $p < 0.01$). These data indicate that the weight of the clutch slows gravid females to about 70% to 80% of the female's unburdened speed (Fig. 3). Since immediately post-parturient females ran just as quickly as pre-ovulatory specimens, the slowing cannot be attributed to any general "loss of condition" in gravid lizards. Instead, the clutch itself is responsible for the reduced mobility. Using log-transformed data on relative speeds,

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Table 1. Repeatability of relative velocity estimates on scincid lizards

Species	Mode of reproduction	$\bar{x}$ snoutvent length of adult ♀♀ (mm)	$\bar{x}$ RCM gravid ♀♀	Ratio of ♀ velocity to ♂ velocity			Sample size	
				Run (1)	Run (2)	Run (3)	♀♀	♂♂
Anotis maccoyi	oviparous	52	0.00	0.95	0.97	–	6	7
			0.33					
Lampropholis guichenoti	oviparous	43	0.35	0.85	0.72	0.73	4	4
Leiolopisma coventryi	viviparous	42	0.30	0.96	0.98	0.99	9	13
			0.46	0.85	0.93	–	15	11
Leiolopisma entrecasteauxii	viviparous	56	0.21	1.01	1.01	1.05	23	13
			0.42	0.85	0.89	–	19	8
Sphenomorphus tympanum	viviparous	88	0.00	1.10	0.98	–	10	5

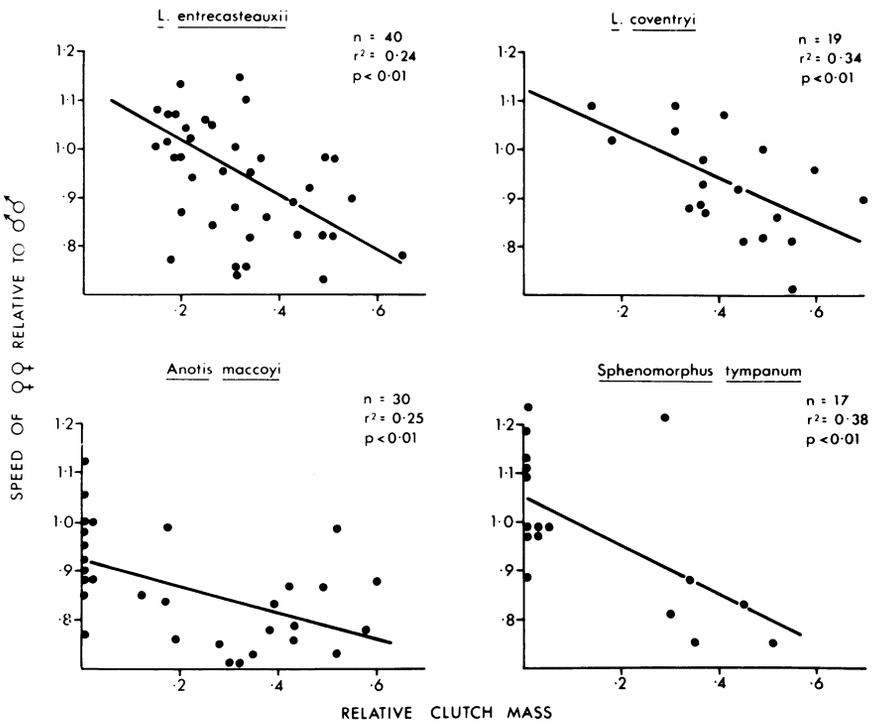


Fig. 2. Effect of Relative Clutch Mass on running speeds of scincid lizards. Each point represents one animal. See text for methods

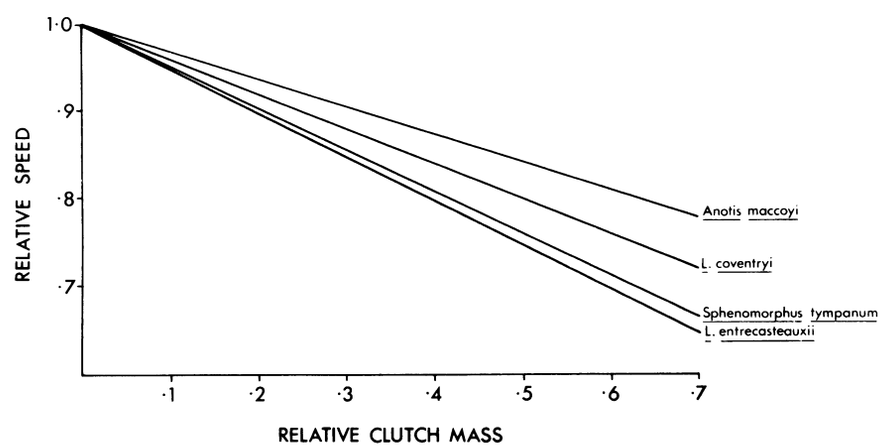


Fig. 3. Interspecific comparison of running speed decrements in gravid scincid lizards. Regression lines transformed to show speeds of ♀♀ relative to mean speed of unburdened ♀♀

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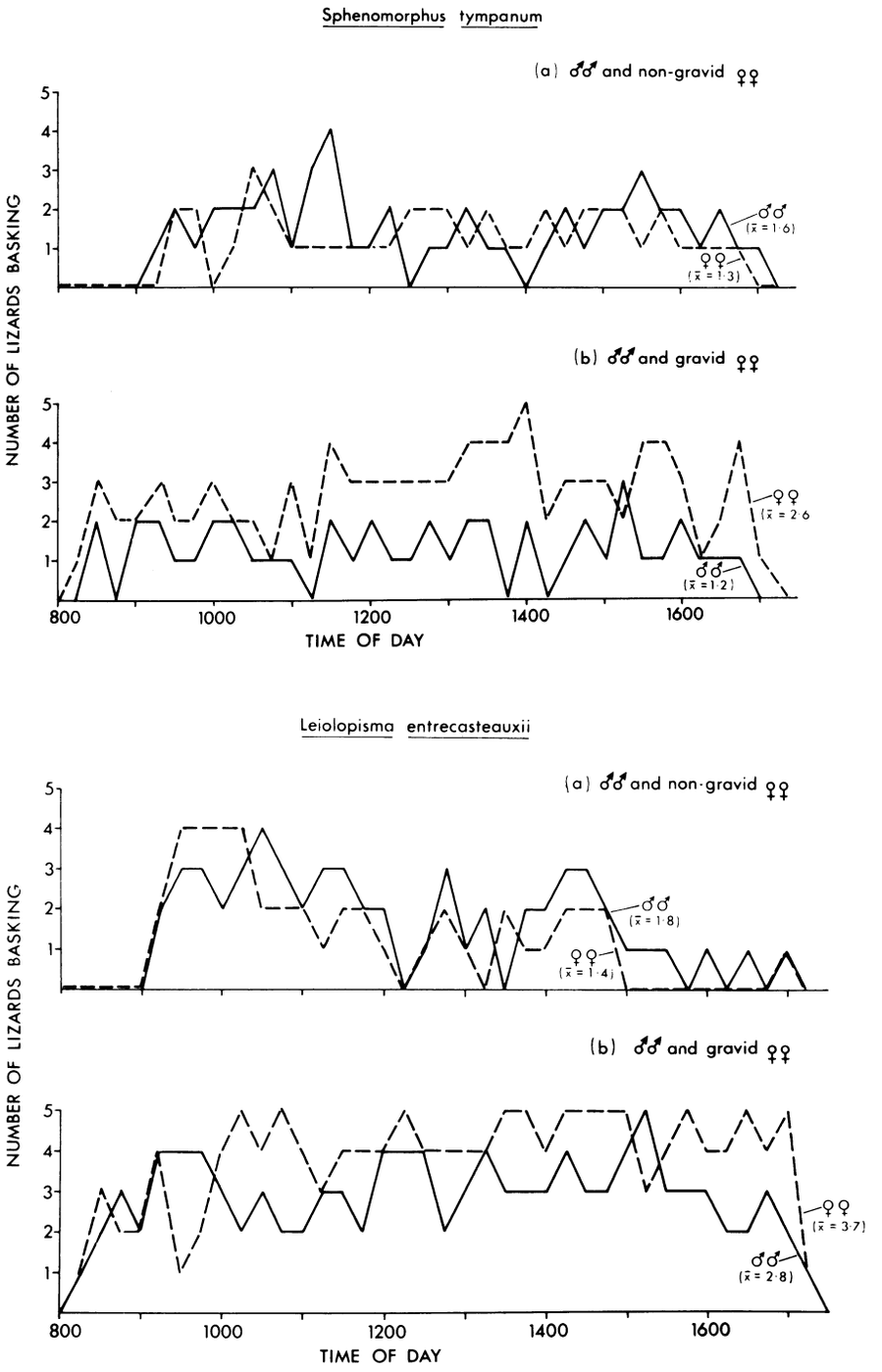


Fig. 4. Effect of reproduction on incidence of basking in two species of scincid lizards in outdoor enclosure. See text for explanation

a covariance test between the four species shown in Fig. 2 reveals no significant interspecific differences in slopes (Fig. 3; d.f.=112, 3, $F=0.86$, n.s.), but considerably different intercepts (d.f.=115, 3, $F=7.31$, $p<0.001$).

(2) Predation Trials. Eight of the 16 *Leiolopisma coventryi* were consumed by the white-lipped snakes. Of these eight lizards, 7 were gravid females and only one a male. This result shows a strong bias for the predator to take the gravid female skink rather than the simultaneously-offered male skink ($n=16$, $\chi^2=4.5$, $p<0.05$).

(3) Basking Trials. There was no significant difference in basking frequency between males and nongravid females (Fig. 4: *L. entrecasteauxii*, $n=102$, $\chi^2=1.41$, 1 d.f. $p>0.20$; *S. tympanum*, $n=94$, $\chi^2=0.68$, 1 d.f., $p>0.30$). However, *gravid* females basked more than males (*L. entrecasteauxii*, $n=250$, $\chi^2=4.62$, 1 d.f., $p<0.05$; *S. tympanum*, $n=147$, $\chi^2=11.44$, 1 d.f., $p<0.01$). I conclude that reproduction increases the incidence of basking in females of both species.

(4) Faeces Weights. In the four most common skinks, faeces production of gravid females did not differ from that of conspecific

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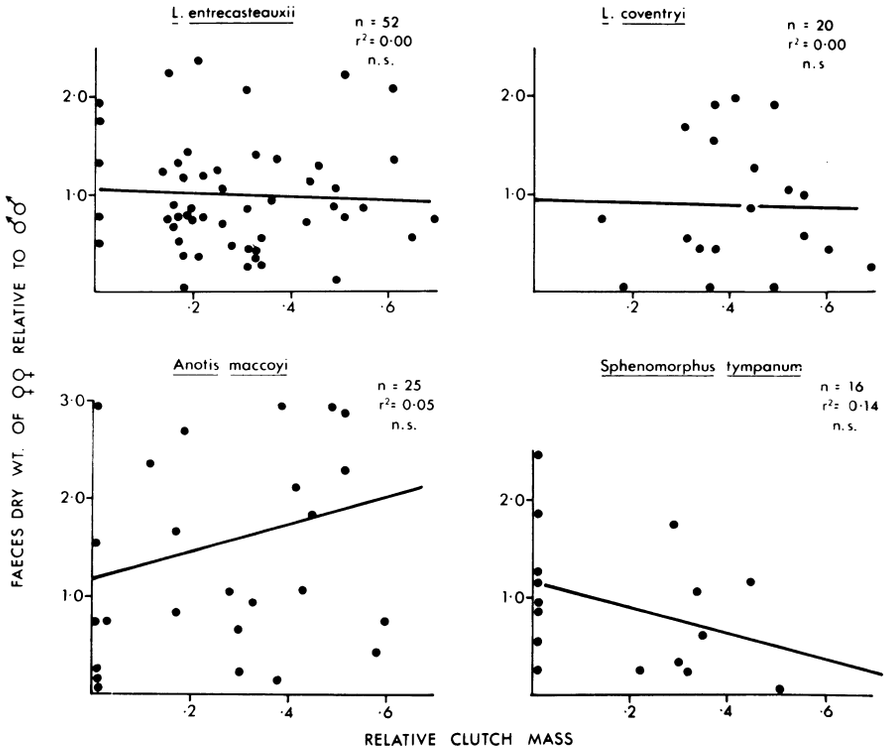


Fig. 5. Effect of Relative Clutch Mass on faeces production by female scincid lizards during 3 days after capture. See text for methods

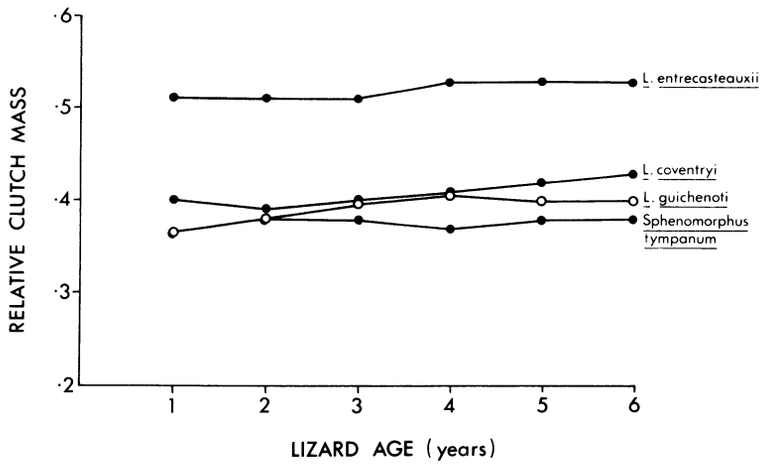


Fig. 6. Relative Clutch Mass remains constant with age in 4 scincid species. Based partly on data from Pengilley (1972); see text for explanation

males (median test, 1 d.f., $p > 0.5$ in all cases). Similarly, no significant relationship was observed between RCM and faeces production (Fig. 5). These data suggest that reproduction does not reduce daily food consumption rates in the female skinks studied.

(5) Relative Clutch Mass. Growth data (and hence, body sizes at each age) were available for four of the species studied (Pengilley 1972). In all these lizards, RCM remained constant with age (Fig. 6).

Discussion

I now examine the two major types of hypothetical reproductive costs: trade-offs with survival and with energy allocation. (1) *Survival Costs.* There *is* a trade-off between current reproductive expenditure and survival (hence, probable future reproductive success) in the montane skinks. Evidence for the existence of a survival "cost" to reproduction comes from three points: (a) the weight of the clutch slows females considerably (Figs. 2 and 3), and field and laboratory observations suggest that speed is essential in avoiding predators; (b) in laboratory trials, gravid female lizards are more vulnerable to snake predation than are conspecific males; and (c) gravid females bask for prolonged periods (Fig. 3), an activity that surely exposes them to diurnal predators (e.g. the Kookaburra, *Dacelo gigas,* is a large predatory bird common at Corree Flats).

Further indirect evidence on reproductive "costs" in the montane skinks comes from Pengilley's (1972) mark-recapture study. Pengilley found that midsummer samples of *L. entrecasteauxii* contained more females than males ($p < 0.01$) if the samples were collected by hand, but more males than females ($p < 0.01$) in sam-

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Table 2. Effects of reproduction on thermoregulation in female reptiles

Species	Mode of reproduction	Thermoregulatory effect	Authority
(1) Snakes			
Notechis scutatus	viviparous	gravid ♀♀ bask more	Shine 1979
Pseudechis porphyriacus	,,	,,	Shine 1979
Agkistrodon contortrix	,,	,,	Fitch 1960
Crotalus viridis	,,	gravid ♀♀ bask more, ♀ BT higher	Hirth and King 1969
Vipera berus	,,	gravid ♀♀ bask more	Vittanen 1967
Thamnophis ordinoides	,,	♀ BT higher (?)	Stewart 1965 but see Gibson and Falls 1979
T. sirtalis	,,	,,	
Nerodia sipedon – Ontario	,,	gravid ♀♀ bask more	Shine, unpubl.
– Texas	,,	gravid ♀♀ do *not* bask	Shine, unpubl.
N. fasciata	,,	♀ BT less variable*(?)	Osgood 1970
N. taxispilota	,,	,, *(?)	Osgood 1970
Lichanura roseofusca	,,	gravid ♀♀ bask more*	Kurfess 1967
Coluber constrictor	oviparous	no change ♀ BT	Hirth and King 1969
Masticophis taeniatus	,,	,,	Hirth and King 1969
Morelia spilotes	oviparous, brood	♀ BT raised metabolically	P. Harlow, pers. comm.
Python molurus	,,	,,	Van Mierop and Barnard 1978
(2) Lizards			
Leiolopisma entrecasteauxii	viviparous	gravid ♀♀ bask more*	Present study
Sphenomorphus tympanum	,,	,, *	Present study
Hoplodactylus maculatus	,,	♀ BT higher*	Werner and Whitaker 1978
Lacerta vivipara	,,	♀ BT lower*	Patterson and Davies 1978
Sceloporus cyanogenys	,,	,, *	Garrick 1974
S. orcutti	oviparous	no change ♀ BT	Mayhew 1963
Amphibolurus inermis	,,	,,	Heatwole 1970
Cnemidophorus, 5 spp.	,,	♀ BT *slightly* lower	Schall 1977

* = Record based on captive specimens

ples from pit-traps. This disparity suggests that gravid females either moved about less than males, or else were more easily caught by hand than were males (perhaps because of the female's lowered mobility – Fig. 2).

Casual observations suggest that females of many reptile species suffer similar reproductive "costs". Gravid females often appear to be physically burdened by the weight and volume of the clutch. Also, prolonged basking is common in gravid animals (Table 2). Interspecific variation in the nature and degree of reproductive "costs" probably is widespread (e.g. Tables 2 and 3). Data on North American watersnakes, *Nerodia sipedon*, suggest geographic variation within a species: basking by gravid females is common in cold climates, but rare in warmer areas. Even if basking occurred throughout the range of a species, geographic differences in predator abundance could result in marked differences in the degree to which reproduction is a "cost" to survivorship.

(2) Energy Allocation Trade-Offs. Reproduction may influence energy budgets in two ways: by decreasing total energy intake (feeding), or by utilizing energy that otherwise would be available for bodily growth. In the first category, a reduction in feeding while gravid seems to be common among reptiles (Table 3), although apparently not in the montane skinks (Fig. 5). At first sight, the continued feeding of gravid skinks seems inconsistent with their lowered mobility (discussed above). Field observations solved this paradox: lizards rarely used "top speed" to capture prey. Instead, they moved quite slowly over to prey items (insects), and siezed them with a sudden short lunge. Even when heavily burdened, gravid females could feed normally. In contrast, rapid movement was commonly used for escape from predators (humans or snakes), and it is not surprising to find that gravid females were vulnerable to snake predation in laboratory trials.

The second type of energy "cost" accrueing from reproduction is more difficult to investigate. Given that an animal has only a finite amount of available energy, this energy must be apportioned between maintenance expenditures (metabolism), bodily growth, and reproduction. A larger clutch size presumably decreases the energy available for bodily growth; since fecundity depends on body size (Pengilley 1972, Shine unpubl.), fecundity at *later* reproductions may be decreased by a higher fecundity at the present reproduction. Theoretical models suggest that this energy allocation trade-off may constitute a real "cost" of reproduction, and play a role in determining optimal reproductive expenditure (e.g. Williams 1966, Gadgil and Bossert 1970, Schaffer 1974). These models indicate that total lifetime reproductive success may be increased by lowering present fecundity and thereby gaining higher future fecundity. However, this result holds true only when: (1) annual survivorship is high (so that the benefits of a higher subsequent fecundity are actually realized) and (2) later fecundity is considerably increased for a minor decrease in present fecundity.

Available data on lizard populations suggest that these two conditions are unlikely to be met. (1) Turner (1978) has reviewed survivorship data on lizards: most studies reveal annual survival rates of less than 0.5 ($\bar{x}=0.28$, S.E.$=0.03$, $n=44$). (2) In lizards, Relative Clutch Mass (RCM) rarely exceeds 0.5 (Vitt and Congdon 1978): that is, the weight of the clutch is generally less than half the weight of the body. Hence, an extra gram of bodily tissue

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Table 3. Effect of reproduction on feeding in female reptiles

Species	Mode of reproduction	Is food intake reduced?	Authority
(1) Snakes			
Acanthophis antarcticus	viviparous	yes	Mirtschin 1976
Drysdalia coronoides	,,	*no*	Shine 1980
Notechis scutatus	,,	yes	Shine 1979
Pseudechis porphyriacus	,,	yes	Shine 1979
Agkistrodon contortrix	,,	yes	Fitch and Shirer 1971
Crotalus enyo	,,	*no**	Tryon and Radcliffe 1977
C. horridus	,,	yes	Keenlyne 1972
C. unicolor	,,	yes*	Kauffeld and Gloyd 1939
C. viridis	,,	yes	Fitch and Glading 1947
Sistrurus catenatus	,,	yes	Keenlyne and Beer 1973
Vipera berus	,,	yes	Prestt 1971
Thamnophis sirtalis	,,	yes	Gregory and Stewart 1975
Tropidoclonion lineatum	,,	yes*	Ramsey 1946
Acrantophis madagascariensis	,,	yes*	Branch and Erasmus 1976
Lichanura roseofusca	,,	yes*	Kurfess 1967
Lampropeltis triangulum	oviparous	yes*	Tryon and Hulsey 1976
Morelia spilotes	oviparous, brood	yes*	P. Harlow, pers. comm.
Python molurus	,,	yes*	Van Mierop and Barnard 1978
P. sebae	,,	yes	Fitzsimons 1930
Ophiophagus hannah	,,	yes	Leakey 1969
(2) Lizards			
Egernia striolata	viviparous	yes	Bustard 1970
Leiolopisma coventryi	,,	*no*	Present study
L. entrecasteauxii	,,	*no*	Present study
L. otagoense	,,	yes*	Watchman 1979
Sphenomorphus tympanum	,,	*no*	Present study
Chamaeleo pumilis	,,	*no*	Burrage 1973
C. namaquensis	oviparous	*no*	Burrage 1973
Anotis maccoyi	,,	*no*	Present study
Cyclura carinata	,,	yes	Iverson 1979
Dipsosaurus dorsalis	,,	yes	Norris 1953
Iguana iguana	,,	yes	Rand 1978
Lampropholis guichenoti	,,	*no*	Present study
Eumeces egregius	oviparous, brood	yes	Mount 1963
E. fasciatus	,,	yes	Fitch 1954
E. obsoletus	,,	yes	Fitch 1955
E. septentrionalis	,,	yes	Breckenridge 1943
(3) Crocodilians			
Crocodylus niloticus	oviparous, brood	yes	Pooley 1977
C. porosus	,,	yes (?)	Deraniyagala 1939

* = Record based on captive specimens

(growth) cannot increase subsequent fecundity by more than about half a gram. This constraint means that energy diverted from reproduction to body growth in the current season will yield a fairly low increment in fecundity at subsequent seasons. For example, a 10% decrease in first-year fecundity is unlikely to boost second-year fecundity by more than 5%. Given this low return for a decrease in current fecundity, coupled with a low probability of living long enough to enjoy the higher fecundity, energy allocation trade-offs are unlikely to be important determinants of lizard reproductive "tactics". In anthropomorphic terms, what theory suggests is that lizards should not reduce attainable levels of current fecundity in order to gain a subsequent benefit in fecundity from larger body size.

In contrast, theoretical models indicate that *survival* costs should play a large role in shaping reproductive strategies in lizards. Trade-offs between survival and fecundity (1) are less affected by low mean survivorships, and (2) are not constrained by RCM, or by any other obvious upper limit (e.g. one could imagine a 1% decrease in fecundity enabling a 10% increase in female survivorship). Hence, the evolutionary adjustment of fecundity levels in lizards should be more sensitive to survival trade-offs rather than energy allocation trade-offs. From a theoretical point of view, the relationship between fecundity and survivorship is likely to be the most important reproductive "cost" in lizards.

Three limitations of this conclusion should be recognized: (i) at annual survivorships higher than 0.6, as is common in snakes (Turner 1978), the energetics trade-offs may be important; (ii) the models assume that energy diversion to body growth does not increase survival; and (iii) the effective "benefit in later fecundity per cost in present fecundity" may be higher than the RCM

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if reproduction decreases food intake (Table 3). If this happens, the energy saving from deferred reproduction may be higher than suggested by the RCM. Overall, however, the models indicate that trade-offs between reproductive expenditure and growth rates should *not* be important determinants of life-history tactics in lizards.

This conclusion has obvious implications for the measurement of "Reproductive Effort" (RE) in reptiles. RE is defined in terms of the "costs" accruing from given levels of reproductive investment; assessing RE is equivalent to assessing these costs (Williams 1966, Schaffer 1974). Hence, energy allocation measures (e.g. Hirschfield and Tinkle 1975) are unlikely to offer useful estimates of RE, because the trade-off they assess (fecundity *versus* growth) is probably of minor importance in the evolution of lizard life-history tactics. Measurements of the *survival* costs of reproduction, although more difficult to quantify, may be the most useful single RE estimate for most lizard species.

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