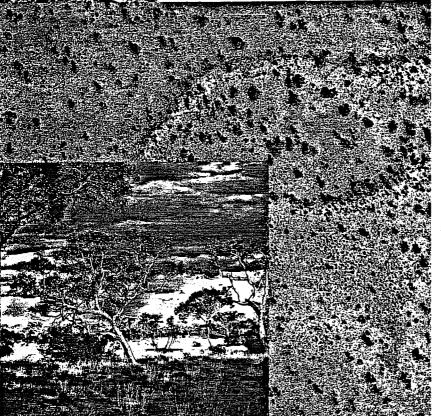
Landscope (1992) 7:10-16.

A LAMB OF LIZARDS

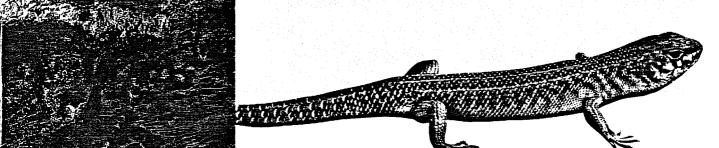


Story and pictures by Eric R. Pianka

Why are there so many lizards in Australian deserts? How do they live through wildfire? How can they compete so well with each other, and with other species? What is the future of their spinifex home?

Professor Eric Pianka, a research scientist from the University of Texas, is fascinated by the beauty and the lizards of Australia's deserts.

- Inset: Ground-level view of a study area before a thunderstorm. This site supports 35 species of lizards.
- Middle Photo: Low-level photograph
 of a study site (about 1km x 1km),
 showing sandridges, marble gums
 (larger dark green spots) and spinifex
 (light green ground cover). Termite
 mounds are small circular patches of
 open red sand. Forty-seven species
 of lizards occur here.
- Outer Photo: Satellite image showing a 150km x 150km patch of the Great Victoria desert. Light beige and pale green patches are fire scars. (Australian Centre for Remote Sensing)

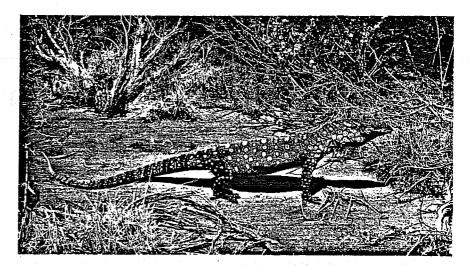




ithin the Great Victoria Desert of Western Australia, sands are rich in iron, usually a delicate pale rusty red, almost flesh coloured. Long undulating sandridges provide attractive curves to create a sensuous image of mother Earth. Equally curvaceous, evergreen marble gum trees (Eucalyptus gongylocarpa) with their smooth white bark adorn this splendid landscape. The dominant ground cover is spinifex (Triodia basedowi), a perennial grass that grows in hummocks or tussocks, a growth form found only in Australia. Rain is infrequent and blue skies prevail most of the time. Taken together, it is a clean, spectacular and most enchanting place, an extensive wilderness area of Crown land containing largely pristing habitats, still relatively undisturbed by human activities aside from the introduction of exotics, which include camels, cats, foxes, and of course rabbits.

Few people have much of an inkling of just what a tremendous biological treasure lies in the Australian deserts. Nowhere else on earth are so many kinds of lizards found living together - at least 47 different species occur on one sandridge site! In addition to familiar forms such as the thorny devil (Moloch horridus) and the perentie (Varanus giganteus), there are a dozen species of exquisitely beautiful nocturnal geckos and another dozen-plus wary and secretive skinks, as well as many others including flap-footed legless pygopodid lizards.

Why are the Australian deserts so rich in species of lizards? The challenge of explaining this high diversity, and of understanding what goes on between component species, is awesome. Compared with Australia the North American deserts are impoverished, with only a dozen species of lizards; in the Kalahari semidesert of southern Africa, only 20 species occur. How do so many lizards avoid competition and manage to coexist? How do they partition resources such as food and microhabitats? Ecologists still know surprisingly little about exactly how diverse natural ecological systems function - ecological understanding that is much needed and will be critical to our own survival as well as that of other species of animals and plants. In fact, the Australian deserts probably offer the last opportunity to



study the regional effects of disturbance on local diversity.

LIVING TOGETHER

Lizards divide up environmental resources in three major ways: by being active at different times, by spending time in different places, and by eating different foods. Such ecological differences reduce competition, allowing coexistence. Many lizard species are food generalists, eating a wide variety of arthropods. Some other species of lizards are dietary specialists, with certain species eating only ants, others termites. and still others almost nothing except other lizards. One species, Pygopus nigriceps, preys heavily on scorpions. Like the North American iguanid horned lizards (genus Phrynosoma), the Australian agamid (Moloch horridus) eats virtually nothing but ants. Such pairs of convergent species are known as ecological equivalents, occupying roughly similar ecological roles in different biogeographic regions. Lizards also differ in their choice of microhabitats: some climb, others are terrestrial, while still others are fossorial, swimming through the sand. Some species frequent the open spaces between spinifex tussocks, whereas others seldom leave the protective cover of spinifex.

Lizards are ectotherms - they obtain their heat from the environment. Animals that usually produce their own heat internally are called endotherms. All plants and nearly all animals are ectothermic; the only continuously endothermic animals are birds and mammals (though even some of these become ectothermic at times). Many ectothermic lizards actually regulate their body temperatures very precisely during periods of activity by appropriate





behaviour. An active desert lizard may have a body temperature every bit as high as that of a bird or mammal; the terms 'warm-blooded' and 'cold-blooded' are misleading and should be abandoned.

Lizards constitute an extremely conspicuous element of the vertebrate faunas of most deserts, especially warmer ones - indeed, in his book The Red Centre the Australian mammalogist H. H. Finlayson referred to the vast interior deserts of Australia as 'a land of lizards'. The reason is ectothermy, which enables the body's metabolism to slow right down, allowing lizards to capitalise on scant and unpredictable food supplies. Moreover, along with other ectotherms. lizards are low-energy animals. In contrast, endothermy is much more energy-expensive; one day's food supply for a small bird will last a lizard of the same weight for over a month. Ectothermy thus has distinct advantages

Top left: Australia's largest lizard, the perentie (Varanus giganteus), which reaches a total length of more than two metres and eats rabbits. Presumably these lizards originally preyed on small marsupials such as hare-wallabies. Photo - E Pianka

Middle left: A climbing nocturnal gecko (Diplodactylus ciliaris), found on large shrubs and small trees, often in association with sandridges. These geckos defend themselves by squirting out a noxious mucus from glands in their tails.

Photo - E Pianka

Below left: A large herbivorous desert blue-tongued skink (*Tiliqua* multifasciata). Photo - E Pianka

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. Hence ectothermy confers a competitive advantage on lizards over endotherms in desert environments.

FIRE IN THE DESERT

Hummock grass, a plant life form unique to Australia, is very flammable. Spinifex tussocks are perfectly designed for combustion, consisting of hemispherical clumps of numerous match-stick sized blades of dry curled grassfilled with flammable resins, loosely interpenetrating one another and laced with ample air spaces. With such ideal tinder, one match is all that is required to start a bonfire. Spinifex has been called an 'ideal pyrophyte'. Some

authorities think that the extensive grasslands in Australia were formed and maintained by regular Aboriginal burning, and that over many thousands of years Aborigines acted to select members of plant communities for resistance to fire or for an ability to come back quickly following a fire. Most early explorers and historians of Australia commented on the extent to which the Aborigines exploited fire. Spinifex grasses give off dark smoke which can be seen from afar. Australian Aborigines used fire to send long-distance smoke signals, to manage habitats and keep terrain open, as well as to facilitate capture of various animals for food.

Upon ignition, an isolated grass tussock generates an egg-shaped thermal field around it. At low wind velocities, isotherms for such a field are symmetric and close to the tussock, but as wind speed increases, the thermal field

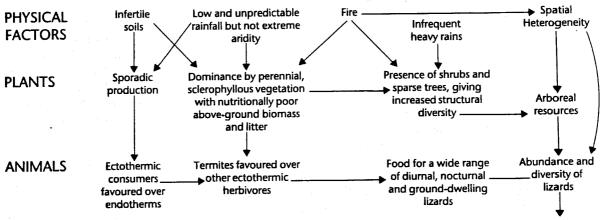
*Morton, S.R. and C.D. James. 1988. The diversity and abundance of lizards in arid Australia: a new hypothesis.' American Naturalist 132: 237-256.

FACTORS INFLUENCING LIZARD DIVERSITY

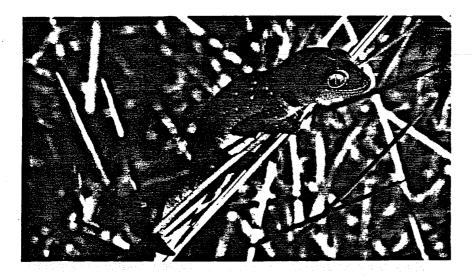
At least a dozen different factors contribute to the high diversity of lizards in arid Australia:

- unpredictable rainfall
- 2 nutrient-poor soils
- 3 the unique hummock life form and physical structure of spinifex grasses
- 4 the low nutrient content of spinifex
- 5 abundant and diverse termite faunas
- 6 nocturnality
- 7 fossoriality (sand swimming)
- 8 arboreality
- 9 habitat specificity
- 10 usurpation of ecological roles occupied by other taxa elsewhere
- 11 biogeographic and historical factors
- 12 a complex fire-succession cycle that creates and maintains habitat variety via disturbance

Most of the above mechanisms were incorporated into a megahypothesis recently proposed by Steve Morton and Craig James at the CSIRO.* This causal network relates a wide range of factors to the diversity of lizards in arid Australia, as follows. Unpredictable rainfall and nutrient-poor soils result in scant and erratic primary production, favouring spinifex grasses that are poor in nitrogen and relatively unusable fodder for most herbivores except termites, which in turn constitute a food resource particularly suitable for ectothermic lizards. Moreover, aperiodic heavy rainfall promotes woody vegetation, therefore supporting arboreal and litterdwelling species of lizards. Although not included in their scheme, fire and fire-induced spatial heterogeneity are easily added.



LIZARD RADIATION





becomes asymmetric and begins to elongate, especially downwind. If other tussocks are then captured within the field, they too ignite and the fire spreads. Due to the geometry of thermal fields, fires tend to burn along broad continuous fronts at low wind velocities, whereas at higher wind velocities, elongated narrow tongues of flame are produced. Fires are more likely to break up at higher wind velocities due to these elongated tongues of flame.

Previously burned areas have sparser vegetation and act as gigantic firebreaks. Sandridges and termitaria (termite nests) create smaller vegetationless areas that also act as local firebreaks, but with fundamentally different geometries and at very different spatial scales. Airborne flaming materials, termed 'firebrands', may jump over unburned areas to rekindle new fires on the downwind side of a fire, sometimes resulting in multiple fire fronts (these can extinguish one another when one runs into another's swath). 'Sleepers', embers created from burning eucalyptus hardwood, lie dormant in burned areas, only to reignite at the edges days or even weeks later when new strong winds come up. New secondary bush fires begin that take off at an angle, resulting in an interesting net-like pattern that generates a patchwork of refuges. Major factors that determine the frequency, extent and geometry of grass fires include temperature, combustibility, plant biomass and spatial distribution, natural firebreaks, and of course winds, which as explained above are of paramount importance.

A fire-succession cycle helps to explain the high lizard diversity of the Australian interior. Fires are a

predictable event in arid Australia, and generate a mosaic of patches of habitat at various stages of post-fire succession. As a more or less regular agent of disturbance. fires contribute substantially to maintaining diversity in Australian desert lizard systems. Bush fires are usually started by lightning, and can rage completely out of control for weeks on end across many square kilometres of desert. Fires vary considerably in intensity and extent. Eucalyptus trees are fire-resistant and usually survive a hot but brief ground fire carried by the exceedingly flammable Triodia grass tussocks. Moreover, fires frequently spread like a net, missing an occasional isolated grass tussock or even large tracts. Effects on lizards and lizard microhabitats are drastic, yet vary from place to place. Many or even most individual lizards may live through the burn itself, only to succumb in the firereduced habitat that can last for years. Fires attract hawks and crows, which feed on fire-killed animals and take advantage of the lack of cover to catch survivors.

Some lizard species with open habitat requirements (such as Ctenophorus isolepis, Ctenophorus inermis and Ctenotus calurus) reinvade and repopulate burned areas rapidly. Other species (such as Delma butleri, Omolepida branchialis, and/or Diplodactylus elderi) require large spinifex tussocks for microhabitats, and become very rare or vanish after a burn. However, such 'climax' species (those living in long-undisturbed habitat) continue to exist in isolated pockets and patches of unburned habitat. Spinifex rejuvenates rapidly from live roots as well as by seedling establishment. Newly Left: This nocturnal gecko (Diplodactylus elderi) seldom leaves the protective cover of large, long-unburned spinifex tussocks. It also defends itself with a tail-gland mucus secretion.

Photo - E Pianka

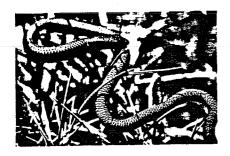
Right: The thorny devil (*Moloch horridus*), a spiny agamid that has specialised on ants as food.

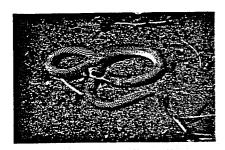
Photo - E Pianka

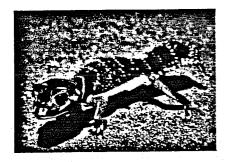
burned areas are very open with lots of bare ground and tiny, well-spaced clumps of *Triodia*. Unburned patches, in contrast, are composed of large ancient tussocks, frequently close together with little open space between them. As time progresses, *Triodia* clumps grow and 'close in', gradually becoming more and more vulnerable to carrying another fire.

Throughout this process, lizard microhabitats (and associated food resources) change. Lizard numbers fluctuate along with them. Numbers also alter substantially through fire succession, with some common species becoming quite rare. Rare species do not always remain rare and may be vitally important to hold a system together, allowing the system to respond to changing environmental conditions. A particular lizard species can even go extinct within a given area (known as a 'sink' habitat), but by surviving in an adjacent patch (a 'source' habitat) can still survive in the region. Periodic recolonisation of 'sinks' from 'sources' allows such species to persist in the overall landscape.

Satellite imagery provides a powerful new way to study the dynamics and geometry of wildfire. In inland Australia, cloud cover is usually low or non-existent, and excellent imagery is the rule. This facilitates analyses on a region-wide basis.







Top: The snake-like flap-footed pygopodid lizard (*Delma butleri*), another denizen of large spinifex tussocks that have gone long unburned. Photo - E Pianka

Middle: Another flap-foot (*Pygopus rapriceps*), which is nocturnal and feeds primarily on scorpions.

Photo - E Pianka

Bottom: The knob-tailed gecko (Nephrurus levis) is nocturnal and is found in spinifex habitats on sandplains. A sister species (Nephrurus levis) is found on sandridges.

Photo - E Pianka

Fire spreads rapidly through spinifex grassland under suitable wind conditions.

Photo - David Pearson

Whereas ash absorbs infrared, unburned vegetation reflects it. The sizes and geometry of fires can be readily measured and fire scars traced through time. Frequency distributions of the ages and sizes of fire scars can also be estimated and examined to see how often a particular area is burned.

In such a large natural region, habitat patches at different stages of post-fire recovery can reach a dynamic

equilibrium: new burns continually arise from older, thicker, more combustible stages of fire succession. Reflectance properties (visible and invisible reflections) recorded in space could allow scientists to estimate the present state of all animal and plant life (biotas) in the region, as well as the climate during the immediate past. Careful field work is needed to learn the extent to which changes over time in patterns of reflectance can be extrapolated to firesuccession patterns on the land. Although a great deal more remains to be known, monitoring habitats and biotic diversity from satellites could ultimately prove to be possible in arid regions.

VANISHING WILDERNESS

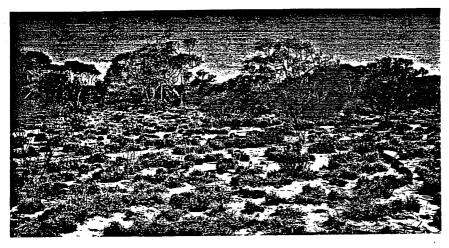
Many people consider biology, particularly ecology, to be a luxury that they can do without. Even many medical schools in the USA no longer require that their pre-medical students obtain a biological major. Basic biology is not a luxury at all, but rather an absolute necessity. Despite our human-centred attitudes, other life forms are not irrelevant to our own existence. As proven products of natural selection that have adapted to natural environments over millennia, they have a right to exist, With human populations burgeoning and pressures on space and other limited resources intensifying, we need all the biological knowledge that we can possibly get.

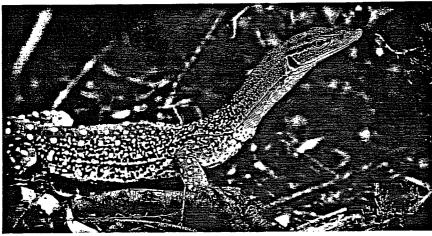
Ecological understanding is particularly vital. There has to be a great

urgency to basic ecological research, simply because the worldwide press of humanity is rapidly driving other species extinct and destroying the very systems that ecologists seek to understand. No natural community remains pristine. Pathetically, many will disappear without even being adequately described, let alone remotely understood. As existing species go extinct and even entire ecosystems disappear, we lose forever the opportunity to study them. Knowledge of their evolutionary history and adaptations vanishes with them: we are thus losing access to valuable biological information itself. Indeed, as H. Rolston remarks in 'Duties to Endangered Species' (BioScience 35, 1985), 'destroying species is like tearing pages out of an unread book, written in a language humans hardly know how to read'. Just as ecologists in many parts of the world are finally beginning to learn to read the unread (and rapidly disappearing) 'book', they are encountering governmental and public hostility and having a difficult time attracting support.

Australia has been undergoing a gradual natural process of desertification for the last million years, but that process has accelerated greatly during the past century due to human activities, particularly agricultural clearing and overgrazing and the burning of fossil fuels. As our population burgeons and we destroy the last remaining natural habitats, earth's atmosphere is being altered at an ever-increasing rate, leading







to weather modification. Long-held meteorological records the world over are being broken: a few years ago, the lowest low ever recorded (during Hurricane Gilbert) in late summer was followed in winter by the highest high on record. On 21 February 1991, Perth experienced the highest temperature (46.2°C) ever recorded in 150 years of habitation. Global warming is having its impact on virtually all plants and animals, including humans, and its effects will continue to intensify into the foreseeable future. Crop failures and other ecocatastrophes seem to be inevitable.

Fires were once a major agent of disturbance in all grasslands and semideserts, including African savannas and the North American tall grass prairies. Most of these ecosystems have now been reduced to mere vestiges, and controlled burning and/or fire control are practised by humans almost everywhere. The inland Australian desert is one of the last remaining areas where natural wildfires are still a regular and dominant feature of an extensive natural landscape largely undisturbed by humans. (Aborigines do increase the frequency of fires, but most are started

Typical west Great Victoria Desert vegetation - spinifex and marble gums. Photo - David Pearson

Gould's sand goanna, a generalist predator of insects, other lizards and small mammals.

Photo - David Pearson

by lightning.) The Australian deserts constitute an exceedingly valuable system for the study of large-scale community ecology.

Inroads on the wilderness have gone far enough. In both North America and in the Kalahari, most of my study sites have succumbed to farming and urbanisation, as have deserts almost everywhere. So far, the spinifex desert has been able to resist the advancing human exploiters. Some people dream of the day that technological 'advances', such as water movement plans or distillation of sea water, will make it possible to replace the desert with vast agricultural fields or even cities. I fervently hope that this never happens, for if it ever should, the quality and dignity of our lives will be sadly diminished.





Ctenotus piankai and Ctenotus helenae. During 1966-68, Eric Pianka and his ex-wife Helen discovered half a dozen undescribed species of skinks.

Eric Pianka is Denton A. Cooley Centennial Professor of Zoology at the University of Texas at Austin. His textbook, Evolutionary Ecology, has been translated into Japanese, Polish, Russian and Spanish. He has researched lizard ecology in North America and the Kalahari Desert as well as in Western Australia. In 25 years he has made four trips 'down under', once as a Guggenheim fellow (1978-79), living four full years in the outback. He is the acknowledged pioneer of research on the ecology of lizards in the WA part of the Great Victoria Desert; one of his two doctorates is a D.Sc from the University of Western Australia. In 1990-91, he came back as a Fulbright Senior Research Scholar under the auspices of the Australian-American Educational Foundation. He was hosted by the Zoology Department at the University of Western Australia and by CALM, and funded by the National Geographic Society.

Professor Pianka describes his work in Australia as 'rediscovering what Aborigines once knew and writing it down in scientific English'. He seems to have taken Australia to his heart; even 'those pesky face flies' haven't kept him from coming back again and again. He hopes to return several more times during the coming decade, although global warming threatens to alter the landscape.

He recently received grants from NASA (the US National Aeronautics and Space Administration) and NSF (the National Science Foundation) to undertake a full scale landscape ecology analysis of fires using satellite imagery.