



FAUNA
of
AUSTRALIA



**25. NATURAL HISTORY OF
THE SQUAMATA**

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The domain of Natural History includes the study of animals in their natural environment, largely by observational means. It encompasses various aspects of behaviour and ecology at the levels of the whole organism, population and community, and leads to conclusions about evolution and adaptation. Those aspects selected for treatment in this chapter partly reflect our own conception of Natural History and partly the requirement not to overlap unduly with contributions of other authors. In particular, we leave discussion of physiological ecology to the authors of Chapter 24, and only discuss experimental approaches, laboratory data, or investigations at the organ, tissue or cellular level where they have particular relevance to field studies—and then only briefly. The emphasis has been placed on the Australian fauna, and reference to the worldwide literature is made for comparative purposes or to illustrate principles not exemplified by Australian studies. The detail with which we treat particular topics is tempered by recent reviews which deal with many aspects of the ecology of lizards and snakes (Huey, Pianka & Schoener 1983; Pianka 1986; Heatwole & Taylor 1987; Siegel, Collins & Novak 1987; Gans & Huey 1988; Greer 1989).

ENVIRONMENTAL RELATIONS

An ectotherm obtains its heat from its external environment, whereas an endotherm produces most of its own heat internally by means of oxidative metabolism. The vast majority of animals are ectothermic. Continuously endothermic animals are found among birds and mammals, though even many of these become ectothermic at times. Reptiles generally are ectotherms, but some squamates, especially the larger ones, are at times at least partially endothermic (see Heatwole & Taylor 1987).

A related pair of useful terms are sometimes confused with the above designations. Animals that maintain relatively constant internal body temperatures are homeotherms, whereas those whose temperatures vary widely and closely track those of the environment, are called poikilotherms. Many ectothermic snakes and lizards have preferred temperatures and regulate their body temperatures rather precisely by appropriate behavioural means during their activity periods. When inactive, their body temperatures fluctuate and follow that of the environment. Thus they are neither strictly poikilothermic nor homeothermic. Some diurnal species bask and use the sun as a heat source and are called heliotherms. Others select substrates of particular temperatures, although they track the temperature of their immediate environment, and do not experience the full range of available conditions. These are called thigmotherms. An active desert lizard may have a body temperature just as high as that of a bird or mammal; the layman's terms 'warm-blooded' and 'cold-blooded' are thus quite misleading and should be abandoned.

Many different pathways of heat gains and heat losses exist (Heatwole & Taylor 1987) and balancing a heat budget requires very different adaptations under varying environmental conditions. At different times of day, ambient thermal conditions may change from being too cold to being too warm for a particular animal's optimal performance. Animals living in hot deserts must be able to minimise heat loads and to dissipate heat efficiently to avoid overheating. In contrast, those that live in colder places, such as at high altitudes, must be adept at acquiring and retaining heat.

Because thermoregulation clearly has costs and risks as well as benefits, an emerging conceptual framework envisions an optimal level of regulation that depends on the precise form of the constraints and interactions among costs and benefits arising from a particular ecological situation (Huey & Slatkin 1976).

Thermoregulation often involves both physiological (Lillywhite 1987b; Chapter 24) and behavioural adjustments. As an example of the latter, consider a typical terrestrial diurnal desert lizard (Bradshaw & Main 1968; Heatwole 1970). During the early morning, when ambient temperatures are low, such a lizard locates itself in the warmer microclimates of the environmental thermal mosaic, and basks in the sun with its flattened body as perpendicular as possible to the sun's rays, thereby maximising heat gain. As ambient temperatures quickly rise, the lizard climbs up off the ground into cooler air and orients itself facing into the sun's rays, thereby reducing its heat load. Often these behavioural adjustments are too effective and carry the animal beyond the limits of its preferred temperatures, and it must make further, compensatory changes in posture or location. Diurnal lizards and snakes often repeatedly 'shuttle' back and forth between sun and shade as their temperatures alternately rise too high and fall too low. At high temperatures, they may seek shade or retreat into burrows. Many lizards change their colour and their heat reflectance properties, becoming dark and heat-absorbent at colder times of day but light and heat-reflectant at hotter ones (Rice & Bradshaw 1980). When these expedients fail, some lizards resort to panting (Heatwole 1970; Heatwole, Firth & Webb 1973).

Snakes have similar behavioural repertoires including basking, flattening, posturing towards the sun and shuttling (Heatwole & Johnson 1979) and in addition have one not common in lizards—coiling as a means of retaining body heat during cool periods (Cogger & Holmes 1960; Shine & Slip 1988b).

Thermoregulatory patterns are related to activity cycles. Two major strategies of thermoregulatory precision seem to be pursued by diurnal lizards (Heatwole, Lin, Villalón, Muñiz & Matta 1969). Some species are active only when they can thermoregulate precisely and consequently alter their activity period seasonally, from a short activity peak centring on midday at cooler times of year to a bimodal cycle which avoids midday heat at warmer periods. Others sacrifice thermoregulatory precision to maximise the length of the activity period and are active most of the daylight hours, during which time they are thermally passive. There may be seasonal and/or geographic shifts in mean body temperature of active animals (Heatwole 1970).

Some species may not fit conveniently into either of these categories. Shine (1987c) found that the diurnal, surficial *Pseudechis porphyriacus* adjusts its time and kind of activity in such a way that, while active, its body temperature stays between 28° and 31°C over a variety of seasons, localities and ambient temperatures. However, a later study (Shine & Lambeck 1990) revealed seasonal shifts in body temperature.

Thermoregulatory patterns are also related to habitat. Some squamates are climbers, others subterranean, while still others are strictly surface dwellers. Among the latter, some tend to be found in open areas whereas others frequent the edges of vegetation. By contrast, many burrowing species are relatively passive to environmental temperature. Arboreal lizards may display narrower variances in body temperature than do terrestrial ones (Pianka 1966).

Differences in temporal patterns of activity, the use of space, and body temperature relationships are hardly independent. Rather, they constrain one another in complex and sometimes obscure ways. For example, thermal conditions associated with particular microhabitats change in characteristic ways in time. A choice basking site at one time of day becomes an inhospitable hot spot at another time. Perches of arboreal lizards receive full sun early and late in the day when ambient air temperatures tend to be low and basking is therefore desirable, but these same tree trunks are shady and cool during the heat of midday when heat avoidance behaviour becomes necessary (Huey & Pianka 1977). In contrast, the fraction of the ground's surface in the sun is low early and late when shadows are long, but reaches a maximum at midday. Terrestrial

heliothermic lizards may thus experience a shortage of suitable basking sites early and late in the day. Moreover, during the heat of the day, their movements through relatively extensive patches of open sun can be severely curtailed. Hence ground-dwelling lizards encounter fundamentally different and more difficult thermal challenges than do climbing species.

Perching sites may vary widely between the cool morning and evening periods (Heatwole 1970). In the morning some desert lizards prefer bushes rather than sand, as the former results in less conductive heat loss to cold substrates. In the evening, warmth can be obtained from sun-heated sand and basking occurs on mounds of sand rather than on bushes.

Radiation and conduction are the most important means of heat exchange for the majority of diurnal lizards, although the thermal background in which these processes occur is strongly influenced by prevailing air temperatures. Ambient air temperatures are critical to nocturnal lizards as well as to certain very cryptic diurnal species.

In an analysis of the costs and benefits of lizard thermoregulation, Huey & Slatkin (1976) identified the slope of the regression of body temperature against ambient environmental temperature as a useful, inverse indicator of the degree of passiveness in regulation of body temperature. On such a plot of active body temperature versus ambient temperature, a slope of one indicates true poikilothermy or totally passive thermoconformity (a perfect correlation between air temperature and body temperature results), whereas a slope of zero reflects the other extreme of perfect thermoregulation. Lizards span this entire spectrum. Among active, diurnal, heliothermic species, regressions of body temperature on air temperature are nearly flat, and for several species, including some quite small ones, slopes do not differ significantly from zero. Slopes of similar plots for nocturnal species are typically closer to unity. Various other species—nocturnal, diurnal and crepuscular—particularly Australian ones, are intermediate, filling in this continuum of thermoregulatory tactics (Pianka 1986).

A straight line can be represented as a single point in the coordinates of slope versus intercept. These two parameters are plotted for linear regressions of body temperatures on air temperatures for 82 species of lizards in Figure 25.1. Each data point represents the least-squares linear regression of body temperature against air temperature for a given species of desert lizard. Interestingly, these data points fall on another, transcendent, straight line. The position of any particular species along this spectrum reflects a great deal about its complex activities in space and time, and the line plotted in Figure 25.1 thus offers a potent linear dimension on which various species can be placed in attempts to formulate general schemes of lizard ecology (Pianka 1986). Various other ecological parameters, including reproductive tactics, can be mapped onto this emergent spatial-temporal axis (Pianka 1986).

The intriguing ‘intercept’ of the intercepts (38.8°C) approximates the point of intersection of all 82 regression lines and presumably represents an innate design constraint imposed by lizard physiology and metabolism. It is presumably not an accident that this value also corresponds more or less to the body temperature of homeotherms, particularly mammals!

Different taxa of squamates have somewhat different body temperatures when active (Fig. 25.2). Among the Australian representatives for which data are available, the frequency of lizards with high preferred temperatures is greater than for snakes. Among the snakes, more pythons tend to have higher temperatures than do elapids, and among the lizards more dragons (agamids) and goannas (varanids) operate at higher temperatures than do skinks, which in turn are higher than geckos and pygopodids (Fig. 25.3). These differences reflect, at least in part, the activity cycles and habitats of these groups. Skinks

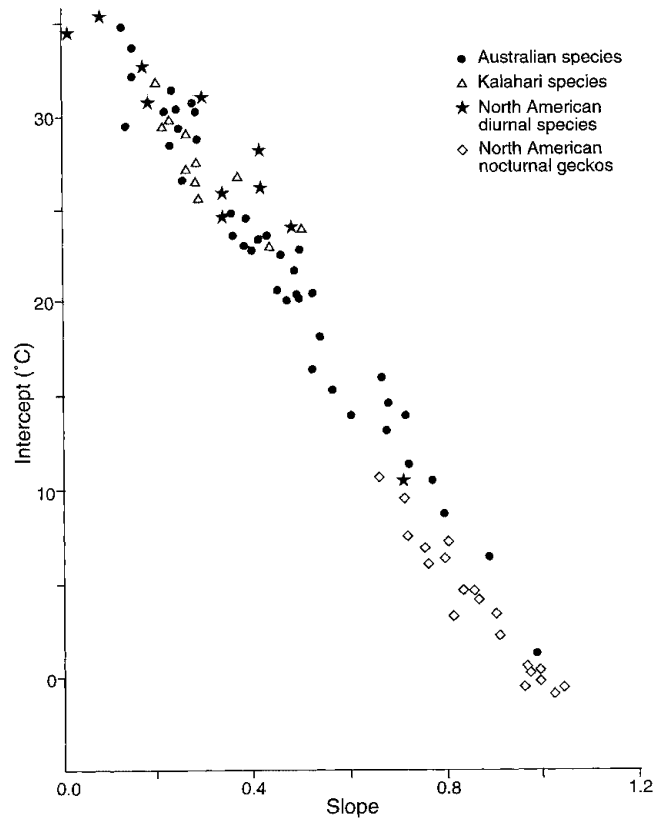


Figure 25.1 Relationship of the intercepts and slopes of lines relating body temperature to air temperature in a number of species of lizards. Each symbol represents one species (From Pianka 1986) [W. Mumford]

have a wide range of habits and preferred temperatures. Those species toward the lower values in Figure 25.2 are burrowing forms, whereas those at the higher end of the spectrum are diurnal, surficial ones. Similarly, the geckos with low preferred temperatures are nocturnal and the few with high preferences are diurnal. Clearly, the thermal relations of active squamates vary widely among taxa and are profoundly influenced by their spatial and temporal patterns of activity.

Reptiles in the field are not always able to achieve the body temperatures they prefer in a laboratory gradient, but rather operate over a wider activity range. Geckos depart more widely from equality of field and laboratory temperatures than do other lizard taxa, and often operate below preferred levels in the field (Fig. 25.4).

Cool forests have few lizard species and individuals; they may simply be too shady and too cold to provide adequate basking sites. Birds and mammals on the other hand do quite well in such areas, partly because of their endothermy. By contrast, lizards constitute an extremely conspicuous element of the vertebrate faunas of most deserts, especially warmer ones. Indeed, the mammalogist Finlayson (1943) referred to the vast interior deserts of Australia as 'a land of lizards'. Like other ectotherms, lizards obtain their bodily heat primarily from the external environment, as opposed to endotherms such as birds and mammals which can produce their own heat internally by means of oxidative metabolism. Moreover, along with other ectotherms (Pough 1980b), lizards are low-energy animals. Bennett & Nagy (1977) underscored the great 'economy of the saurian mode of life' by pointing out that one day's food supply for a small bird will last a lizard of the same body size for over a month. Ectothermy presumably has

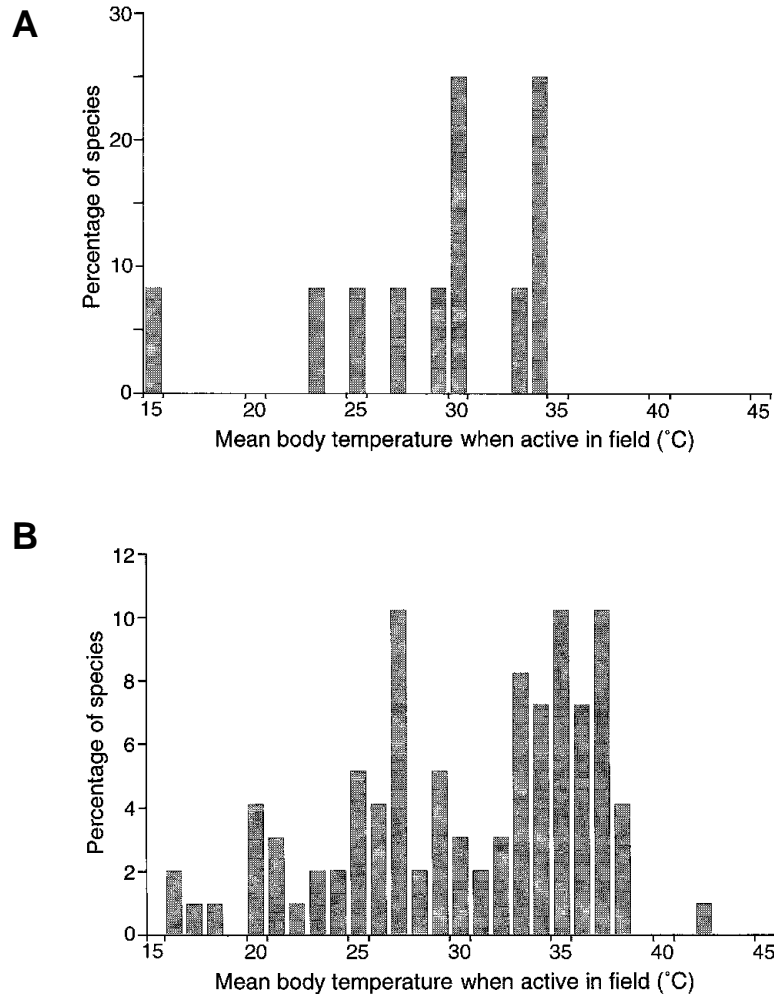


Figure 25.2 Frequency distribution of mean body temperatures of squamate species active in the field. **A**, snakes; **B**, lizards. (Data from Heatwole & Taylor 1987; Greer 1989) [W. Mumford]

distinct advantages over endothermy under the harsh and unpredictable conditions that prevail in deserts (Schall & Pianka 1978). By means of this thermal tactic, snakes and lizards can conserve water and energy by becoming inactive whenever difficult physical conditions occur, such as during drought, the heat of midday, or shortages of resources. Birds and mammals must sustain these inhospitable periods at a substantially higher metabolic cost. Ectothermy thus confers lizards with the ability to capitalise on scant, unpredictable resources.

Water also has an important role in the ecology of squamates. Australia is largely desert and there are some unique adaptations to aridity among its desert lizards. Noteworthy is the imbibing of water from moist sand by the thorny devil, *Moloch horridus* (Pl. 5.6). The interscalar spaces are arranged in such a way that they carry water by capillarity from the moist sand to the corner of the lizard's mouth (Bentley & Blumer 1962).

Weather may influence different segments of the population differently. Differential survival of one sex over the other would alter sex ratios in the population. The egg stage may be particularly vulnerable. For example, Bustard (1968d) noted impairment of hatching success of eggs of the gecko *Gehyra*

variegata when rainfall was slight during the incubation period, and Cogger (1978) found that *Ctenophorus fordi* suffered high egg mortality during a hot, dry summer.

Squamates are influenced by the geometry of their habitat, and population densities may reflect availability of particular structures. *Ctenophorus nuchalis* requires a small bush for a sun perch in close proximity to a taller shade perch (Heatwole 1970). Areas where perches are too widely spaced are unsuitable for these lizards and they do not occur. Thus, the population density of this species is partly controlled by spacing of vegetation. Similarly, the densities of the gecko *Oedura ocellata* is related to the availability of loose bark under which it shelters; almost all suitable sites are occupied (Bustard 1971). Densities of the water skink, *Eulamprus quoyii*, correlate well with the abundance of rocks in open areas. These structures are important as basking platforms (Law & Bradley 1990) and as shelter from predators (Daniels & Heatwole 1990).

Squamates that construct their own burrows are not so restricted by naturally occurring shelter and can extend their capacity to exploit their environment. The example of *Ctenophorus nuchalis* cited above is relevant. This species tires at midday after a dash of only a few metres and it digs burrows at intervals between its sun and shade perch, thereby always having available a retreat within its sprint distance (Heatwole 1970).

The complex burrow system of *Egernia striata* is a very important feature of the Australian sandy deserts (Pianka & Giles 1982). These skinks dig elaborate tunnels which are used as diurnal retreats by many species of nocturnal geckos, including *Heteronotia binoei*, *Nephrurus levis*, and *Rhynchoedura ornata*. They are also exploited as refuges by various diurnal lizards, such as *Ctenophorus isolepis* and *Varanus eremius* and the large elapid snakes, *Pseudechis australis* and *Pseudonaja nuchalis*. The burrows are elaborate, with several interconnected openings often as far as a metre apart, and vaguely reminiscent of a tiny rabbit warren. Most of the removed sand is piled up in a large mound outside one 'main' entrance (Pianka & Giles 1982).

A sympatric, but smaller species, *Egernia inornata*, digs a much simpler burrow, consisting of a U-shaped tube with but one arm of the 'U' open. The other arm of the 'U' typically stops just below the surface of the ground and can be broken through for use as an emergency escape hatch. The entrances to tunnels of *E. inornata* face north or north-west. Whereas *E. striata* is mainly active in summer, *E. inornata* is active during cooler periods by virtue of being crepuscular and less seasonal. Sitting in a northward-facing burrow entrance during the day would expose it to the relatively warm northern sky. Thus, the interspecific difference in orientation of burrows between these two species may reflect their differences in seasonality and activity period.

Foraging and Diet

Many predators attack their prey from ambush, but others usually hunt while on the move. These two modes of foraging have been called the 'sit-and-wait' versus the 'widely-foraging' tactic, respectively (Pianka 1966). Of course, these designations are somewhat artificial, although numerous animal groups seem to fall rather naturally into either one category or the other. For example, agamids and geckos primarily sit and wait for their prey, whereas many skinks forage widely. Some species are more versatile, such as the scincid *Ctenotus taeniolatus*, which uses both foraging tactics; juveniles spend proportionately more time in active foraging than do adults (Taylor 1986). The water skink, *Eulamprus quoyii*, is an active forager on land but adopts a sit-and-wait tactic at the water's edge when feeding on aquatic prey (Daniels 1987).

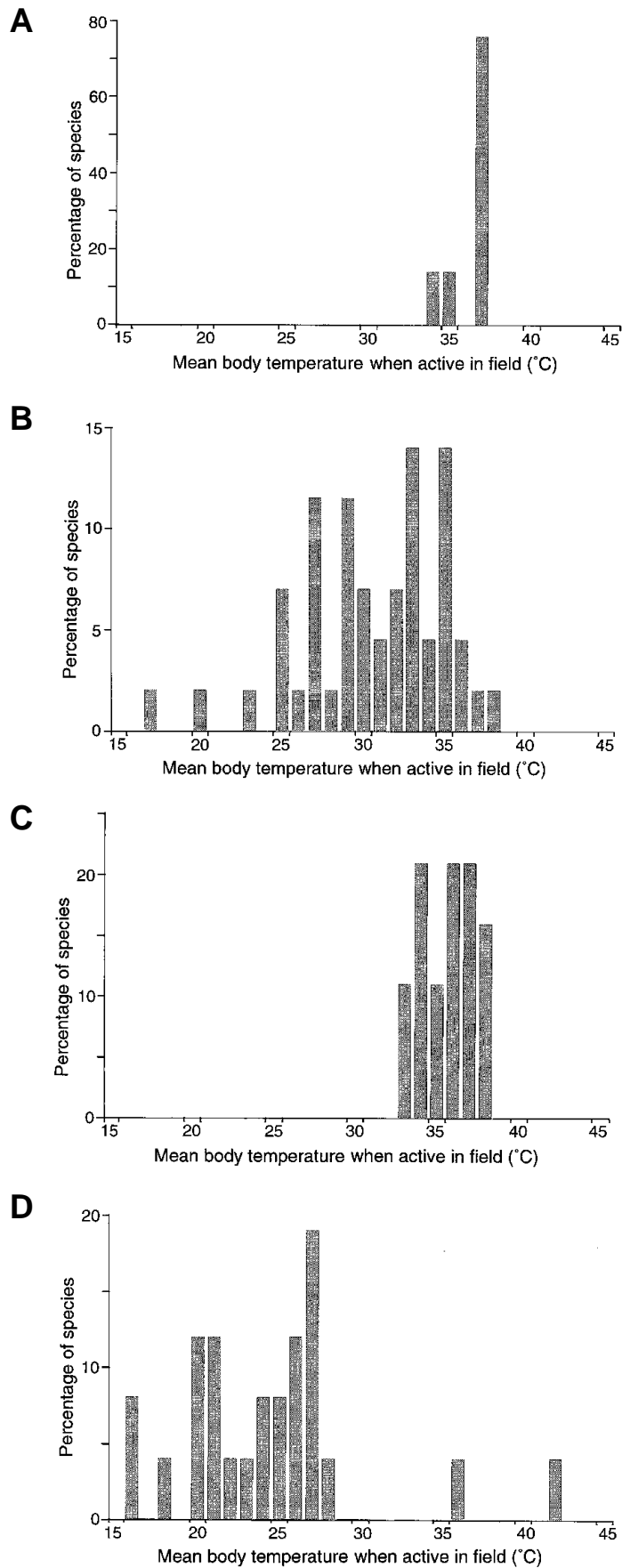


Figure 25.3 Frequency distribution, by family, of mean body temperature for lizards active in the field. **A**, Varanidae; **B**, Scincidae; **C**, Agamidae; **D**, Gekkonidae. (Data from Heatwole & Taylor 1987; Greer 1989)

[W. Mumford]

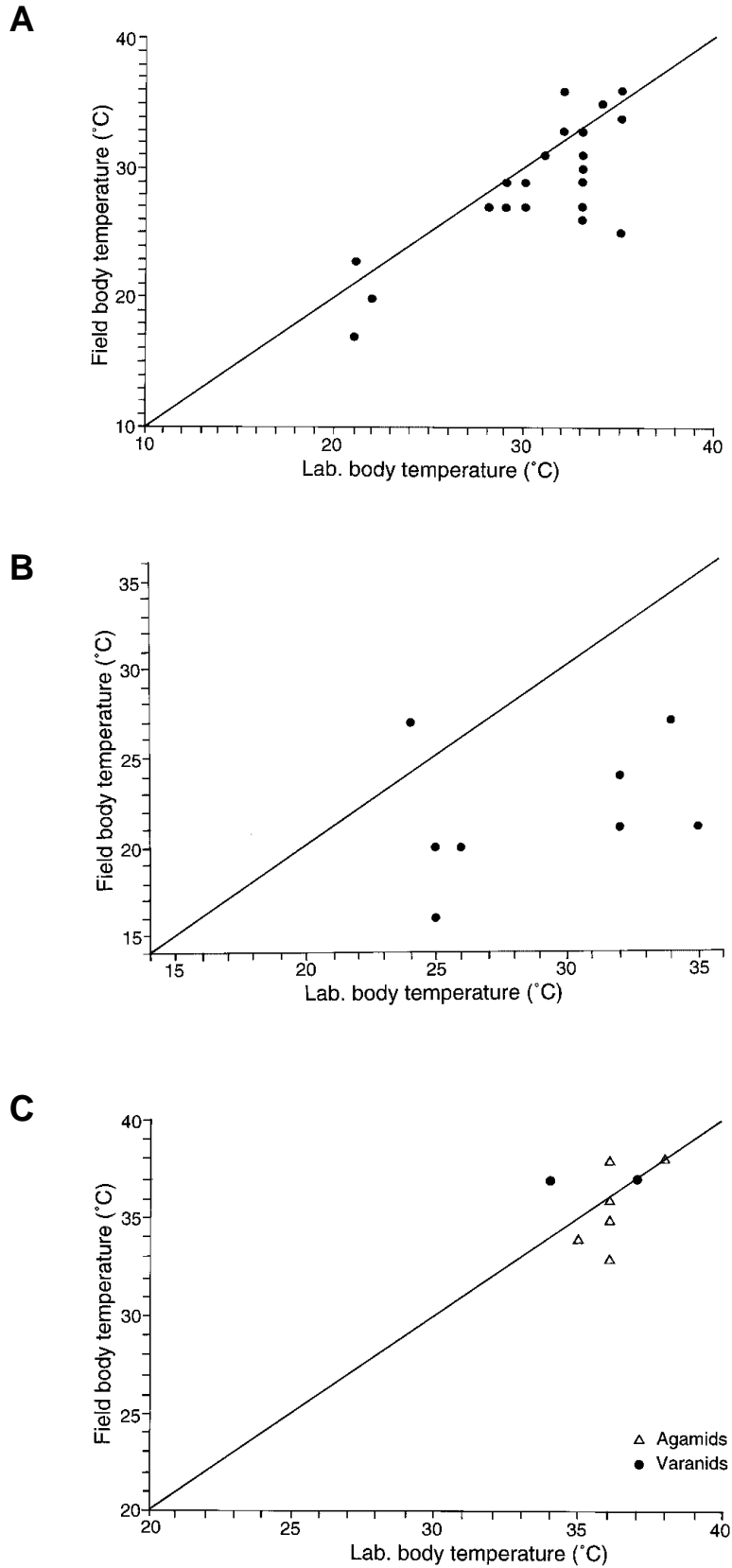


Figure 25.4 Relationship between mean body temperature of lizards active in the field and mean temperature preferred in a laboratory gradient. The diagonal line indicates equality of field and laboratory temperatures. **A**, Scincidae; **B**, Gekkonidae; **C**, Agamidae, Varanidae. The data are a subset of the data used in Fig. 25.3. (Data from Heatwole & Taylor 1987)

[W. Mumford]

Desert sites in North America and Australia support similar numbers of species of sit-and-wait foragers, whereas this mode of foraging is distinctly impoverished in the Kalahari (Pianka 1986). Markedly fewer species forage widely in western North America and in the Kalahari than in the Australian deserts. Intercontinental comparisons of proportions of total species in various foraging modes are also instructive. A full 60% of North American lizard species are sit-and-wait foragers, compared to only 16% in the Kalahari and 18% in Australia.

Overall energy budgets of widely-foraging species are approximately half as great again as those of sit-and-wait species (Huey & Pianka 1981). As would be expected, sedentary foragers tend to encounter and eat rather mobile prey whereas more active, widely-foraging predators consume less active prey.

Because they are moving more or less continually, widely-foraging species tend to be more visible, and therefore suffer higher predation rates. Widely-foraging species fall prey to lizard predators that hunt by ambush whereas sit-and-wait lizard species tend to be eaten by predators that forage widely, generating "crossovers" in foraging mode between trophic levels. Widely-foraging lizard species are also more streamlined and have longer tails than sit-and-wait species (Huey & Pianka 1981).

Another spin-off of foraging mode involves reproductive tactics. Clutch sizes of widely-foraging species tend to be smaller than those of sit-and-wait species, probably because the former simply cannot afford to weight themselves down with eggs to as great an extent as can the latter (Vitt & Congdon 1978). Foraging style constrains reproductive prospects.

Most Australian lizards are opportunistic, generalised insectivores. However, some are dietary specialists, eating only a very narrow range of prey items. For example, among pygopodids, *Lialis burtonis* (Pl. 4.10) eats principally small skinks (Patchell & Shine 1968a, 1968c) and *Pygopus nigriceps* (Pl. 4.12) eats more scorpions than most other lizards. The diet of the agamid *Moloch horridus* is restricted to ants (Pianka & Pianka 1970). Other species are termite specialists, including the nocturnal geckos *Diplodactylus conspicillatus* and *Rhynchoedura*, as well as some diurnal skinks (*Ctenopus* species) (Pianka 1969c). Food specialisation on termites and ants is economically feasible because these social insects normally occur in a clumped spatial distribution and hence constitute a concentrated food supply. Still other lizard species, while not quite so specialised, also have narrow diets.

Most lizards have much more catholic diets. Thus, Australian goannas include arthropods, frogs, reptiles, birds, mammals and carrion in their diet and some extend their prey to fish as well (Table 25.1). Diet varies interspecifically, especially between semi-aquatic and terrestrial species, and within a species differs seasonally and geographically (Shine 1986d). Pianka (1968, 1970a, 1970b, 1971b, 1982) tracked four species (*Varanus giganteus*, *V. gouldii*, *V. tristis* and *V. eremius*) as a means of studying their foraging. All ranged widely, and daily forays typically covered a distance of a kilometre. *Varanus gouldii* (Pl. 9.10) appeared to encounter most of its food by digging, whereas the tracks of *V. tristis* usually led almost directly from tree to tree, which presumably they climbed in search of food. *Varanus eremius* is attracted to fresh holes and diggings, and almost invariably will visit any man-made digging within a day or two. In a typical foraging run, an individual *V. eremius* often visits and goes down into several burrows belonging to other lizard species, especially the complex burrow systems of *Egernia striata*. In contrast to *V. gouldii*, it seldom does its own digging, but rather catches its prey above ground. Its tracks have been observed intercepting those of another smaller lizard with evidence of an ensuing tussle, and they have been seen to attack another lizard from ambush.

Table 25.1 Diets of some Australian varanid lizards, expressed as the percentage of items by number in the stomach. Populations of *Varanus gouldii*, *V. mertensi*, *V. mitchelli* and *V. panoptes* sampled from northern and western Australia are denoted by (a) and (b) respectively.

Species	Mammals	Birds	Lizards	Snakes	Reptile eggs	Frogs	Fish	Aquatic insects	Non-aquatic insects	Other aquatic arthropods	Other non-aquatic arthropods	Other	Source	
<i>Varanus brevicauda</i>	–	–	–	–	15	–	–	–	85	–	–	–	Pianka 1970a	
<i>Varanus caudolineatus</i>	–	–	20	–	–	–	–	–	63	–	16	2	Pianka 1969a	
<i>Varanus eremius</i>	–	–	35	–	–	–	–	–	50	–	3	12	Pianka 1968	
<i>Varanus gilleni</i>	–	–	63	–	–	–	–	–	38	–	–	–	Pianka 1969a	
<i>Varanus gouldii flavirufus</i>	<1	<1	10	–	37	–	–	–	39	–	11	–	Pianka 1970b	
<i>Varanus gouldii</i>	(a)	<1	–	3	<1	7	2	<1	–	79	<1	6	–	Shine 1986d
	(b)	–	14	7	–	–	–	–	–	57	–	21	–	Shine 1986d
<i>Varanus mertensi</i>	(a)	<1	<1	–	<1	4	4	3	20	6	56	4	–	Shine 1986d
	(b)	1	1	–	–	2	5	5	15	36	32	2	–	Shine 1986d
<i>Varanus mitchelli</i>	(a)	1	1	1	–	2	1	37	4	33	5	13	1	Shine 1986d
	(b)	–	–	–	–	3	5	14	3	22	–	54	–	Shine 1986d
<i>Varanus panoptes</i>	(a)	1	<1	3	<1	2	7	1	<1	80	1.5	4	–	Shine 1986d
	(b)	–	5	5	–	–	16	–	–	68	–	5	–	Shine 1986d
<i>Varanus tristis</i>	–	2	8	0	12	–	–	–	76	–	–	2	Pianka 1971b	

A surprising number of Australian lizards are omnivorous and include plant food as either a supplementary or principal component of their diet. For example, up to 82% of the gut contents of *Egernia cunninghami* may be plant material (Barwick 1965), and skinks of the genus *Tiliqua* (Pl. 6.1, 6.3) are fond of fruit as well as of snails, arthropods and carrion. Among the agamids, *Pogona barbata* supplements its insect diet with flowers and soft herbage, and the water dragon, *Physignathus lesueurii*, feeds on fruits, insects and frogs (Cogger 1992).

Within a species there may be temporal and spatial variation in composition of the diet. The type of food may change opportunistically in response to fluctuating prey abundances and availabilities (Pianka 1986; Shine 1986c; Taylor 1986).

In an environment with a scant food supply, a consumer cannot afford to bypass many inferior prey items because mean search time per item encountered is long and expectation of prey encounter is low (MacArthur & Pianka 1966). In such an environment, a broad diet maximises the return per unit effort, and favours generalisation. In a food-rich environment, however, search time per item is low since a foraging animal encounters numerous potential prey items. Under such circumstances, substandard prey items can be bypassed economically because expectation of finding a superior item in the near future is high. Hence, rich food supplies favour selective foraging and lead to narrow food niche breadths. Some lizards eat a greater diversity of foods in dry years (presumably times of low food availability) than in average ones, but contract their diet during periods of prey abundance (Pianka 1970c). The winged alates of termites, which appear in

huge numbers after heavy summer rains, can form the sole food of desert lizards, even for species that do not normally consume termites. During such fleeting moments of great prey abundance, there is little, if any, competition for food and dietary overlap among members of the assemblage may be nearly complete.

Biologically significant variation occurs between species in utilisation of certain relatively minor food categories. Thus, Hemiptera-Homoptera, mantids-phasmids and various flying insects, such as wasps, Diptera, and Lepidoptera tend to be better represented in the diets of climbing lizard species than they are among terrestrial species. Likewise, geckos tend to consume more nocturnal arthropods (scorpions, crickets, roaches, and moths) than do most diurnal species, although certain diurnal lizards capture nocturnal prey in their diurnal retreats (Huey & Pianka 1983). Such prey items are thus indicators of spatial and temporal patterns of activity.

Relatively few foods dominate diets of desert lizards (Pianka 1986). Prey resource spectra are broadly similar between three continents, although notable quantitative differences occur. In North America, 84% of the diet comprises seven food groups. They are, in decreasing order by volumetric importance, beetles, termites, insect larvae, grasshoppers plus crickets, ants, plant materials, and vertebrates. In the Kalahari, termites, beetles and ants far outweigh all others, and form 71% of the total. In Australia, the five most important categories comprise 77% of the total. In decreasing order of importance, they are vertebrates, termites, ants, grasshoppers plus crickets, and beetles. The same three categories, termites, beetles and ants, constitute major prey items in all three continental desert-lizard systems. Termites assume a disproportionate role in the Kalahari, as do vertebrate foods in Australia, which are largely a reflection of varanid diets.

Whereas most lizards eat arthropods, primarily insects, Australian snakes generally prey upon vertebrates (Table 25.2). There are exceptions (Mushinsky 1987). Australian pythons feed largely on birds and mammals with other vertebrates being of lesser importance, and then primarily in the diet of juveniles (Slip & Shine 1988a). Many of the Australian elapids have broad diets including frogs, reptiles and mammals. Shine (1977a, 1987d) found that differences in proportions of these categories in the diet is the result of opportunistic feeding and depends largely on habitat. Snake species living in wetter habitats eat more frogs whereas those from drier habitats eat more lizards. Mammals and birds are less common because of relative unavailability in preferred habitats. There are also age differences, with juveniles tending to take lizards and frogs rather than mammals or birds (Shine 1989).

There are, however, specialist feeders. Many of the smaller elapid species eat lizards, especially skinks (Table 25.2). The taipan, *Oxyuranus scutellatus*, feeds mainly on small mammals, the bandy-bandy, *Vermicella annulata*, (Pl. 8.4) feeds solely on typhlopids (Shine 1980d) and some species of *Simoselaps* feed exclusively on eggs of squamates (Scanlon & Shine 1988). In addition, some species depart from the norm and eat invertebrate prey instead of, or in addition to, vertebrates. Some of the small Australian elapids eat arthropods (Table 25.2) and typhlopids are specialist feeders on ants and termites (Cogger 1992).

Australia has an unusually high number of aquatic snake species, including the families Acrochordidae, Colubridae (*Amphiesma* and various genera of the subfamily Homalopsinae), Laticaudidae and Hydrophiidae, in all about 40 species. Most of these eat fish and/or crustaceans (McCosker 1975; Cogger 1992). Some of the freshwater ones include frogs in their diet. The Australian sea snakes *Emydocephalus annulatus* and *Aipysurus eydouxii* feed solely on fish eggs (Voris 1966; Heatwole 1987).

25. NATURAL HISTORY OF THE SQUAMATA

Table 25.2 Diets of Australian snakes, summarised by genus. The number of taxa indicates the number of species, with the number of populations in parentheses. Diet data, expressed as the percentage of number of items in the stomach, are shown as the maximum and minimum percentages for species within each genus. The median percentage is shown in parentheses for those genera in which data for 6 or more species and/or populations were summarised.

Taxon	No. of taxa	Mammals	Birds	Lizards	Snakes	Reptile eggs	Frogs	Fish	Inverts	Source
TYPHLOPIDAE										
<i>Ramphotyphlops</i>	4	–	–	–	–	–	–	–	100	Shine & Webb 1990
BOIDAE										
<i>Aspidites</i>	2	6–44	3	47–81	3–10	2–3	–	–	–	Shine & Slip 1990
<i>Chondropython</i>	1	44	56	–	–	–	–	–	–	Shine & Slip 1990
<i>Liasis</i>	7	33–100	3–25	11–67	5	–	5–33	–	–	Shine & Slip 1990
<i>Morelia</i>	3(4)	69–100	8–10	17–23	–	–	–	–	–	Shine & Slip 1990; Slip & Shine 1988a
ACROCHORDIDAE										
<i>Acrochordus</i>	1	–	–	–	–	–	–	100	–	Shine 1986b
COLUBRIDAE										
<i>Boiga</i>	1(3)	7–47	19–54	28–56	–	–	6–12	–	–	Shine 1991c
<i>Dendrelaphis</i>	1(3)	8	–	29–39	–	–	54–95	–	5	Shine 1991c
<i>Tropidonophis</i>	1(2)	2	–	4	–	–	94–98	2	–	Shine 1991c
ELAPIDAE										
<i>Acanthophis</i>	1	32	9	53	–	–	6	–	–	Shine 1980a
<i>Austrelaps</i>	1(6)	2–3	–	37–90	1–5	2	10–61	–	3–4	Shine 1977b, 1987d
<i>Cacophis</i>	3	–	–	93–100	2	–	6	–	–	Shine 1980a
<i>Demansia</i>	4	–	–	73–100	–	–	9–27	–	–	Shine 1980d
<i>Denisonia</i>	2	–	–	–	–	–	95–96	–	4–5	Shine 1983c
<i>Drysdalia</i>	1	2	–	44–100	–	–	5–53	–	3	Shine 1981b
<i>Echiopsis</i>	1	13	2	52	–	–	32	–	2	Shine 1982
<i>Furina</i>	1	–	–	100	–	–	–	–	–	Shine 1981a
<i>Hemiaspis</i>	1	–	–	65	–	–	35	–	–	Shine 1977a
<i>Notechis</i>	1	3	2	2	–	–	92	–	–	Shine 1977a
<i>Pseudechis</i>	5(13)	2–75(11)	3–18	14–75(39)	1–29(8)	5	15–86(60)	+	7–12	Shine 1977a, 1987b
<i>Pseudonaja</i>	7(11)	5–100(48)	1–3	24–100(46)	1–6	1–25	2–41(6)	–	–	Shine 1977a, 1989
<i>Rhinoplocephalus</i>	4	–	–	89–100	5–11	–	1–6	–	–	Shine 1984a, 1988a
<i>Simoselaps</i>	10	–	–	25–100(100)	–	25–100	–	–	–	Shine 1984b
<i>Suta</i>	9(10)	–	–	59–100(98)	1–17	1–14	3–5	–	–	Shine 1977a, 1983c, 1988a
<i>Tropidechis</i>	1	48	7	4	–	–	41	–	–	Shine & Charles 1982
<i>Vermicella</i>	1	–	–	–	100	–	–	–	–	Shine 1980e

Most of the Australian elapids and pythons are active foragers. For example, the genus *Demansia* (Pl. 8.6; Shine 1980d) is convergent with diurnal, surficial colubrids in ways of facilitating chase and capture of fast-moving prey. By contrast, the highly camouflaged death adder, *Acanthophis antarcticus*, is an ambush strategist and in this regard is convergent with viperids (Shine 1980c) as is the boid *Morelia spilota* (Slip & Shine 1988a).

Acanthophis antarcticus is also the only Australian elapid known to use ‘caudal-luring’ (Fig. 35.1; Chizar, Boyer, Lee, Murphy & Radcliffe 1990). The tail of juveniles, in contrast to the otherwise cryptic colouration, is banded and resembles a caterpillar. On the approach of potential prey, the snake wriggles the tip of the tail in a worm-like fashion to lure its victim within striking range. The only lizard known to practise caudal luring is the snake-like, legless pygopodid *Lialis burtonis* (Murray, Bradshaw & Edward in press). Its tail is not distinctively marked.

LIFE HISTORY

Most lizards and snakes lay eggs, but some species retain their eggs internally and give birth to living young. Oviparous species may retain the eggs for varying times and lay them at different developmental stages; viviparity is merely one end of a continuum in which the eggs are retained to the hatching stage (Shine 1983b). Viviparity, or live-bearing, has arisen independently almost 100 times among squamates, even several times within a single genus (Shine & Bull 1979; Shine 1985a). Viviparity and egg retention probably has evolved because of the advantage it confers in enabling successful reproduction in cooler regions at high elevations and high latitudes (Tinkle & Gibbons 1977; Shine & Bull 1979) and it may be a current determinant of geographic distributions (Shine 1987b). In the south-eastern highlands of Australia, viviparous skinks can maintain temperatures 7°C higher than the nest temperatures of oviparous skinks and accordingly produce young a month earlier than the egg-laying forms (Shine 1983d).

Some species reproduce only once every second or third year, others but once each year, while still others lay two or more clutches per year. A multivariate statistical analysis of life history patterns identified the same three clusters among both snakes and lizards (Dunham, Miles & Reznick 1988)—single brooded oviparous species, multiple brooded oviparous species, and single brooded viviparous species. In addition, a fourth cluster emerged for a few biennial viviparous lizards and snakes.

Among Australian species (Heatwole & Taylor 1987), agamids are oviparous and generally have two, or even three, clutches per year. Geckos are oviparous and have only one clutch. Skinks have single clutches each year; tropical species are oviparous but both oviparity and viviparity are represented among temperate ones. Most Australian elapids are viviparous with only one annual brood, but some such as *Vermicella* (Shine 1980d) and *Pseudonaja* (Shine 1977b) are oviparous, and the latter may have more than one clutch per year. Females of *Tropidechis* (Shine & Charles 1982) and of the hydrophiid sea snake *Aipysurus laevis* (Burns 1985) only reproduce every second year.

Average clutch size varies from one egg to 50 or more among different species of lizards and snakes (Fitch 1970). Clutch size is fixed at one or two eggs in certain families (geckos, pygopodids) and genera. Across species, modal clutch size among lizards is two, whereas it is six to eight among snakes (Fitch 1970). Greer (1989) reviewed clutch sizes in Australian lizards, and reported ranges of one to three in pygopodids, one or two in geckos, two to 35 in varanids and one to 35 in agamids. Skinks had clutch sizes of one to 11, except in *Hemisphaeriodon gerrardii* which has been reported to have clutches up to 53

eggs. Values for elapid snakes tended to be higher than for lizards, and ranged from five to 38, except for the low clutch size of two to seven eggs in *Suta gouldii* (Heatwole & Taylor 1987). Larger species tend to have larger clutch sizes than smaller species (James & Shine 1988) (Fig. 25.5).

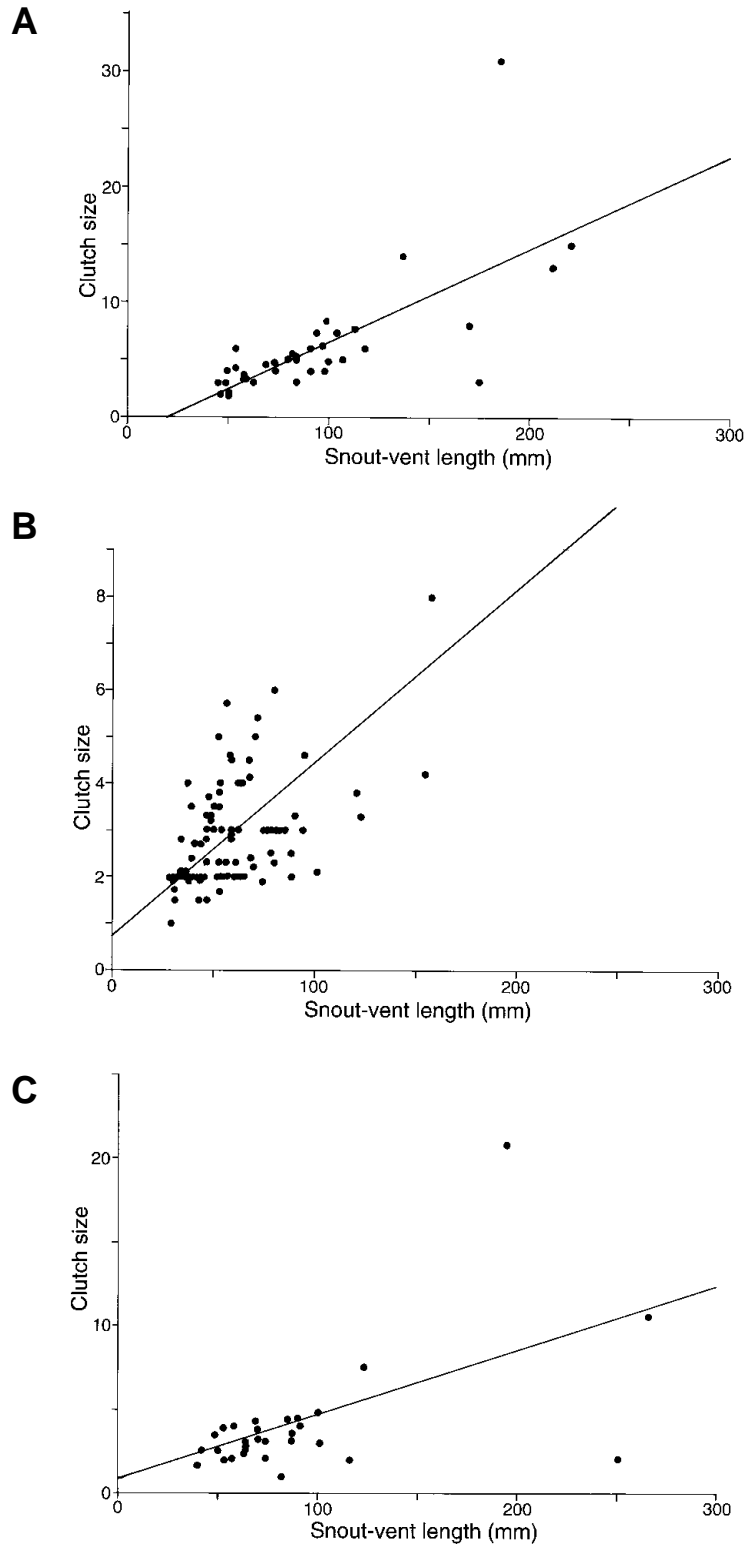


Figure 25.5 Relationship of mean clutch or brood size to mean body length of adult females of Australian skinks. **A**, Agamidae, all oviparous; **B**, Scincidae, oviparous; **C** Scincidae, viviparous. (Data from Greer 1989) [W. Mumford]

Substantial spatial and temporal variation in clutch size exists within species. For example, in the double-clutched agamid, *Ctenophorus isolepis*, the average size of 67 first clutches (3.01 eggs, August to December) was distinctly smaller than that for 41 second clutches (3.88 eggs, January to February) (Pianka 1971a). Females increase in size during the season, and, as in most lizards and snakes (Heatwole & Taylor 1987; Seigel & Ford 1987), larger individuals tend to lay larger clutches. Interestingly, these same females appear to invest relatively more in their second clutches than they do in their first clutch. Average volume for 25 first clutches was only 11.2% of female weight, but increased to 15.1% in 15 second clutches (Pianka & Parker 1975b).

Changes in fecundity with fluctuations in food supplies and local conditions from year to year or location to location are known. Females tend to lay larger clutches in years with above-average precipitation and presumably ample food supplies (Hoddenbach & Turner 1968; Pianka 1970c; Parker & Pianka 1975; Dunham 1980).

The bulk (weight or volume) of a clutch or litter mass, expressed as a fraction of a female's total body weight is known as 'relative clutch mass', or RCM. It ranges from as little as 4 to 5% in some species up to 20 to 30% in others. Ratios of clutch or litter weight to female body weight correlate strongly with various energetic measures (Ballinger & Clark 1973; Vitt 1977) and have been used as crude indices of a female's instantaneous investment in current reproduction. In Australia, tropical lizards have about 20% lower relative clutch masses than do those from the temperate zone (James & Shine 1988).

The size (or weight) of an individual oviducal egg or newborn progeny is an inverse measure of the extent to which a juvenile lizard must grow to reach adulthood. It varies widely among lizards, from 1 to 2% up to 17% of adult weight (Pianka 1986). Small species of snakes have a greater ratio of offspring size to adult size than do larger species (Shine 1978a). Species that protect their offspring by egg-brooding or which bear living young produce larger, though fewer, progeny than related oviparous species lacking parental care (Shine 1978c).

Any two components of the triad of clutch size, female reproductive investment, and expenditure per progeny uniquely determine the third. However, the forces of natural selection moulding each of these differ substantially. Clutch or litter weight presumably reflects an adult female's best current investment tactic in a given environment at a particular moment, whereas expenditure on any given individual progeny is probably more closely attuned to the average environment to be encountered by a juvenile. Clutch or litter size is thus the direct result of the interaction between an optimal parental reproductive tactic and an optimal juvenile size, and clutch size is simply the ratio of the former divided by the latter.

Food-specialisation may be a factor in this interaction. Among Australian geckos, species with relatively restricted termite diets tend to lay comparatively larger eggs and hence have higher expenditures per progeny than do those with more catholic diets (Pianka & Pianka 1976). Habitat type also may be important. Shine (1988b) found that the aquatic species in each of four lineages of snakes had lower reproductive investments and carried the clutch further anteriorly in the body than did terrestrial ones. He suggested that the important role of the posterior part of the body in swimming is a constraint on the weight of young that can be carried.

Timing reproduction so that young begin life under conditions most favourable for their survival and growth has obvious selective advantage, and clearly such timing varies latitudinally and with patterns of seasonal change. Heatwole & Taylor (1987) recognised 11 different kinds of reproductive cycles in Australian squamates depending on the phenology of spermatogenesis, ovulation and

mating in relation to seasons or to wet and dry periods. In most tropical areas, squamates tend to breed in the wet season. However, in Australia, the wide variety of reproductive cycles includes year-round breeders, wet season breeders and even dry season breeders (James & Shine 1985).

In terms of reproductive cycle, perhaps the most unusual Australian squamate is *Ctenophorus maculosus*, in which mature males mate with mature females in spring, but with first-year ones in late summer which apparently retain the sperm until they reach sexual maturity the following spring (Mitchell 1973).

Timing of reproduction may vary with yearly differences in the triggering environmental cues. In an eight-year study, Bradshaw, Saint Girons & Bradshaw (in press) found that *Ctenophorus nuchalis* and *C. caudicinctus* from the same geographic area responded in different ways to annually variable patterns of rainfall. As a result there were some years of breeding synchrony between these two species but they were out of phase in other years.

Growth rate in squamates varies interspecifically, between the sexes and with age, nutritional state and extent of stored energy (Andrews 1982). It is usually rapid in hatchlings or newly born, declines toward sexual maturity and thereafter is even slower until maximum size is attained. Growth is partly influenced by temperature, moisture, appetite and availability of food but may also be controlled by intrinsic factors (see Heatwole & Taylor 1987).

In *Ctenophorus ornatus* growth rates are variable (Bradshaw 1971; Baverstock 1975). In favourable years mortality is similar between rapidly growing and slowly growing lizards. During cold winters slow-growers have high mortality but are relatively unaffected by long, dry summers. The reverse is true of the fast-growing ones which are cold-hardy but sensitive to drought. When an unusually hot, dry summer followed an exceptionally cold winter (a rare event) mortality was high and the populations declined (Bradshaw 1981).

Weather may influence different segments of the population differently. Differential survival of one sex over the other would alter sex ratios in the population. The egg stage may be particularly vulnerable (Packard & Packard 1988). For example, Bustard (1968d) noted impairment of hatching success of eggs of the gecko *Gehyra variegata* when rainfall was slight during the incubation period, and Cogger (1978) found that *Ctenophorus fordi* suffered high egg mortality from desiccation.

Longevity and age of attainment of sexual maturity varies widely among species of squamates. Some species of lizards are essentially annuals. They reach maturity early and many adults of a given year class die by the time their offspring mature. Accordingly, there are marked shifts in population structure. Examples of short-lived Australian species are *Ctenophorus isolepis* (Pianka 1971c) and *Ctenophorus fordi* (Cogger 1978). Other species mature slowly and are long-lived, and intermediates lie along the spectrum between these extremes. *Egernia cunninghami* lives for eight years or longer (see Heatwole & Taylor 1987) and sometimes groups of at least three generations can be observed living together in crevices in limestone outcrops. The 'family groups' of *Egernia stokesii* may also include multiple age groups (Pl. 6.5). Australian snakes may be unusual, as Shine (1978a) noted that six species he studied reached sexual maturity earlier than most previously-studied snakes from other continents.

Within a given species, females may mature later than males. Shine (1978a) suggested that this arises from two selective pressures. The first of these is fecundity, which is proportional to body size in females (but not in males) and therefore larger females tend to leave more offspring. Secondly, early maturation and consequent production of small clutches may not warrant the considerable risks associated with reproduction that are peculiar to females and which are independent of body size.

In squamates the two sexes often differ in adult size, and in some sexually dimorphic species males are larger, in others the females are. The difference arises either by both sexes growing at equal rates until sexual maturity is reached and then one sex continuing to grow, or the larger sex showing faster growth rates at an early age, before sexual maturity (Andrews 1982). In *Acrochordus arafurae*, even neonates display sexual dimorphism in size (Shine 1986d). The ultimate causes of sexual differences in size are probably variable and include both social and ecological factors. Shine (1978b) found a high correlation between male combat in snakes and the occurrence of sexual dimorphism in size in which males were the larger sex. Male *Pseudechis porphyriacus* engage in combat and displace rival courting males and even disrupt mating couples (Shine, Grigg, Shine & Harlow 1981), and large male size may be an advantage in such struggles. Dimorphism in which females are larger can be attributed to the greater fecundity attendant on large size in females, noted above. This generalisation does not fit all snakes, as in some species, body size seems to be related to sex-specific differences in trophic niche, where the two sexes differ in food habits, head morphology and/or foraging sites (Shine 1986c; Camilleri & Shine 1990).

Numbers of males and females are usually, though not always, equal at hatching or birth. The sex ratio may become skewed at a later age. Often it is difficult to ascertain whether this has resulted from differential mortality, or is an artifact of behavioural differences between the sexes (Parker & Plummer 1987). The greatest discrepancy in sex ratios occurs in parthenogenetic species, in which females lay fertile eggs without having been inseminated by a male. Parthenogenesis is rare in squamates although it is scattered over a number of families. In Australia, three genera of geckos (*Heteronotia*, *Nactus* and *Lepidodactylus*) are known to have species that either wholly lack males or have parthenogenetic populations as well as bisexual ones (Moritz & King 1985).

Predators and Defence

Predation is seldom seen by observers and is difficult to quantify. Indeed, it is seldom known how many species of predators a given species has, or what their relative importances are. The only attempt to provide such information for an Australian species is that of Daniels & Heatwole (1984). They listed 102 known or potential predators for the semi-aquatic skink, *Eulamprus quoyii*, of which 14% were believed to have a significant impact.

Most commonly, squamates respond to predators by remaining motionless, thereby preventing detection by visually hunting predators, by flight, or by presenting an aggressive display either as bluff or as an overt attack. These are not mutually exclusive and may occur in sequence within a given species (Greene 1988).

Cryptic colouration is common in Australian squamates, but perhaps is illustrated best by the death adder, *Acanthophis antarcticus*, a species seldom seen unless nearly trodden upon. Mouth-opening displays by various agamids and other squamates are well known. *Pogona barbata*, for example, opens the mouth to expose its yellow lining and erects the gular region as a 'beard' (Pl. 5.8; Throckmorton, de Bavay, Chaffey, Merrotsky, Noske & Noske 1985). Tongue protrusion in the scincid genus *Tiliqua* (Pl. 6.2, 6.4), erection of the neck frill in the frill-necked lizard (*Chlamydosaurus kingii*, Pl. 5.9), and rearing up and spreading the hood in large elapids (Fig. 25.6A; Pl. 8.8) are remarkable and all have become famous. In the last example real danger underlies such threats. The bandy-bandy, *Vermicella annulata*, (Fig. 25.6B; Pl. 8.4) reacts to disturbance by elevating its conspicuously banded body into vertical loops (Bustard 1969b).

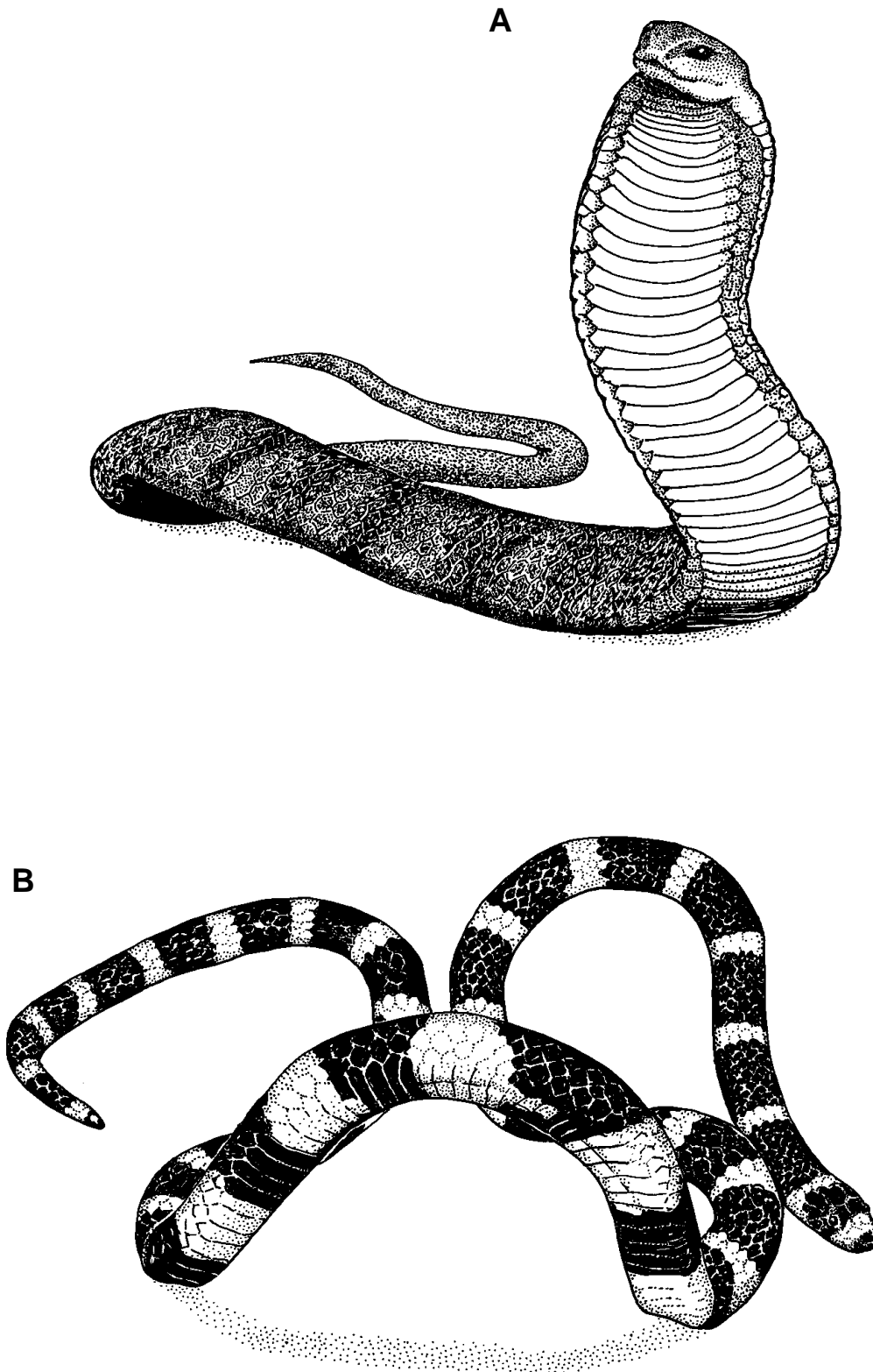


Figure 25.6 Displays of snakes. **A**, a tiger snake, *Notechis scutatus* rears up and flattens its neck in the typical aggressive display of elapids; **B**, a bandy-bandy, *Vermicella annulata*, elevates part of its body in a defensive display typical for this species. (A, from photo by David Stammer; B, from photo by Richard Shine) [M. Cilento]

If one tactic is ineffective, switching to another may be necessary, and timing of such switches may be crucial for survival. For example, once detected, a cryptic species may need to flee. If flight is left too late escape may no longer be possible, but if initiated too early, it may attract attention prematurely. The distance that an animal will permit a potential predator to approach before flight is called the 'approach distance'. In some lizards it varies inversely with degree of crypsis, well-camouflaged species having a shorter approach distance than those which are more conspicuous (Heatwole 1968). Bauwens & Thoen (1981) found that gravid females tend to rely on crypsis longer than males or non-gravid females and also stay closer to safe retreats. These behaviours compensate for slower locomotion occasioned by the load of eggs.

Approach distance also varies with temperature in a compensatory way. Lizards initiate escape earlier when they are cold and sluggish than when they are at higher temperatures and have faster responses (Rand 1964). *Ctenophorus nuchalis* allows closer approach when it is near a safe retreat, such as the entrance to its burrow, than when it is in the open (Heatwole 1970). Hertz, Huey & Nevo (1982) found that some agamids would flee when body temperatures were high enough to permit rapid running, but when colder would stand their ground and attack aggressively. This phenomenon also occurs in the Australian *Tympanocryptis cephalus* (Pianka pers. obs.).

Age and gender may influence the capacity of lizards to escape predators. Huey, Dunham, Overall & Newman (1990) studied variation in locomotor performance and showed that male lizards were faster than females, and that older adults had slightly greater stamina than young adults but were slower.

The immediate orientation and location of water skinks, *Eulamprus quoyii*, and the physical characteristics of their habitat, determine which of several escape tactics is used (Daniels & Heatwole 1990). Diversity of escape responses is higher in habitats which are structurally more diverse. Unmolested lizards usually face the water, and flee in the direction they are facing when disturbed. Running is energetically less taxing than either swimming or diving, and flight to the shelter of rocks is employed more often than aquatic escape. Where rocks are abundant they are used for escape more often than in less rocky areas. Escape to the water is less often employed where currents are swift. By choosing the least expensive option, in terms of energy, only a small part of their locomotor capacity is used in any given escape attempt, and leaves sufficient reserves for repeated attempts if necessary.

The tail is important in protection of many lizards against predation. This organ has diversified greatly and serves a wide variety of functions, including a role in locomotion and hence in escape from predators. Many climbing species, such as the Australian sandridge agamid *Gemmatophora longirostris*, have evolved extraordinarily long tails which serve as effective counterbalances. Tail removal experiments (Snyder 1962) have shown that such long tails also enable lizards to raise their forelegs up off the ground and to run on their hind legs alone, which is faster than tetrapodal locomotion. Prehensile tails are used as a fifth leg in climbing by some arboreal lizards.

Several Australian geckos of the genus *Diplodactylus* have glandular tails that secrete and store a smelly, noxious mucus. When disturbed, these lizards squirt large amounts of this sticky substance (Rosenberg & Russell 1980). Surprisingly, their tails are fragile and easily shed, though quickly regenerated. The related species *Diplodactylus conspicillatus*, which has a non-glandular and very stubby, bony tail, is a nocturnal termite specialist that hides in the vertical shafts of abandoned spider holes during the day. This gecko is thought to point head-downwards and use its tail to block off the tunnel. Similarly, a species of skink, *Egernia depressa*, wedges itself into tight crevices in mulga tree hollows and rocks, blocking off the entrance with its strong, spiny tail.

The tails of many species of lizards (especially among juveniles) are brightly coloured or otherwise conspicuous, and evidently function to lure a predator's attack away from the more vulnerable and less dispensable parts of the animal. The Australian desert skink, *Ctenotus calurus*, lashes and quivers its bright azure blue tail alongside its body continuously as it forages slowly through the open spaces between plants. Similarly, tiny *Morethia butleri* juveniles twitch their bright, red tails as they move around in the litter beneath *Eucalyptus* trees.

Some species can lose their tails voluntarily, or with minimal external force, a process known as autotomy. Many geckos, pygopodids and skinks exhibit autotomy, whereas most agamids, varanids and snakes do not. Lizards with tough tails usually cannot regenerate a very complete tail, whereas autotomous lizards quickly regenerate a new tail from the stub. Although re-grown tails are occasionally almost indistinguishable from the original externally, their internal support structure is cartilaginous rather than bony. Many autotomous lizards possess special adaptations for tail loss, including weak fracture planes within each tail vertebra, muscular attachments that facilitate autotomy and tail movement after dismemberment, as well as mechanisms for rapidly closing off blood vessels and healing.

The freshly dismembered tails of autotomous species, or pieces thereof, typically thrash around wildly. Writhing of autotomised tails distracts predators, thereby enhancing escape by the tail's erstwhile owner (Dial & Fitzpatrick 1983). When threatened, some species raise or move the tail making it a more likely target for attack than the rest of the body (Johnson & Brodie 1974).

Certain small predators, such as the pygmy varanids *Varanus gilleni* and *V. caudolineatus*, may actually 'harvest' the exceedingly fragile tails of geckos that are too large for them to subdue intact (Pianka 1969b). Some skinks, including many *Ctenotus* species, return to the site where their tail was lost and swallow the remains of their own tail! Few, if any, other vertebrates display auto-amputation and self cannibalism.

Temperature affects autotomy. Daniels (1984) found that cold *Oedura marmorata* retained the tail longer than warm individuals. By contrast, *Gehyra variegata* autotomises its tail more readily and parts with a greater portion of it, at both low and high temperature extremes than at intermediate temperatures (Bustard 1968b).

Tail size may also be important. Adults of *Oedura marmorata* have relatively larger tails than juveniles. They are better able to avoid predatory attacks by species of the dasyurid genus *Antechinus*, apparently because larger tails have a greater distractive quality than small ones when autotomised (Daniels, Flaherty & Simbotwe 1986).

Loss of the tail seems to disturb lizards surprisingly little, as individuals often resume basking and foraging within minutes, as if nothing had happened. There are longer term consequences, however. The tail is an organ of fat storage in many lizards and its loss depletes part of the energy reserve of the animal. Smyth (1974) and Taylor (1984) found that there was a significant reduction in number and/or energy content of eggs or young in skinks that had lost their tails in comparison with those with intact tails. When deprived of food, tailless *Oedura marmorata* have shorter survival times than those with complete tails (Daniels 1984). In periods of food shortage, the immediate advantage of autotomy in escaping predators would have to be balanced against the long-term disadvantage arising from loss of stored energy. Accordingly, under suboptimal conditions these geckos show a reluctance to autotomise. One might expect that lizards would conserve tail lipids by losing only that portion of the tail under attack. That expectation is not fulfilled in *O. marmorata*, which autotomises the entire tail regardless of the position of attack (Daniels 1985c).

Not all side-effects of autotomy are disadvantageous. In contrast to previous studies indicating locomotion was impaired by tail loss, Daniels (1983) found that *Oedura marmorata* increased its running speed, and presumably its ability to flee from predators, after autotomy. Different modes of escape may be differently affected by autotomy. In *Eulamprus quoyii* loss of the tail results in greatly reduced swimming speeds, but slightly increased running speeds (Daniels 1985a).

Tail-break frequency has been used to estimate intensity of predation, and in some species has been correlated with density of predators (for example, Pianka 1967). However, this method has numerous problems and limitations (Schoener 1979). Efficient predators that leave no surviving prey obviously will not produce broken tails, but nevertheless may exert substantial predation pressures. Broken and regenerated tails may therefore reflect lizard escape ability or predator inefficiency better than intensity of predation. Furthermore, conspecific fighting may lead to broken tails. In his review, Arnold (1988) noted that it is difficult to unravel the contributions of intraspecific conflict, age, predation efficiency and intensity, and ease of autotomy, and that this approach to predation rate had sampling, methodological and interpretive problems. He concluded that tail-break frequencies are often unreliable indices of predation; clearly this method should be used cautiously and only when sufficient data are available to assess independent effects on break frequencies, a condition that seldom applies.

Social Behaviour

The repertoire of social behaviour in squamates includes courtship and mating, aggression, parental care, and limited aggregation and communal activities. Australian species have received little attention in this regard in comparison with overseas species.

In lizards, courtship may involve elaborate posturing and displays. Often the same movements are involved in aggressive displays and whether mating or combat ensues depends on the sex of the individual toward which the display is directed, and/or the responses it makes. Brattstrom (1971b) has noted that head bobbing and fast waving of the forelimb in *Pogona barbata* is a challenge. If the individual towards which it is directed is a female mating may ensue, but if it is a male fighting may result unless the recipient male adopts a submissive posture and/or waves its forelimb slowly. Similar behaviour occurs in some other species of Australian agamids (Carpenter, Badham & Kimble 1970; Shine 1990). Male varanids exhibit 'shuddering' of the head when courting (Carter 1990).

Intraspecific aggression takes various forms. In many snakes aggression between males takes the form of rearing up by antagonists, which attempt to depress the head and neck of the opponent (Gillingham 1987). In the Australian elapids *Pseudechis porphyriacus* and *Austrelaps superbis* (Shine & Allen 1980; Shine *et al.* 1981) prolonged bouts of ritual combat occur between males, and direct attack, including biting, occurs. In lizards, aggression often centres around defense of a territory, and may involve females as well as males. It is widespread among Australian agamids and skinks (for example, see Brattstrom 1971b; Done & Heatwole 1977) and has been suggested for some geckos (Bustard 1968d, 1969a). Under conditions of crowding, defense of territories may break down and be replaced by a dominance hierarchy, with the more dominant individuals having the advantage in feeding, mating and selection of basking sites (Done & Heatwole 1977).

Selection of an appropriate ovipositional site and concealment of recently deposited eggs are both widespread in lizards and snakes and can be interpreted as rudimentary parental care, as it enhances survival of the young. In addition,

Shine (1988c) recognised four categories of post ovipositional parental care in squamates: the female defends the nest briefly against conspecific females; the female remains with the eggs and guards them against predators or pathogens; the female coils around the eggs and warms them by shivering thermogenesis, and protects them against predators; the female aids newly born or newly hatched young. Parental care among Australian squamates seems rare. Some Australian pythons coil around their eggs and incubate them (Slip & Shine 1988b). There is inconclusive, anecdotal evidence suggesting parental care in some varanids (Shine 1988c).

Most aggregations of squamates are seasonal or short-term (Gregory, Macartney & Larsen 1987). The spectacular denning of large numbers of snakes in winter, so characteristic of North America, is unknown in Australia, although the skink *Lampropholis guichenoti* has been reported in small winter hibernacula (Powell, Heatwole & Heatwole 1978). The whipsnake *Demansia psammophis* nests communally (Covacevich & Limpus 1972).

Home Range and Movements

Few species of terrestrial vertebrates wander randomly. Most restrict their activities to a discrete and familiar area, or to home ranges. In squamates home ranges often include one or more shelter sites, such as burrows or rock crevices, food sources and basking perches. They may overlap with the home ranges of other individuals of the same species, especially those of mates and young. A home range (or part of it) when defended against other individuals, is called a territory.

In general, snakes tend to have less well defined, and often larger, home ranges than do lizards of equivalent sizes. In both groups, but especially in snakes, an individual may remain in a small area for considerable time, before moving to a new home range some distance away (Shine & Slip 1988d). Juveniles frequently have smaller home ranges than adults, and the sexes may differ in average home range size. Gravid females may be especially sedentary (Shine 1979). Bradshaw (1971) studied a population of *Ctenophorus ornatus* in which juveniles emigrated from the area in which they hatched, probably because of harassment by adult males. They set up home ranges in marginal areas where predation upon them was high. The survivors returned to preferred habitat as sexually mature individuals one to three years later, replacing the previous generation, now in decline. Thus, there are 'adult' areas and 'juvenile' areas with individuals moving between them in ontogenetic shifts of home range.

Most home range data are from terrestrial, surficial species. The aquatic filesnake *Acrochordus arafurae*, has an exceptionally large home range (up to 4.7 ha) and individuals move on average 141 m during a single night during the wet season (Shine & Lambeck 1985). Information on burrowing snakes is practically non-existent.

Squamate Assemblages and Resource Partitioning

An assemblage is that part of a biotic community that is made up of all organisms of a particular taxon, such as the Squamata. Like the entire community, an assemblage has structure that can be characterised in terms of species richness (number of species), taxonomic composition, guild membership and equitability (apportionment of individuals among species) (Heatwole & Taylor 1987). Reviews of reptilian assemblages by Heatwole (1981c, 1982), Scott (1982), Pianka (1986) and Heatwole & Taylor (1987) indicate that species richness is affected by latitude, elevation, climate (rainfall, evapotranspiration, amount of sunshine), soil fertility, habitat diversity and structural complexity of the vegetation. Most assemblages are inequitable in that

they are characterised by a few abundant species and many less common ones. Various of these generalisations have received support from analysis of Australian assemblages (for example, Kitchener, Chapman, Dell & Muir 1980; Milewski 1981; Heatwole & Butler 1981).

Australian squamate assemblages from arid areas are richer than those from equivalent habitats on other continents (Pianka 1969b, 1973, 1985, 1986). Many factors have been postulated to account for this, and include: unpredictable precipitation; nutrient-poor soils; the unique hummock life-form and physical structure of *Triodia* (spinifex) grasses; abundant and diverse termite fauna; nocturnality; fossoriality; arboreality; habitat specificity; usurpation of ecological roles occupied by other taxa elsewhere; a complex fire-succession cycle that creates and maintains habitat heterogeneity via disturbance; biogeographic and historical factors (Pianka 1989).

Morton & James (1988) proposed a causal network relating a wide range of climatic, edaphic and biotic factors to the diversity of lizards in arid Australia (Fig. 25.7). In their network, unpredictable rainfall and nutrient-poor soils result in scant and erratic primary production, favouring *Triodia* grasses which are poor in nitrogen. These grasses form relatively unusable fodder for most herbivores except termites, which in turn constitute a food resource that is particularly suitable for exploitation by ectothermic lizards. Moreover, aperiodic, heavy rainfall promotes woody vegetation, thereby supporting arboreal and litter-dwelling species of lizards. Pianka (1989) added fire and fire-induced spatial heterogeneity to their scheme.

Resources are not partitioned randomly in squamate assemblages, but have been shown to be highly organised (Winemiller & Pianka 1990). Species differ in the foods they eat, in the times they are active and in the habitats and microhabitats they exploit (see above; Webb 1985); that is, they occupy different niches. Such ecological differences often have been interpreted as strategies reducing interspecific competition, and in many instances supporting evidence is strong. However, other factors, such as predation, also may influence the kinds and numbers of species that make up an assemblage, and thermoregulatory demands and social factors may alter the assemblage structure through their influence on habitat selection and use (see Heatwole & Taylor 1987).

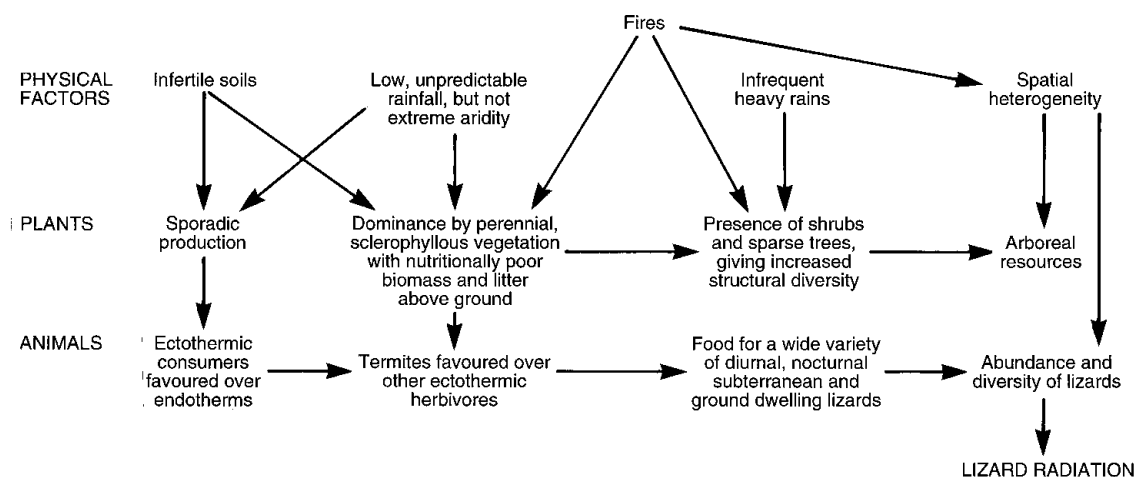


Figure 25.7 Web of ecological forces hypothesised to account for high lizard species richness in arid Australia. (After Morton & James 1988) [D. Wahl]

Different assemblages sometimes contain unrelated species that have parallel niches and have independently developed similar adaptations, morphologies, physiologies and ecologies. Such convergent species-pairs, which occupy similar niches in different assemblages, are known as ecological equivalents. *Moloch horridus* from arid Australia and *Phrynosoma* spp. from American deserts are both spiny lizards subsisting on a diet of only ants (Pianka & Pianka 1970). Some snakes have jointed teeth that facilitate capture and handling of their prey of skinks with osteoderms in the scales; an Australian legless lizard, *Lialis burtonis*, is an ecological equivalent which also feeds on skinks (Fig. 28.6) and has independently evolved hinged teeth (Patchell & Shine 1986b).

Parasites and Disease

Squamates suffer from bacterial, fungal and viral infections, are hosts to endoparasitic protozoans, trematodes, cestodes, nematodes and lingulitids, are attacked by ectoparasitic mites and ticks, and are fed upon by blood-sucking flies and mosquitoes. They also have tumours and skin warts, and suffer from degenerative arterial maladies (Bellairs 1969). Manuals on the diagnosis and treatment of these diseases have been published (Frye 1973, 1990; Cooper & Jackson 1981; McCracken 1988). Incidences of infection sometimes are high in wild populations (for example, 25% for malaria in some lizards, Schall, Bennett & Putnam 1982; 35 to 40% for ticks on one species of gecko and 10% for mites on another, Bustard 1968d, 1969a). Among captive squamates, two of the most prevalent problems are ectoparasitic mites and mouth rot. One Australian parasite, the acanthocephalan *Sphaerechinorhynchus rotundicapitus*, has two semi-aquatic squamate hosts. It occurs in the rectum and large intestine of *Pseudechis porphyriacus*. Eggs released into the water are eaten by aquatic arthropods, which form prey of the skink *Eulamprus quoyii*. Infected lizards are preyed on by the snake, thus completing the cycle (Daniels 1990).

Infection in squamates leads to changes in thermoregulatory behaviour and an increase in body temperature ('behavioural fever') (Firth & Turner 1982), and metabolic rate, stamina and fat reserves may be altered. Reproduction can also be affected via reduced clutch size (Schall *et al.* 1982). Daniels (1985b) noted that voluntary diving time in Australian water skinks (*Sphenomorphus quoyii*) was greater in individuals infected by acanthocephalans than in uninfected animals.

Ticks have been reported from only 32 species of Australian squamates (Roberts 1970). Information is almost certainly incomplete as many species probably have not been examined. However, analysis of Roberts' data suggests that only the larger species of lizards and snakes are host to ticks. Few small squamates are represented and then only by rare records of only one species of tick whereas most of the larger reptiles harbour several species. Varanid lizards and the larger species of skinks and snakes were especially prominent in the list of hosts. With the exception of a single record, geckos were absent.

Of the eight genera and 58 species of ticks known from Australia, only 11 species in two genera (*Amblyomma* and *Aponomma*) have been reported reliably from squamates. Two additional genera are doubtfully recorded (one species each). Most of the tick species found on squamates are common to a number of species, including both lizards and snakes, and some occur on mammals as well. Four species account for most of the tick infestations. *Amblyomma moreliae* is the most widespread, in terms of hosts, and is recorded from 18 species in all squamate families, except the burrowing pygopodids and typhlopids. *Aponomma fimbriatum* is known from 15 host species, and *Amblyomma limbatum* and *Aponomma hydrosauri* each from 10 species.

Ectoparasitic mites infest a variety of Australian squamates and 38 species of lizards and snakes have been recorded as harbouring them (Domrow & Lester 1985; Domrow 1987); this list must be considered incomplete. Unlike ticks, mites infest small species of host as well as large ones. Many ectoparasitic mites attack warm-blooded hosts. Of the 19 genera and 107 species of chiggers (Prostigmata: Trombiculidae) recognised from Australia only seven genera (37%) and 14 species (13%) have been recorded from squamates. Similarly, of the 46 genera and 217 species of Australian ectoparasitic Mesostigmata, only three genera (7%) and seven species (3%) have been found on lizards and/or snakes. The most common hosts for mites are skinks (25 species), particularly for trombiculids. Prostigmatic mites were recorded most often on geckos (6 species).

Economic Significance of Snakes and Lizards

In addition to their scientific and aesthetic worth as wildlife, Australian squamates have an enormous, practical value. Most lizards are generalist insectivores and would be expected to play a role in controlling pest insect populations. However, there have been few attempts to evaluate their contribution quantitatively, or to make a monetary assessment of it. Crome (1981) found that lizards in an area suffering from dieback did not feed on the major defoliators of trees and therefore were not an agent of control of the malady. Similar studies in other systems, where size and habitat of harmful insects overlap to a greater extent with potential saurine predators are badly needed.

Many snakes and varanids prey on mammals and are potentially of benefit in controlling rodents. Again, information is mostly anecdotal. Many rural properties still keep carpet snakes in farm buildings as a means of rodent control, and in the recent past even urban warehouses carried out this practice.

Australian reptiles are highly prized in the pet trade and pythons and varanids exported illicitly net high prices, sometimes in excess of \$1000 per animal. Reptile smuggling continues unabated and the pet trade threatens some species. It may be worth considering licensing the raising in captivity of selected species for export. Coupled with harsher penalties for infringements and more efficient surveillance of wild populations, this might serve as a conservation measure for endangered species.

Reptile leather is a prized commodity and sea snakes are harvested in Australia for this purpose. Given the reproductive properties and population characteristics of these animals it is unlikely that this industry can be sustained, except at a very low level, without depleting stocks.

Snakes and goannas, and their eggs are part of the traditional Aboriginal diet. In the Northern Territory, the larger, gravid females of the freshwater file snake, *Acrochordus arafuræ*, are harvested selectively for food. Because this species reproduces infrequently, human predation has an effect out of proportion to the numbers taken (Shine 1986a).

Not all impacts of reptiles on humans are beneficial. Some reptiles serve as reservoirs for human diseases, for example, equine encephalitis. The larger venomous snakes pose a threat to the safety of humans and their domestic animals. However, with improved techniques for treating snake bite and better preparedness of the medical profession, threat to human life by snakes in Australia has become minimal. Snake venom is extremely valuable because of its uses in medicine and biochemical research. Several enterprises in Australia milk snakes and sell venom. Indeed, the venom of some sea snakes ranks among the most expensive substances for its weight in the world (Heatwole 1987).