HELLENIC ZOOLOGICAL SOCIETY

# Lacertids of the Mediterranean region

## A Biological Approach

REPRINT

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Athens, Bonn, Alicante
1993

*Valakos, Böhme, Pérez - Mellado, Maragou (eds), (1993)*
*Lacertids of the Mediterranean region, pp. 121-154*

## Chapter 9

# The many dimensions of a lizard's ecological niche

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## Introduction

The ecological niche is defined as the sum total of the adaptations of an organismic unit, or as all of the various ways in which a given organismic unit conforms to its particular environment (Pianka, 1974). The niche concept has gradually become inextricably linked to the phenomenon of interspecific competition, and, in the U.S. it is increasingly becoming identified with patterns of resource utilization (Pianka 1981). Niche relationships among competing species are frequently visualized and modeled with bell-shaped resource utilization curves along a continuous resource gradient, such as prey size or height above ground. Emphasis on resource use is operationally tractable.

Lizard niches are multidimensional, complex and elusive. At least five major dimensions which are not independent should be recognized (Table 1). Space, time, and food correspond to the place niche, the temporal activity niche and

*Table 1.* Dimensions of the Lizard Niche

1. **Spatial Niche**
    - Habitat
        - deserts, shrubby habitats, forests, grasslands, etc.
        - sandridges
        - sandplains
        - rocky outcrops
    - Microhabitat
        - arboreal → terrestrial
        - open versus vegetation
        - fossoriality
        - aquatic
        - diurnal, nocturnal retreats
    - Anatomical Correlates - Convergent Evolution
        - fringed toe lamellae, shovel snouts, prehensile tails
2. **Temporal Niche**
    - Time of Activity
    - Nocturnal and Diurnal species
    - Thermoregulatory tactics continuum (thermoconformers → thermoregulators)
3. **Trophic Niche**
    - Dietary Niche Breadth
        - generalists → specialists
            - ants
            - termites
            - scorpions
            - other lizards
            - birds
            - mammals
            - some plant foods
    - Anatomical Correlates -- head length x prey size, hinged teeth
    - Mode of Foraging
        - ambush hunters, sit-and-wait predators
        - widely foraging
        - search vs. pursuit, energetic costs & profits, etc.
4. **Reproductive Tactics**
    - clutch size, reproductive effort, expenditure per progeny
    - Viviparity
5. **Predator Escape Tactics**
    - speed, agility, mimicry, camouflage, spines, tail length, body shape
    - autotomy

the trophic or dietary niche. Reproductive tactics and predator escape tactics must also be included. The spatial niche includes habitat and microhabitat. The temporal niche includes both seasonal and diurnal patterns of activity. Use of space and time are inextricably intertwined.

## Habitat and Microhabitat

Lizards inhabit a broad range of habitats, including deserts, grasslands, chaparral, rock outcrops, deciduous forest and rainforest. Certain species of lizards are climbers, others subterranean, while still others are surface dwellers (although most lizards exploit burrows as retreats). Among the latter, some tend to be found in open areas whereas others frequent the edges of vegetation. Because such spatial and temporal differences limit the frequency of encounters between species as well as expose them to differing food resources, any potential effects of interspecific competition would tend to be ameliorated. Indeed, avoidance of competition is perhaps the most plausible basis for the evolution and maintenance, and thus the very existence, of such niche differences. (Other possibilities, such as physiological design constraints and predator avoidance tactics, need also be considered.) We can learn a lot from careful study of lizard ecology.

In the North American deserts, zebra-tailed lizards *(Callisaurus draconoides*) are usually in the open sun when first sighted; in contrast, side-blotched lizards (*Uta stansburiana*) are most frequently found underneath shrubs. Other iguanid species, such as *Sceloporus magister* and *Urosaurus graciosus*, are almost always found in trees at some distance above ground. *Urosaurus* frequents smaller branches in the tree canopy where it captures most of its insect prey, whereas *Sceloporus* uses tree trunks as perches from which they make forays to the ground to feed (such species perhaps should not be labelled "arboreal" or "semiarboreal," but rather should be called climbing ground feeders). Such climbing lizards exploit a distinctly different microhabitat than true ground-dwelling species which forage at considerably greater distances away from trees; hence any potential for competition for food should be reduced by this differential use of space.

Microhabitat utilization frequencies for various species of lizards in each of three continental desert systems were summarized by Pianka (1986). Overall frequencies of use of various microhabitat elements, along with total numbers of undisturbed lizards observed in each, are listed in Table 2. Considerable intercontinental variation in the incidence of use of different microhabitats is evident: for example, in the two southern hemisphere deserts, substantially more lizards are arboreal and subterranean.

*Table 2.* Microhabitat utilization by all lizards in each of three different continental desert systems (percentages).

| Microhabitat | North America | Kalahari | Australia |
|---|---|---|---|
| Subterranean | 0.0 | 12.1 | 0.8 |
| Terrestrial | 96.0 | 73.1 | 78.1 |
| Open Sun | 45.3 | 18.6 | 16.4 |
| Grass Sun | 3.1 | 3.2 | 15.8 |
| Bush Sun | 30.0 | 11.4 | 3.8 |
| Tree Sun | 3.5 | 2.6 | 0.7 |
| Other Sun | 3.2 | 0.1 | 0.5 |
| Open Shade | 1.7 | 11.4 | 13.6 |
| Grass Shade | 0.1 | 5.7 | 18.4 |
| Bush Shade | 5.6 | 15.9 | 5.5 |
| Tree Shade | 1.0 | 3.7 | 2.3 |
| Other Shade | 2.4 | 0.4 | 1.4 |
| Arboreal | 4.2 | 14.8 | 21.1 |
| Low Sun | 0.4 | 2.6 | 1.5 |
| Low Shade | 0.2 | 2.3 | 7.9 |
| High Sun | 1.8 | 4.2 | 2.1 |
| High Shade | 1.8 | 5.8 | 9.6 |
| Total Number of Lizards | 2,945 | 4,795 | 6,129 |

The diversity of microhabitats used* by various species of North American desert lizards (also termed "microhabitat niche breadths") varies from 1.0 in the specialized night lizard, *Xantusia vigilis* (found only in the fallen rubble underneath Joshua trees) to 3.87 in the much more generalized side-blotched lizard, *Uta stansburiana* (found in 11 of the 14 microhabitats exploited by American lizards - Pianka, 1986). Among all 11 species of North American desert lizards, microhabitat niche breadth averages 2.19 (standard deviation =

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* Measurements based on proportional utilization using Simpson's (1949) index of diversity as an index of microhabitat niche breadth.

1.0, $N = 11$). In the southern hemisphere deserts, subterranean lizards add a 15th microhabitat resource state. Among 22 species of Kalahari lizards, observed microhabitat niche breadths vary from 1.0 in the very specialized fossorial *Typhlosaurus* skinks to nearly 6.0 in two species of climbing skinks (genus *Mabuya*) and the terrestrial lacertid *Ichnotropis squamulosa* (mean = 3.36, SD. dv. = 1.44, $N = 22$). Mean microhabitat niche breadth is significantly greater ($t = 2.41$, df = 31, $P = 0.025$) in the Kalahari than in North America. In many of the 60 Australian species, microhabitat niche breadth is low (mean = 3.02, SD. dv. = 1.38, $N = 60$, Pianka 1986), due partially to small sample sizes (Australian microhabitat niche breadths do not differ significantly from those in North America or in the Kalahari by t-tests). Fig. 1 summarizes these data. However, numbers of lizards observed and their microhabitat niche breadths are uncorrelated ( $r = 0.037$) -- many uncommon species, such as *Menetia greyi* and *Heteronotia binoei*, are nevertheless relatively generalized.

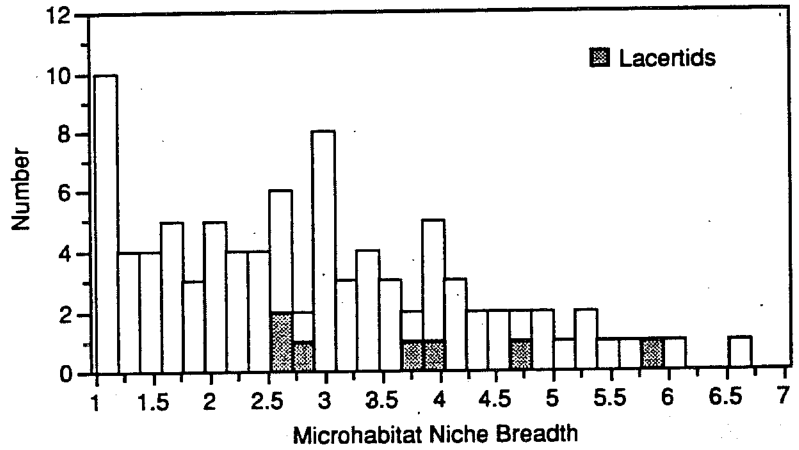

*Fig. 1.* Histogram of microhabitat niche breadths among 83 species of desert lizards from three continents, North America, southern Africa, and Australia. Kalahari lacertids, which have relatively broad spatial niche breadths, are highlighted.

Microhabitat niche breadths are, on average, broadest in the Kalahari, narrowest in North America, and intermediate in Australia. Estimates of the diversity of microhabitats actually used by the entire saurofaunas of each of the study areas are listed in Table 3. Note that microhabitat diversity is lowest in North America and most variable from site to site in the Kalahari. The diversity of microhabitats used by Australian desert lizards is high.

*Table 3.* Estimates of the diversity of microhabitats used by entire saurofaunas at various study areas.

| | North America | Kalahari | Australia |
|---|---|---|---|
| | 2.77 | 6.58 | 8.82 |
| | 2.67 | 9.10 | 7.86 |
| | 2.41 | 4.44 | 7.56 |
| | 2.52 | 4.32 | 6.66 |
| | 2.56 | 10.56 | 6.36 |
| | 2.18 | 5.93 | 5.37 |
| | 2.99 | 6.80 | 6.96 |
| | 2.89 | 3.24 | 5.05 |
| | 3.25 | 9.35 | 7.36 |
| | 3.58 | 8.05 | 8.06 |
| Mean | 2.78 | 6.84 | 7.01 |
| St. Dev. | 0.41 | 2.42 | 1.18 |

## Temporal Patterns of Activity

Even a casual observer quickly notices that various species of desert lizards differ markedly in their times of activity. Some species are active early in the morning, but other species do not emerge until late morning or mid day. Most geckos and pygopodids and some Australian skinks are nocturnal.

Times of activity of most lizards are relatively consistent from day to day and change more or less regularly with the seasons. Many species of diurnal lizards exhibit a bimodal daily pattern of activity (early-late) during the warm summer months, but a single mid-day period of activity at cooler times of the year. Such seasonal shifts in time of activity facilitate thermoregulation by allowing the lizards to encounter a similar thermal environment at different times of year. Standardizing times of activity to "time since sunrise" (diurnal species) or "time since sunset" (nocturnal species) corrects for such seasonal shifts in activity times and allows comparisons among species and between communities. Sympatric species often differ in their activity patterns, with some emerging earlier than others. Such sequential replacements of lizard species during the day are illustrated for four species of North American desert lizards (Fig. 2) and for five sympatric species of Australian *Ctenotus* skinks (Fig. 3). Differences in time of activity may result in exposure to different prey

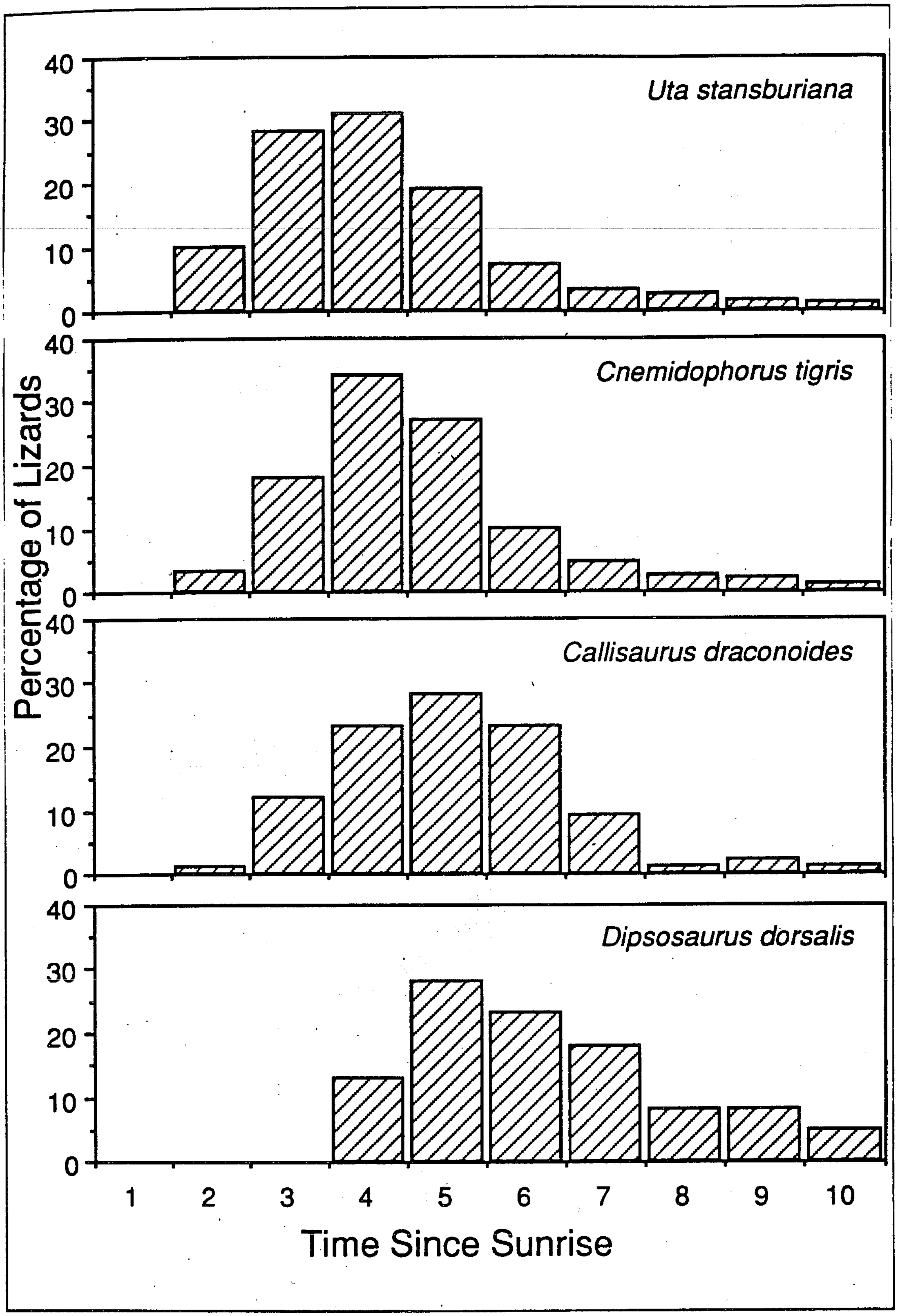

*Fig. 2.* Times of activity of four species of North American flatland desert lizards

resources. Some species, such as the iguanid *Dipsosaurus dorsalis*, the scincid *Ctenotus leae*, and the lacertid *Nucras tessellata*, may actually avoid predators by being active during the heat of mid day.

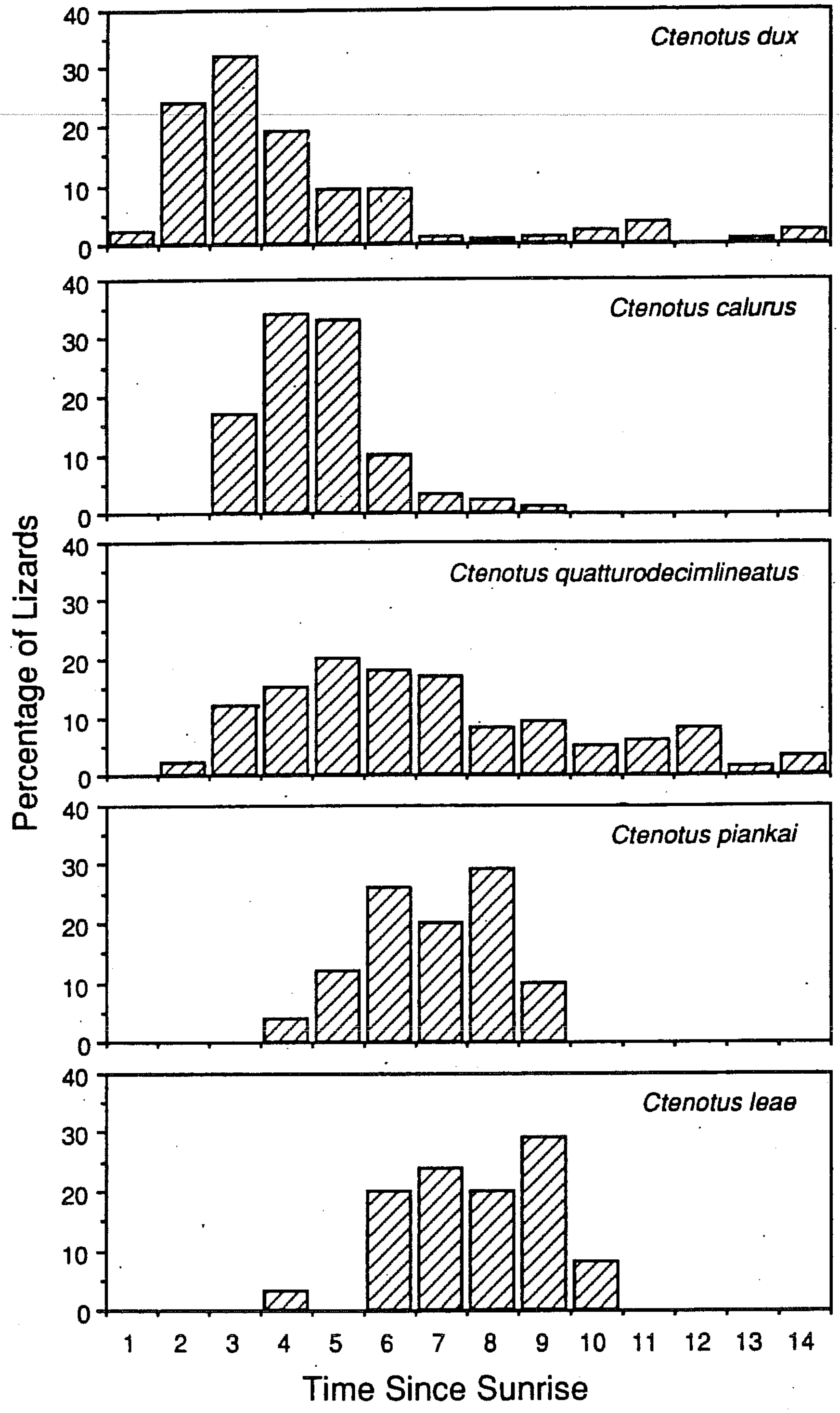

*Fig. 3.* Times of activity among five sympatric congeneric species of Australian desert skinks (from Pianka 1986).

## Thermoregulation

Thermoregulation has been the focus of attention in lizard ecology and natural history since the classic paper of Cowles and Bogert (1944). Animals that maintain relatively constant internal body temperatures are ***homeotherms***, whereas those whose body temperatures vary widely from time to time, often approximating the temperature of their immediate environment, are called ***poikilotherms***. A related pair of useful terms are sometimes confused with these two terms. An ***ectotherm*** obtains its heat from its external environment, whereas an ***endotherm*** produces most of its own heat internally by means of oxidative metabolism. All plants and the vast majority of animals are ectothermic; the only continuously endothermic animals are found among birds and mammals (but even many of these become ectothermic at times). Some poikilotherms including large lizards are at times at least partially endothermic. Many ectothermic lizards actually regulate their body temperatures fairly precisely during periods of activity by appropriate behavioural means, thus achieving homeothermy. An active desert lizard may have a body temperature just as high as that of a bird or mammal (the misleading layman's terms "warm-blooded" and "cold-blooded" should be abandoned).

When averaged over a long enough period of time, heat gained by an organism must be exactly balanced by heat lost to its environment; otherwise the animal either warms up or cools off. Many different pathways of heat gains and heat losses exist. 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 lizard's optimal performance. Lizards living in hot deserts must avoid overheating by being able to minimize heat loads and to dissipate heat efficiently; in contrast, those that live in colder places such as at high altitudes must be adept at acquiring and retaining heat.

Environmental temperatures fluctuate in characteristic ways at different places over Earth's surface, both daily and seasonally. In the absence of a long-term warming or cooling trend, environmental temperatures at any given particular place remain roughly constant when averaged over an entire annual cycle. The range in temperature within a year is much greater at high latitudes than it is nearer the equator. A lizard can balance its annual heat budget by being entirely passive and simply allowing its temperature to mirror that of its environment. Such a passive thermoregulator is known as a thermoconformer. Of course, it is also an ectotherm. Another extreme is to maintain an absolutely constant body temperature by physiological and/or behavioral means, dissipating (or avoiding) excess bodily heat during warm periods but retaining (or gaining) heat during cooler periods. Such creatures that carefully regulate their internal temperatures are known as thermoregulators. Both endotherms and ectotherms regulate their body temperatures. There is a continuum between the two extremes of perfect conformity and perfect regulation. Regulation is never perfect. Because thermoregulation clearly has costs and risks as well as profits, 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 and Slatkin, 1976). Thermoregulation often involves both physiological and behavioral adjustments; as an example of the latter, consider a typical terrestrial diurnal desert lizard. During the early morning, when ambient temperatures are low, such a lizard locates itself in warmer microclimates of the environmental thermal mosaic (e.g., small depressions in the open or on tree trunks), basking in the sun with its body as perpendicular as possible to the sun's rays and thereby maximizing heat gained. With the daily march of temperature, ambient temperatures quickly rise and the lizard seeks cooler shadier microhabitats. Individuals of some species retreat into burrows as temperatures rise; others climb up off the ground into cooler air and orient themselves facing into the sun's rays, thereby reducing heat load. Many lizards change colors and their heat reflectance properties, becoming dark and heat absorbent at colder times of day but light and heat reflectant at hotter times. Such adjustments allow individual lizards to be active over a longer time interval than they could be if they conformed passively to ambient thermal conditions; no doubt they are also more effective competitors and better able to elude predators as a result of such thermoregulatory behaviors.

Lizards constitute an extremely conspicuous element of the vertebrate faunas of most deserts, especially warmer ones. Indeed, the Australian mammalogist Finlayson (1943) referred to the vast interior deserts of Australia as "a land of lizards." Like other ectotherms, lizards obtain their bodily heat solely 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, lizards are low-energy animals. Bennett and Nagy (1977) underscore 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 distinct advantages over endothermy under the harsh and unpredictable conditions that prevail in deserts. By means of this thermal tactic, lizards can conserve water and energy by becoming inactive during the heat of midday, during resource shortages, or whenever difficult physical conditions occur (such as during heat waves or droughts). Birds and mammals must weather out these inhospitable periods at a substantially higher metabolic cost. Ectothermy thus confers lizards with the ability to capitalize on scant and unpredictable food supplies and other resources; presumably this gives lizards a distinct competitive advantage over endotherms in many desert environments.

Hot, arid regions typically support rich lizard faunas, whereas cooler forested areas support fewer lizard species and individuals. Lizards can enjoy the benefits of a high metabolic rate during relatively brief periods when conditions are appropriate for their activity and yet can still become inactive during adverse conditions. By facilitating metabolic inactivity on both a daily and a seasonal basis, ectothermy thus allows lizards to capitalize on unpredictable food supplies. Moreover, most endothermic diurnal birds and mammals must wait out the hot midday period at considerable metabolic cost, whereas lizards can effectively reduce temporal heterogeneity by retreating underground, becoming inactive, and lowering their metabolic rate during harsh periods (some desert rodents estivate when food and/or water is in short supply). Ectothermy probably contributes to the apparent relative success of lizards over birds and mammals in arid regions (Schall and Pianka, 1978). Forests and grasslands are probably simply too shady and too cold for ectothermic lizards to be very successful because these animals rely on basking to reach body temperatures high enough for activity; birds and mammals, in contrast, do quite well in such areas due to their ability to maintain activity via endothermy.

Students of thermoregulation have often noted an apparent upper thermal limit of about 40°C for most of the Earth's eukaryotic creatures (most plants, invertebrates, and vertebrates). This thermal "lid" has frequently been used as evidence for an extremely archaic and inflexible fundamental physiological process (perhaps some enzyme fundamental to all life processes, such as a dehydrogenase, denatures). Major exceptions are certain heat-tolerant bacteria and blue-green algae, inhabitants of hot springs and oceanic volcanic vents. These prokaryotic organisms may well have arisen before the origin of the heat-sensitive metabolic pathway that limits eukaryotes.

An example of such a physiological design constraint involves the thermal relationships of vertebrates, spanning classes from reptiles to mammals (Pianka, 1985, 1986). Detailed consideration of behavioral thermoregulation in lizards enables a fairly accurate prediction of the active body temperatures of mammalian homeotherms. A provocative biological "constant" can be identified that suggests asubstantial degree of physiological inertia.

An intriguing hypothesis for the evolution of homeothermy was offered by Hamilton (1973), who suggested that homeothermy is a by-product of advantages gained from maintaining maximum body temperatures in the face of such an innate physiological ceiling. Ecologically optimal temperatures do not always coincide with physiological optima (Huey and Slatkin, 1976).

Not all homeotherms are endotherms; many ectotherms such as lizards have attained a substantial degree of homeothermy by means of behavioral thermoregulation. Typically, these organisms actively select thermally suitable microhabitats, orient their bodies (or parts thereof) to control heat exchange, and/or shuttle between sun and shade as necessary to maintain a more-or-less constant internal body temperature.

Thermoregulation in lizards is not nearly as simple as it might appear to be at first glance, but rather encompasses a wide diversity of very different thermoregulatory tactics among species ranging from ectothermic poikilothermy to and including ectothermic homeothermy. Thermal relations of active lizards vary widely among species and are profoundly influenced by their spatial and temporal patterns of activity. Body temperatures of some diurnal heliothermic species average 38°C or higher, whereas those of nocturnal thigmothermic species are typically in the mid-twenties, closely paralleling ambient air temperatures.

Variance in body temperature varies between species as does the relationship between body temperatures and air temperatures. For example, among North American lizards, two arboreal species (*Urosaurus graciosus* and *Sceloporus magister*) display narrower variances in body temperature than do terrestrial species. Presumably, arboreal habits often facilitate efficient, economic, and rather precise thermoregulation. Climbing lizards have only to shift position slightly to be in the sun or shade or on a warmer or cooler substrate, and normally do not move through a diverse thermal environment. Moreover, arboreal lizards need not expend energy making long runs as do most ground dwellers, and thus climbing species do not raise their body temperatures metabolically to as great an extent as do terrestrial lizards.

Such differences in temporal patterns of activity, the use of space, and body temperature relationships are hardly independent. Rather, they complexly constrain one another, sometimes in intricate and 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 hotspot at a later 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 behavior becomes necessary (Huey and Pianka, 1977a). In contrast, the fraction of the ground's surface in the sun is low when shadows are long early and late, 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.

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 cryptic diurnal species.

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

A straight line can be represented as a single point in the coordinates of slope versus intercept; these two parameters were plotted for linear regressions of body temperatures on air temperatures among some 82 species of lizards by Pianka (1986). Each data point represents the least-squares linear regression of body temperature against air temperature for a given species of desert lizard. These data points fall on yet another, transcendent, straight line (Fig. 4). The position of any particular species along this spectrum reflects a great deal about its complex activities in space and time. The line plotted in this figure is thus a unidimensional surrogate for multidimensional spatial-temporal niche dimensions: it offers a potent linear dimension on which various species can be placed in attempts to formulate general schemes of lizard ecology (Pianka, 1985; 1986 - see also last section of this paper). Various other ecological parameters, including reproductive tactics, can be mapped on to this emergent spatial-temporal axis.

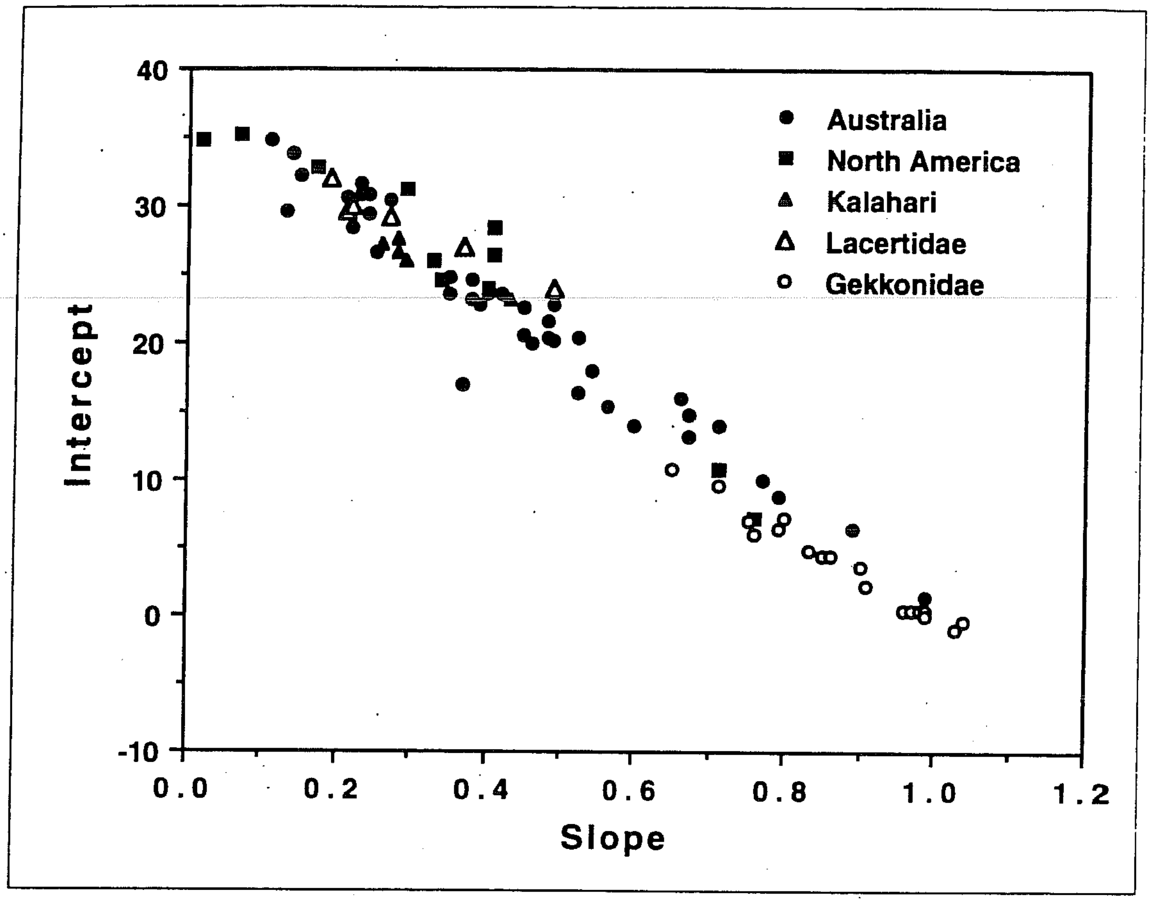

*Fig. 4.* Each data point represents the least squares regression line of active body temperatures against ambient air temperature for a different species of desert lizard (data from Pianka 1986). Various different deserts and taxa are identified. Lacertids are thermoregulators, whereas most geckos are thermoconformers.

The intriguing "intercept" of the intercepts (38.8°C) approximates the point of intersection of all 82 regression lines and represents an innate design constraint imposed by lizard physiology and metabolism. It is no accident that this value also corresponds closely to the body temperatures of homeotherms, particularly mammals!

Birds maintain slightly higher body temperatures than mammals (Hamilton, 1973), and descended from another reptilian stock, the archosaurs, represented today by the crocodilians. Would a comparable study of crocodilian thermoregulation yield a higher intercept of the intercepts? (This prediction could be doomed to failure by the mere fact that crocodilians are aquatic and very large - yet they clearly thermoregulate when out of the water.) Although most insects are so small that convective heat exchange prevents them from attaining body temperatures much higher than that of ambient air, some, such as bumblebees and butterflies, do exhibit behavioral thermoregulation; would a plot for insects show more scatter and a different intercept?

## Diet

Certain species of lizards are dietary specialists, eating an exceedingly narrow range of prey items. For example, the Australian agamid *Moloch horridus* eats essentially nothing except ants, mostly of a single species of *Iridomyrmex*. Convergent North American horned lizards, genus *Phrynosoma*, are also ant specialists - (see also below). Still other species are termite specialists, including the Kalahari lizards *Heliobolus lugubris* and *Typhlosaurus* and the Australian nocturnal *Diplodactylus conspicillatus, Rhynchoedura,* as well as some diurnal *Ctenotus* species. Even though these species consume virtually nothing but isoptera, other species in the same habitat never eat termites as prey. Food specialization 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. Other lizard species, while not so specialized, also have narrow diets. For example, the Kalahari lacertid *Nucras tessellata* and the Australian pygopodid *Pygopus nigriceps* both consume an excessive number of scorpions when compared to other lizard species (Pianka, 1986). *Nucras* forages widely to capture these large arachnids by day in their diurnal retreats, whereas the nocturnal *Pygopus* sits and waits for scorpions at night above ground during the latter's normal period of activity. In North America, no desert lizard has become a scorpion specialist, but the small sand-swimming snake *Chionactis occipitalis* seems to have usurped this ecological role.

Scorpions are solitary prey items, but they are extremely large and nutritious, facilitating evolution of dietary specialization. For similar reasons, specialization on other lizards as food items has evolved in North American leopard lizards (*Crotaphytus wislizeni*) as well as among most Australian varanids. Other lizard species have much more catholic diets, eating a considerably wider variety of foods. Dietary niche breadth also varies within species from time to time and from place to place as the composition of diets change with opportunistic feeding in response to fluctuating prey abundances and availabilities (Pianka, 1986). However, the consistency of lizard diets is remarkable, suggesting a profound impact of microhabitat utilization and foraging mode, as well as various anatomical and behavioral constraints imposed by phylogeny.

Diets of nearly a hundred species of desert lizards were summarized by Pianka (1986) as percentages by volume of various foods in the overall diets of all specimens of each species on all study areas within each desert-lizard system.

Close scrutiny of these data matrices reveals that some species specialize on scorpions, ants, termites, vertebrates, and/or on plants, whereas other species on each continent are much more generalized, eating an extremely wide variety of food categories. No centipedes were found in stomachs of North American lizards, and solpugids are not present in Australia. Food niche breadths* range from 1.06 to 6.53 (mean 4.07, SD. dv. = 1.93, N = 11) among the 11 species of North American lizards, from 1.07 to 8.22 (mean 3.8 5, SD. dv. = 2.09, N = 21) among 21 Kalahari species, and from 1.00 to 10.9 (mean 3.86, SD. dv. = 2.28, N = 59) among the 60 Australian species (Fig. 5). None of these intercontinental variations in food niche breadths are significantly different by t-tests. Estimates of food niche breadths are uncorrelated with the number of lizards on which they are based ( r = 0.11), providing evidence that sample sizes are adequate to characterize patterns of food utilization even among the rarer species. Indeed, species with broad diets are often, though not always, relatively uncommon. Across species, dietary niche breadth is weakly, but significantly (r = 0.27, P = 0.02), positively correlated with microhabitat niche breadth, an indication that food specialists tend to be restricted to fewer microhabitats than food generalists.

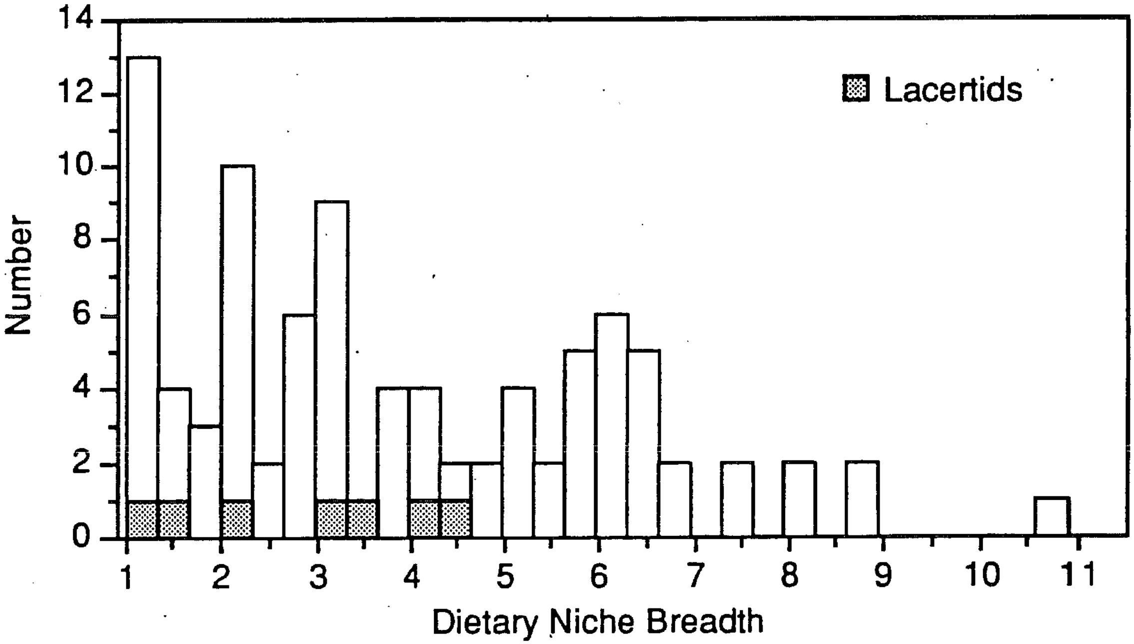

*Fig. 5.* Histogram of dietary niche breadths among 83 species of desert lizards from three continents. North America, southern Africa, and Australia. Kalahari lacertids, which have narrow diets, are highlighted.

Biologically significant variation between species in utilization of certain relatively minor food categories is evident: for example, in the diets of climbing

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* Computed using proportional utilization coefficients with Simpson's (1949) index of diversity.

lizard species, hemiptera-homoptera and mantids-phasmids, as well as various flying insects (wasps, Diptera, and Lepidoptera) tend to be better represented than they are among terrestrial species. Likewise, geckos consume more nocturnal arthropods (scorpions, crickets, roaches, and moths) than do most diurnal species (some diurnal lizards do capture nocturnal prey in their diurnal retreats). Such prey items are thus indicators of spatial and temporal patterns of activity.

*Table 4.* Overall diets of all lizards in each of three different continental desert systems (percentages by volume)

| Prey Item | North America | Kalahari | Australia |
|---|---|---|---|
| Centipedes | 0.0 | 0.0 | 2.0 |
| Spiders | 1.6 | 3.1 | 2.7 |
| Scorpions | 0.7 | 2.9 | 1.5 |
| Solpugids | 1.4 | 1.5 | 0.0 |
| Ants | 9.7 | 13.6 | 16.8 |
| Wasps | 0.9 | 0.8 | 1.4 |
| Locustidae | 11.5 | 6.1 | 8.6 |
| Blattidae | 3.2 | 0.4 | 2.8 |
| Mantids-Phasmids | 0.8 | 0.1 | 0.6 |
| Neuroptera | 0.2 | 0.04 | 0.1 |
| Coleoptera | 18.5 | 16.3 | 5.7 |
| Isoptera | 16.5 | 41.3 | 18.5 |
| Homoptera-Hemiptera | 1.0 | 1.3 | 1.7 |
| Diptera | 0.9 | 0.6 | 0.3 |
| Lepidoptera | 2.1 | 1.4 | 0.6 |
| Insect Eggs | 0.3 | 0.02 | 0.1 |
| All Larvae | 12.1 | 3.6 | 3.3 |
| Vertebrates | 7.8 | 2.3 | 27.1 |
| Plants | 8.3 | 1.2 | 4.2 |
| Misc. Unid. Arthropods | 2.6 | 3.5 | 2.1 |
| Total Volume of Prey | 3174 cc. | 1145 cc. | 2787 cc. |
| Diversity of Foods Consumed by all Species | 8.7 | 4.4 | 6.6 |

Overall diets of entire saurofaunas are summarized and compared in Table 4. Relatively few foods dominate lizard diets. Prey resource spectra are broadly similar between continents (Pianka, 1986), although notable differences occur.

In North America, the seven most important (totalling 84%), in decreasing order by volumetric importance, are: beetles, termites, insect larvae, grasshoppers plus crickets, ants, plant materials, and vertebrates. In the Kalahari, just three food categories far outweigh all others (total 71%): these are termites, beetles, and ants. In Australia, the five most important categories (total 77%, in decreasing order) 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 (largely a reflection of varanid diets). Somewhat surprisingly, the overall diversity of foods consumed by all species of lizards is actually greatest in the least diverse North American saurofauna (8.7), lowest in the Kalahari lizards (4.4), and intermediate in Australia (6.6). Basically comparable figures, although broadly overlapping, emerge from an area-by-area analysis (Pianka, 1986; 1989).

Prey diversity is weakly correlated with certain measures of the variability in average annual precipitation: food diversity is positively correlated with the coefficient of variation in annual precipitation ($r = 0.45$, $P = 0.05$), but is negatively correlated with the mean minus the standard deviation in precipitation. More variable precipitation, and presumably primary productivity, fosters higher insect species diversities (lizard diversity also correlates with variability of precipitation).

## Modes of Foraging

Some predators attack their prey from ambush, whereas others usually hunt while on the move. Over 25 years ago, I termed these two modes of foraging the "sit-and-wait" versus the "widely-foraging" tactic, respectively (Pianka, 1966). Of course, this dichotomy could be somewhat artificial, although numerous animal groups seem to fall rather naturally into either one category or the other*. Members of most lizard families typically exploit either one or the other of these two modes of foraging: thus iguanids, agamids and geckos primarily sit and wait for their prey, whereas teiids and skinks forage widely. Lacertids, however, exploit both modes of foraging, even within the same genus. This evidently natural dichotomy in foraging tactics has had a substantial impact on theories of optimal diets and competitive relationships among species

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* One Namib desert lacertid species, *Aporosaura anchietae*, has been reported to "switch" from sitting and waiting for wind-blown seeds when winds are blowing to foraging widely for insect prey when winds are calm (Robinson and Cunningham, 1978).

(Magnusson *et al.*, 1985; McLaughlin, 1989; Perry *et al.*, 1990; Pietruszka, 1986). Empirical study of the influence of mode of foraging on diets has lagged behind theory. (One of my graduate students, Gad Perry, is working to close this gap.)

Certain dietary differences are associated with this apparent dichotomy in foraging tactics. Sit-and-wait predators rely largely on moving prey whereas widely-foraging predators encounter and consume non-moving types of prey items more frequently. In order for the sit-and-wait tactic to pay off, prey must be relatively mobile and prey density must be high (or predator energy requirements low). The sit-and-wait tactic should be less prevalent during periods of prey scarcity than the widely-foraging method. The success of the widely-foraging tactic is also influenced by prey mobility and prey density as well as by the predator's energetic requirements (which should usually be higher than those of sit-and-wait predators), but the searching abilities of the predator and the spatial distribution of its prey now assume substantial importance. North American and Australian sites 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 (only one species, the teiid *Cnemidophorus tigris*) and in the Kalahari (an average of 4 species per site) than in the Australian deserts (mean number of widely-foraging species per area is 10.1, most of which are skinks in the genus *Ctenotus*). 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; percentages of widely-foraging species are 14% (North America), 27% (Kalahari), and 36% (Australia).

Two species of Kalahari lizards, *Pedioplanis lineo-ocellata* and *Meroles suborbitalis*, sit-and-wait for prey, whereas two other syntopic species, *Heliobolus lugubris* and *Pedioplanis namaquensis*), forage widely for their food (Pianka et al., 1979; Huey and Pianka, 1981). Time budgets of these lacertids reflect their modes of foraging (Pianka, 1986). Foraging widely is energetically expensive and, judging from their relative stomach volumes, those species that engage in this mode of food gathering appear to capture more prey per unit time than do sit-and-wait species. Overall energy budgets of widely-foraging species are nearly twice as great as those of sit-and-wait species (Huey and Pianka, 1981). Sedentary foragers tend to encounter and eat fairly mobile prey whereas more active widely-foraging predators consume less active prey. Compared with sit-and-wait species, widely-foraging lacertid species eat more termites (sedentary, spatially and temporally unpredictable but clumped prey). One widely-foraging species, *Nucras tessellata*, specializes on scorpions (by day, these large arachnids are non-mobile and exceedingly patchily-distributed prey items). Another ramification of foraging mode in these Kalahari lizards concerns exposure to their own predators. Because of their more-or-less continual movements, widely-foraging species expose themselves and tend to be more visible. As a result, they seem to 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 and Pianka, 1981).

Another important spin-off of foraging mode involves reproductive tactics. Clutch sizes of widely-foraging species are 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 and Congdon, 1978). Hence foraging style constrains reproductive prospects (as well as vice versa). Huey and Pianka (1981) summarize many of these ecological correlates of foraging mode.

In an environment with a scant food supply, a consumer presumably 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 and Pianka, 1966). In such an environment, a broad diet maximizes returns per unit expenditure, favoring generalization. In a food-rich environment, however, search time per item is low because a foraging animal encounters numerous potential prey items. Under such circumstances, sub standard prey items can be bypassed economically because expectation of finding a superior item in the near future is high. Hence rich food supplies favor selective foraging and lead to narrow food niche breadths. These arguments are supported by the North American teiid lizard *Cnemidophorus tigris*, which eats a greater diversity of foods in drier than average years (presumably times of low food availability) but like most lizards contracts its diet during periods of prey abundance (Pianka, 1986).

Another, more extreme, example of this phenomenon occurs after heavy summer rains when termites send out their winged reproductives in great abundance and virtually every species of lizard eats nothing but termites (even lizard species that normally never consume termites). During such fleeting moments of extraordinary prey abundance, competition for food is negligible and dietary overlap among members of a desert saurofauna is sometimes nearly complete.

## Reproductive Tactics

Most lizards lay eggs, but some species retain their eggs internally and give birth to living young. Viviparity has arisen at least 25 times among lizards (Shine and Bull, 1985) in eight different families (agamids, anguids, chameleons, geckos, iguanids, lacertids, xantusids and skinks). Clutch or litter sizes vary from one to forty or more among different species of lizards. Some species reproduce only once every second or third year, others but once each year, while still others lay two or more clutches each year. Substantial spatial and temporal variation in clutch size also exists within species.

As just one among many possible examples, in the double-clutched Australian agamid species *Ctenophorus isolepis*, the size of 67 first clutches (August-December) averaged 3.01 eggs whereas the mean of 41 second clutches (January-February) was 3.88. Females grow during the season, and, as in many lizards, larger females tend to lay larger clutches. Interestingly enough, however, these same females invest relatively more on their second clutches than they did on their first clutch: among 25 first clutches, clutch volumes average only 11.2% of female weight, but in 15 second clutches the average was 15.1%. (95% confidence intervals on these means are non-overlapping -- 10.25 to 12.20 versus 13.38 to 16.85, respectively).

Changes in fecundity with fluctuations in food supplies and local conditions from year to year or spot to spot have also frequently been observed: for example, in the North American whiptail *Cnemidophorus tigris* (Family Teiidae) females lay larger clutches in years with above-average precipitation and presumably ample food supplies (Pianka, 1970). Similar phenomena have also been documented in *Xantusia vigilis* (Zweifel and Lowe, 1966) and *Uta stansburiana* and doubtlessly occur in many or even most other lizard species.

Clutch or litter weight (or volume), expressed as a fraction of a female's total body weight, ranges from as little as 4 to 5% in some species to as much as 20-30% in others. Clutch weights tend to be particularly high in some of the North American horned lizards (genus *Phrynosoma*). Ratios of clutch or litter weight to female body weight correlate strongly with various energetic measures and have often been used as crude indices of a female's instantaneous investment in current reproduction (sometimes equated with the elusive notion of "reproductive effort").

In addition to clutch size and female total investment in reproduction, the size (or weight) of an individual oviductal egg or newborn progeny also varies widely among lizards from as little as 1-2% in some species to a full 17% in the live-bearing Kalahari fossorial skink *Typhlosaurus gariepensis*. Such expenditures per progeny are inverse measures of the extent to which a juvenile lizard must grow to reach adulthood.

Of course, any two parties to this triad (clutch size, female reproductive investment, and expenditure per progeny) uniquely determine the third: however, forces of natural selection molding each differ substantially. Thus clutch or litter weight presumably reflects an adult female's best current investment tactic in a given environment at a particular instant in time whereas expenditure on any given individual progeny is probably more closely attuned to the average environment to be encountered by a juvenile. In a sense, then, clutch (or litter) size is the direct result of the interaction between an optimal parental reproductive tactic and an optimal juvenile body size (clutch size is, of course, simply the ratio of the former divided by the latter).

Statistics on clutch/litter sizes, total reproductive investment of females, and expenditure per progeny among 65 species of desert lizards were presented by Pianka (1986), along with similar data on another 20 species of lizards, including both desert and non-desert forms extracted from the literature. Among the species surveyed, average clutch/litter size varies from 1 in the Kalahari skink *Typhlosaurus gariepensis* and the geckos *Gehyra variegata* and *Ptenopus garrulus* to 13 in the Kalahari agamid *Agama hispida*. Clutch sizes in certain horned lizards are still larger, averaging 24.3 in the American iguanid *Phrynosoma cornutum* (the Texas horned lizard). Clutch or litter size and female investment are significantly positively correlated (r = 0.482, P = 0.001), although scatter is considerable. Viviparous species (mostly skinks) tend to have slightly higher investment ratios than do the egg layers. Since expenditure per progeny can be estimated from total investment divided by clutch/litter size, it tends to decrease exponentially with increasing number of progeny (for a fixed total investment). Expenditure per progeny and clutch/litter size are inversely related (r = -0.652, P = 0.001). This correlation is strengthened when both variables are transformed to logarithms (on a log-log plot, the correlation coefficient is -0.810). Clutch size is thus correlated positively with total investment but negatively with investment per progeny. In simple product-moment correlation, the latter two members of the triumvirate, total reproductive investment and expenditure per progeny, are only weakly and not significantly correlated (r = 0.153, P = 0.10), suggesting that these two parameters vary independently of one another and that they may be responsive to different selective pressures. However, when effects of clutch size are held constant by partial correlation, the weak correlation between reproductive effort and expenditure per progeny is substantially improved (partial correlation coefficient = 0.704), an indication, once again, that these three aspects of reproductive tactics are far from independent of one another. Indeed, pairwise partial correlation coefficients between the logarithms of these three variates are all nearly perfect (rxy.z's = 0.910, 0.924, and -0.969). Species fall neatly on a plane in this three space, as evidenced by a principal component analysis using log-transformed variables, which shows that the first two principal components reduce variance by over 99% (Pianka, 1986).

Frequency distributions of average clutch/litter sizes, total investment ratios, and expenditure per progeny among species were summarized by Pianka (1986). Expenditure per progeny varies over more than an order of magnitude, from 1% to 17% of a gravid female's body weight. Interestingly, species with narrow diets often though not always tend to have higher than average expenditures per progeny. Two of the species with the highest expenditures per progeny, *Typhlosaurus gariepensis* and *T. lineatus*, probably experience intense competition: (1) these live-bearing, subterranean skinks exist at very high population densities, (2) individuals are long-lived with delayed maturity, (3) litter sizes are extremely small (means of 1.0 and 1.5, respectively), and (4) females very likely reproduce only biennially (Huey *et al.*, 1974). These two Kalahari fossorial skinks are also extreme food specialists, eating termites to the virtual exclusion of all other prey. The extremely high expenditure per progeny of *Typhlosaurus* may well be necessary to confer newborn animals with competitive ability sufficient to establish themselves in the highly competitive underground environment. Limited evidence indicates that investment per progeny is indeed responsive to and indicative of a lizard's competitive environment. Thus, in *Typhlosaurus lineatus*, offspring are significantly heavier (and expenditure per progeny significantly greater) where this species occurs in sympatry with *T. gariepensis* as compared with allopatric populations (Huey *et al.*, 1974). Other food-specialized species seem also to encounter intense competition: 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 and Pianka, 1976). A similar phenomenon appears to occur in the semi-arboreal African skink *Mabuya spilogaster*: on one study area, it is syntopic with an ecologically very similar species, *Mabuya striata*. Expenditure per progeny in *M. spilogaster* increases significantly (t-test, P = 0.01) from allopatry (mean = 4.39 + 0.21, N = 51) to sympatry (mean = 5.63 + 0.48, N = 19).

Differences between viviparous and oviparous species are relatively slight, although, as noted above, viviparous species appear to invest slightly more in reproduction. Statistically significant differences exist between diurnal and nocturnal species of lizards in these reproductive statistics: nocturnal species have significantly smaller clutch/litter sizes and lower total investment in reproduction, but significantly higher expenditure per progeny (Pianka 1986). These differences between diurnal and nocturnal species stem largely from a simple historical ortaxonomic basis, since geckos and pygopodids dominate the nocturnal saurofauna and have a fixed clutch of only one or two eggs. Two viviparous nocturnal skink species (genus *Egernia*) also tend to have small litters; however, a third oviparous nocturnal skink, *Sphenomorphus richardsoni*, does not have a small clutch size.

Reproductive tactics can be mapped, to a limited extent, on to the spatial-temporal thermoregulation axis plotted earlier. Simple pair-wise product-moment correlation coefficients between the three reproductive variables and the slope-intercepts of body temperature regressions on air temperature are weak although generally statistically significant. The strongest correlation, between the logarithm of clutch size and the intercept of body temperature on air temperature ($r = 0.609$), seems to arise largely as a result of the small clutch sizes and low body temperature intercepts of nocturnal lizards.

Dunham and Miles (1985) undertook a detailed multivariate analysis of the reproductive tactics of 91 species of lizards. A discriminant function analysis describes an axis which has actively foraging species with large body sizes and small clutches at one end and sit-and-wait foragers with small body size and large clutches at the other end. This axis could be exploited as a dimension for construction of a "periodic table of lizard niches" (see last section).

## Predator Escape Tactics

Lizard tails have diversified greatly and serve a wide variety of functions for their possessors. Many climbing species, such as the Australian sandridge agamid *Lophognathus longirostris*, have evolved extraordinarily long tails which serve as effective counterbalances. Long tails enable lizards to raise their forelegs up off the ground and to run on their hind legs alone (bipedality is a faster means of locomotion than tetrapodality). Prehensile tails are used as a fifth leg in climbing by some arboreal lizard species like some geckos ( e.g., *Diplodactylus elderi*), by the true chameleons (*Chameleo*), and by some skinks (*Corucia*).

In several members of the Australian gekkonid genus *Diplodactylus (D. ciliaris, D. elderi, D. strophurus* and relatives), glandular tails secrete and store a smelly noxious mucous. When disturbed, these lizards squirt out large amounts of sticky odoriferous gorp. Surprisingly, tails of these geckos are fragile and easily shed (but quickly regenerated). A related Australian desert gecko *Diplodactylus conspicillatus* has a non-glandular but very short and stubby bony tail: these nocturnal termite specialists hide in the vertical shafts of abandoned spider holes during the day and it is thought that they point head downwards and use their tails to block off these tunnels. Another Australian desert lizard with a similar yet different tail tactic is the climbing skink *Egernia depressa*. These lizards wedge themselves into tight crevices in mulga tree hollows (and rocks), blocking off the entrance with their strong and very spiny tails. Spinily-armored tails are used by numerous other species of lizards in a similar fashion, including the Mexican iguanid *Enyaliosaurus clarki* and the Saharan agamid *Uromastix acanthinurus*. Members of another bizarre group of Australian lizards (genus *Nephrurus*) possess a unique round knob at the tip of their tails. These large nocturnal lizards eat big prey including other species of geckos on occasion. Both sexes carry the curious knob, but its function remains a total mystery. Unlike most geckos, their tails are not exceedingly fragile. In many species of lizards (especially among juveniles), tails are brightly colored and/or very conspicuous, evidently functioning as a lure to attract a potential predator's attack away from the more vulnerable and less dispensible parts of the animal. When approached or followed by a large animal, the zebra-tailed lizard of the western North American deserts, *Callisaurus draconoides*, curls its tail up over its hindquarters and back, exposing the bold black and white pattern underneath and coyly wriggling its tail from side to side. If pursued farther, zebra-tailed lizards resort to extreme speed (estimated at up to 20-30 km/h) and long zig-zag runs. An 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.

Tails of many, but by no means all, lizards break off easily. Indeed, some species can actually lose their tails voluntarily with minimal external force in a process known as autotomy (Arnold, 1988). Freshly dismembered tails or pieces thereof typically thrash around wildly, presumably attracting a predator's attention while the recent owner quietly slips away unnoticed (Vitt *et al.*, 1977). Some skinks, including many *Ctenotus*, 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. Many such 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. Losing its tail has surprisingly little effect on a lizard, as individuals often resume basking and foraging as if nothing had happened within minutes. In such lizard species, of course, tails are quickly regenerated from the stub. Although regrown tails are occasionally almost indistinguishable from the original externally, their internal support structure is cartilaginous rather than bony. Not all lizard tails are easily broken, however. Whereas most iguanids have fragile tails, their close relatives the agamids generally do not. Tails of varanids and true chameleons do not break easily either. Lizards with such tough tails usually cannot regenerate a very complete tail if their original should happen to be lost. The evolutionary bases for these differences, sometimes between fairly closely-related groups of lizards, are evasive. Arnold (1988) argues that easy tail loss is a primitive trait among lizards which has been lost but regained repeatedly among various lizard lineages. 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 to subdue intact (Pianka, 1969).

Tail break frequency could serve as an index to the intensity of predation on lizard populations. It has since been used to attempt to estimate the amount of predation, although there are serious problems and limitations with the procedure (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. Predator densities increase from north to south in western North America (Pianka, 1986; Schall and Pianka, 1980). Correlated with this latitudinal increase in predation, frequencies of broken and regenerated tails are higher at southern sites than at northern localities among four of the five widely-distributed lizard species. In the well-studied species *Cnemidophorus tigris*, frequency of broken tails decreases with latitude (Pianka, 1970); moreover, diversity of predator escape behaviors utilized among members of these various *Cnemidophorus* populations also increases with the frequency of broken and regenerated tails (Schall and Pianka, 1980). A greater variety of escape tactics, a form of behavioral "aspect diversity" (Rand, 1967), presumably reduces the ease with which predators can capture lizard prey.

In the Kalahari desert of southern Africa, juvenile lacertid lizards of the species *Heliobolus lugubris* employ an interesting anti-predator tactic involving deception known as Batesian mimicry (Huey and Pianka, 1977b). These defenseless small lizards mimic noxious "Oogpister" beetles (the Afrikaans translates euphemistically as "eye squirter"), which emit pungent acids, aldehydes, and other chemicals when disturbed. Adult *H. lugubris* lizards are buff-colored and pale red, matching the color of Kalahari sands. Bodies of juveniles are jet black with white spots (juvenile tails are red, matching the sand color). Whereas adults walk with a normal tetrapod lizard gait, with their backs undulating from side to side, juveniles walk stiff-legged, with backs arched vertically, holding their reddish tails flat against the ground (this makes the tail difficult to detect). When pursued, young *H. lugubris* abandon their "beetle walk" and dart rapidly for cover, using normal lizard locomotion. As they reach a size of about 45-50 mm from snout to vent (the size of the largest oogpister beetles), these lizards "metamorphose" into the cryptic adult coloration and permanently abandon the stilt walk. The frequency of broken and regenerated tails is lower in juvenile *H. lugubris* than among closely related lacertids in the same habitats exposed to common predators, suggesting that this beetle mimicry does reduce predatory attacks.

## Fringed Toes and Shovel Noses

An open sandy desert poses severe problems for its inhabitants: (1) wind blown sands are always loose and provide little traction; (2) surface temperatures at midday rise to lethal levels; and (3) open sandy areas offer little food or shade or cover for evading predators. Even so, natural selection over eons of time has allowed lizards to cope fairly well with such sandy desert conditions. Subterranean lizards simply bypass most of the problems by staying underground, and actually benefit from the loose sand since underground locomotion is made easier. Burrowing is also facilitated by the evolution of a pointed, shovel-shaped head and a countersunk lower jaw, as well as by small appendages and muscular bodies and tails.

During the hours shortly after sunrise, but before sand temperatures climb too high, diurnal lizards scurry about above ground in such sandy desert habitats. Sand specialized lizards provide one of the most striking examples of convergent evolution and ecological equivalence. Representatives of many different families of lizards scattered throughout the world's deserts have found a similar solution for getting better traction on loose sand: enlarged scales on the toes, or lamellae, have evolved independently in five different families of lizards: skinks, lacertids, iguanids, agamids, and geckos (Luke, 1986). A skink, appropriately dubbed the "sand fish," literally swims through sandy seas in search of insect food in the Sahara and other eastern deserts. These sandy desert regions also support lacertid lizards (*Acanthodactylus*) with fringed toes and shovel noses. Far away in the southern hemisphere, on the windblown dunes of the Namib desert of southwestern Africa, an independent lineage of lacertids has evolved a similar life form, *Aporosaura anchietae*.

In North America, this body form has been adopted by members of the iguanid genus *Uma*, which usually forage by waiting in the open and eat a fairly diverse diet of various insects, such as sand roaches, beetle larvae and other burrowing arthropods. They also listen intently for insects moving buried in the sand, and dig them up. Sometimes they dash, dig, and paw through a patch of sand and then watch the disturbed area for movements.

All of these lizards have flattened, duckbill-like, shovel- nosed snouts, which enable them to make remarkable "dives" into the sand even while running at full speed. The lizards then wriggle along under the surface, sometimes for over a meter. One must see such a sand diving act to appreciate fully its effectiveness as a disappearing act. Some Namib desert lizards discovered another solution to gain traction on powdery sands: frog-like webbing between the toes as seen in the gecko *Palmatogecko*.

## Interdependence of Niche Dimensions

Any given organism possesses a unique coadapted complex of physiological, behavioral, and ecological traits whose functions complement one another and enhance that organism's reproductive success. Such a constellation of adaptations has been called an optimal design (Rosen, 1967) or an ***adaptive suite*** (Bartholomew, 1972).

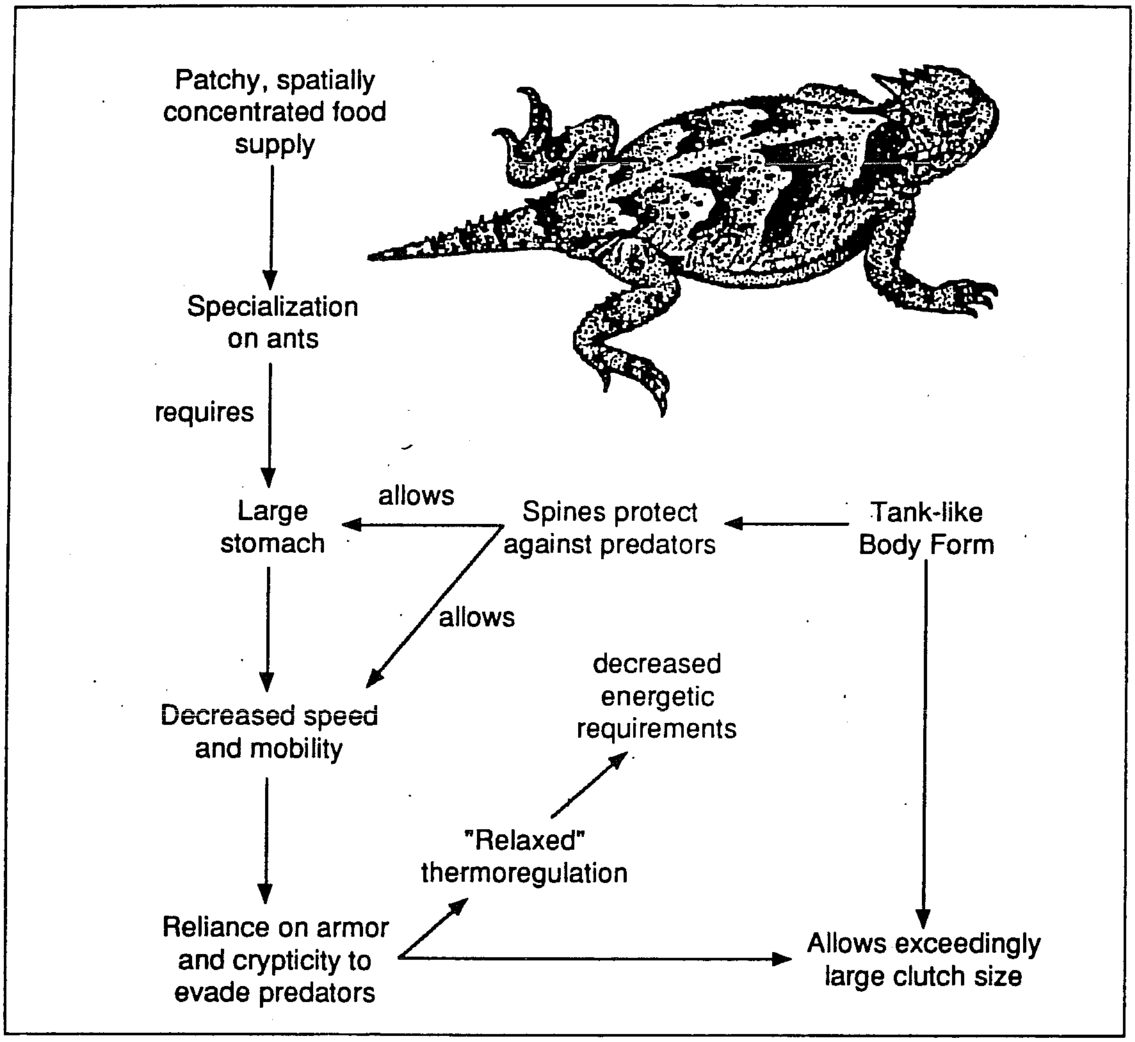

*Fig. 6.* The adaptive suite of anatomical, behavioral, and ecological factors influencing an ant specialist, the desert horned lizard *Phrynosoma platyrhinos*.

Consider the desert horned lizard *Phrynosoma platyrhinos* (Fig. 6). Various features of its anatomy, behavior, diet, temporal pattern of activity, thermoregulation, reproductive tactics, and predator escape tactics, can be profitably interrelated and interpreted to provide an integrated view of the ecology of this interesting animal (Pianka, 1966; Pianka and Parker, 1975). Horned lizards are ant specialists and usually eat essentially nothing else. Ants are small and contain much undigestible chitin, so that large numbers of them must be consumed. An ant specialist must therefore possess a large stomach for its body size. When expressed as a proportion of total body weight, the stomach of this horned lizard occupies a considerably larger fraction of the animal's overall body mass (about 13 percent) than do the stomachs of all other sympatric desert lizard species, including the herbivorous desert iguana *Dipsosaurus dorsalis* (herbivores typically have lower assimilation rates and larger stomachs than carnivores). Possession of such a large gut necessitates a tanklike body form, reducing speed and decreasing the lizard's ability to escape from predators by flight. As a result, natural selection has favored a spiny body form and cryptic behavior rather than a sleek body and rapid movement to cover (as in most other species of lizards). Risks of predation are likely to be increased during long periods of exposure while foraging in the open. A reluctance to move, even when actually threatened by a potential predator, could well be advantageous; movement might attract attention of predators and negate the advantage of concealing coloration and contour. Such decreased movement doubtless contributes to the observed high variance in body temperature of *Phrynosoma platyrhinos*, which is significantly greater than that of all other species of sympatric lizards.

*Phrynosoma platyrhinos* are also active over a longer time interval than any sympatric lizard species. Wide fluctuations in horned lizard body temperatures under natural conditions presumably reflect both the long activity period and perhaps their reduced movements into or out of the sun and shade (most of these lizards are in the open sun when first sighted). More time is thus made available for activities such as feeding. A foraging ant-eater must spend consider able time feeding. Food specialization on ants is economically feasible only because these insects usually occur in a clumped spatial distribution and hence constitute a concentrated food supply. To make use of this patchy and spatially concentrated, but at the same time not overly nutritious, food supply, *P. platyrhinos* has evolved a unique constellation of adaptations that include a large stomach, spiny body form, an expanded period of activity, and "relaxed" thermoregulation (eurythermy). The high reproductive investment of adult horned lizards is probably also a simple and direct consequence of their robust body form (Pianka and Parker, 1975; Vitt and Congdon, 1978). Lizards that must be able to move rapidly to escape predators, such as racerunners

(*Cnemidophorus*), would hardly be expected to weight themselves down with eggs to the same extent as animals like horned lizards that rely almost entirely upon spines and camouflage to avoid their enemies.

## Phylogenetic Constraints and Evolutionary Pathways

Ecologists have only recently begun to adopt a phylogenetic perspective. Related species do not constitute independent observations due to their shared evolutionary histories (Felsenstein, 1985). Phylogenetic relationships among members of a monophyletic group must be known in order to interpret evolution, comparative anatomy and ecology (Felsenstein, 1988; Huey and Bennett, 1986).With a known phylogeny, the evolution of niche transitions can be plotted. Huey and Bennett (1987) and Garland *et al.* (1991) have developed approaches to examine the influence of phylogeny on coadaptation of thermal physiology in some Australian skinks, including several species of *Ctenotus*. Their work provides a foundation for a study of evolution within the genus *Ctenotus* and suggests a hypothesis: the *Ctenotus* adaptive radiation was partially a consequence of the evolution of higher body temperatures (most, but not all, *Ctenotus*, display appreciably higher body temperatures than related skinks).

Given a phylogenetic perspective, anatomical and ecological convergences can be identified. With a known phylogeny, the evolution of niche transitions can be plotted. Comprehensive study of comparative anatomy and ecology of a species-rich genus with a known phylogeny could actually enable prediction of the probable ecologies of unstudied members of that genus, which could then be tested by examination in the field. Such efforts to ascertain evolutionary pathways, as well as the extent to which phylogeny has constrained morphology and ecology, should prove to be most instructive. I plan to undertake such an analysis of the speciose Australian skink genus *Ctenotus* in the near future.

## Towards a Periodic Table of Lizard Niches: Reducing Dimensionality

To order and classify natural phenomena, chemists invented the well-known periodic table of the elements, which allowed them to predict unknown elements as well as certain of their chemical properties and led to our understanding of electron shells. Something analogous, but much more complex than the periodic table of the elements, a "periodic table of niches" might be possible in ecology. Of course, nothing about ecological niches is as simple or discrete as the number of electrons in the outer shell of a chemical element, but most aspects of ecological niches are multidimensional and more continuous.

Powerful multivariate statistical techniques, such as principal components analysis, have been designed to represent the same data but in a new set of orthogonal axes with reduced dimensionality. For original variates that are variously correlated, the first principal component (PC1) is the line through n-dimensional hyperspace that reduces variance by the greatest amount, leaving the smallest residual (unexplained) variance. The second PC is constrained to be at right angles to the first, and reduces the residual variance as much as possible. Likewise for the third PC which is constrained to be a right angles to both the first and second PCs, and so on. Principal components represent combinations of the original dimensions, weighted according to their contribution. With highly correlated data sets, dimensionality can often be greatly reduced. For example, 96% of the variance in a 10-dimensional morphometric hypervolume was "explained" by just the first three principal components (Pianka, 1986).

Nearly 20 years ago, I constructed a very primitive example of a periodic table of niches (Pianka, 1974). Dietary niches repeat themselves in organisms of different sizes that are relatively more or less r- and K-selected. An aphid is more like a lemming and a mantid more like a weasel in their trophic niche, whereas in terms of body size and position on the r-K selection continuum, the aphid and mantid are relatively alike, as are the lemming and the weasel. Other niche dimensions, such as diurnal and nocturnal time of activity, could also be used to construct similar but different periodic tables. My suggestion that a periodic table of lizard niches might actually be possible (Pianka, 1986) was dismissed as "somewhat fanciful" by Gregory (1989). Today I have outlined most of the dimensions required to construct a periodic table of lizard niches. Even though I have not yet been able to achieve this goal, I still hold high hopes that lizard niches can eventually be classified in a space of moderately low dimensionality using axes such as the thermoregulator-thermoconformer continuum (page 133-134) and Dunham and Miles' (1985) discriminant function axis linking mode of foraging to body size and reproductive tactics (page 145). Unfortunately, only 13 of the 82 species used to generate the first axis are included among the 91 species used to generate the second axis. Until more data on lizard niches are gathered, such ananalysis would be premature.

## Summary

Lizards have proven themselves to be almost ideal organisms for ecological studies. Because they are ectotherms, they are often abundant, making them relatively easy to locate, observe, and capture. By facilitating metabolic inactivity on both a daily and a seasonal basis, ectothermy may well confer lizards with an advantage over birds under conditions of low and unpredictable productivity such as in desert regions. Lizards exhibit a wide range of variation

in many morphological, behavioral, physiological, and ecological phenomena. Some species are annuals, whereas others live for decades. Reproductive tactics are readily studied and quite varied. Some species, such as geckos and the iguanine *Anolis*, have invariate small clutch sizes. Other species are exceedingly prolific, laying large clutches of several dozen eggs. Viviparity has arisen repeatedly among different lineages, as have fringed toe lamellae. Both arboreal and terrestrial lizards occur among both nocturnal and diurnal species. Some species such as *Basiliscus* are highly aquatic as well. Lizards inhabit a broad range of habitats, including deserts, grasslands, chaparral, rock outcrops, deciduous forest and rainforest. Lizards exhibit a wide range of thermoregulatory tactics, ranging along a continuum from passive thermoconformers to active thermoregulators. The slope of the regression of body temperature plotted against ambient temperature is a useful index of the position of any given species on this thermoregulation spectrum. A physiological design constraint is suggested by comparative analysis of 82 species from 10 families. This thermoregulation axis can also be exploited as a convenient unidimensional surrogate to represent multidimensional spatial and temporal niche dimensions.

Diets are quite varied among lizards, with some species being generalists and others specializing on only a narrow range of prey. Lizards have specialized on ants, termites, scorpions, other lizards, birds, mammals, and even on some plant foods. Some lizards are ambush hunters, catching prey by sitting and waiting for it to move past. Others are more active, foraging widely for their prey. Although it is energetically more expensive to forage widely and probably more hazardous in terms of attracting the attention of potential predators, foraging widely can be advantageous in increasing contacts with potential prey.

Phylogenetic systematics offers an exciting new framework and perspective for elucidating evolutionary pathways, evolutionary constraints and understanding lizard ecology. Even though the lizard niche is multidimensional and complex , it may eventually prove to be possible to construct a "periodic table of lizard niches" in a space of moderately low dimensionality. However, much more data than are presently available will be required to achieve this goal.

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