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Lizards of the Australian Deserts: Uncovering an Extraordinary Ecological Story

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For 150 years after European settlement of Australia there were no indications that the lizards of the Australian deserts might be exceptional in their species diversity and ecology. However, from the 1950s to the present, and especially from the 1970s, there has been acceleration in the rate of description of new species, a process likely to push the number known from the deserts past 400. Systematic work led rapidly to ecological research showing that the most diverse assemblages of lizards on Earth occur in the spinifex deserts, a phenomenon leading to considerable debate among ecologists on causal mechanisms. Appreciation of the extraordinary nature of the Australian desert lizards has come about through four developments: a cadre of dedicated systematists; explosive expansion in technologies for molecular analysis of species relationships; opening-up of the spinifex country to four-wheel-drive transport; and the vigorous efforts of a few dedicated ecologists.

Introduction

Among the most striking features of arid Australia is its remarkable evolutionary radiation of reptiles—it is a land of lizards. What is also remarkable is the extent to which this fact remained unrecognized for 150 years after European settlement of the continent before emerging in a rush of endeavour from the 1970s onward. This paper inquires into the conjugation of forces leading to such an outburst of scientific activity. It first outlines the course of growth in taxonomic knowledge of reptiles. Then it considers the search for ecological and evolutionary explanations for the phenomenon uncovered by that systematic work, the most diverse assemblage of desert lizards on the planet.

Taxonomy and Systematics

Terrestrial Australian reptiles are comprised of lizards (families Carphodactylidae, Diplodactylidae, Gekkonidae, Pygopodidae, Scincidae, Agamidae and Varanidae) and snakes (Typhlopidae, Pythonidae, Colubridae and Elapidae). All these families except colubrid snakes occur in the deserts. In order to display the time-course in development of taxonomic knowledge we determined the year of description of each currently recognized species, using the most recent distribution maps.[1] A species was included in analysis if substantial parts of its distribution were adjudged to occur within the boundaries of the deserts (as defined by Morton and colleagues[2]).

Figure 1 shows first an extended period of 150 years during which slow and sporadic growth occurred in taxonomic knowledge, noting a dip between 1930 and 1950 due ultimately to stringencies of Depression and World War. The period shows a steady rate of increase in the numbers of species recognized by scientists (Fig. 2). In concert with the times most descriptions were made from specimens sent to European institutions. For example, at the British Museum the brothers George Robert and John Edward Gray described nearly 30 species of Australian desert reptiles between 1825 (*Tiliqua rugosa*) and 1864 (*Lerista gerrardii*; both Scincidae). There seems nothing unusual about the measured growth throughout this period, for it is probably characteristic of the time-course of knowledge of many groups of Australian organisms. Nor were there indications in this taxonomic work that apart from the uniqueness of the individual species, the diversity, richness and abundance of lizards of the Australian deserts might be anything other than unexceptional. Snakes have made up a minor proportion of total reptile species throughout the full span of time.

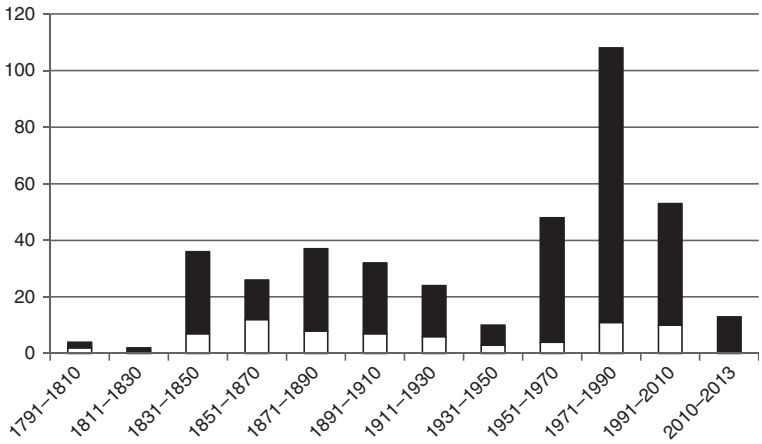

Figure 1. Temporal pattern from the time of European settlement, in 20-year brackets, of the description of species of Australian desert reptiles (lizards black columns, snakes open columns).

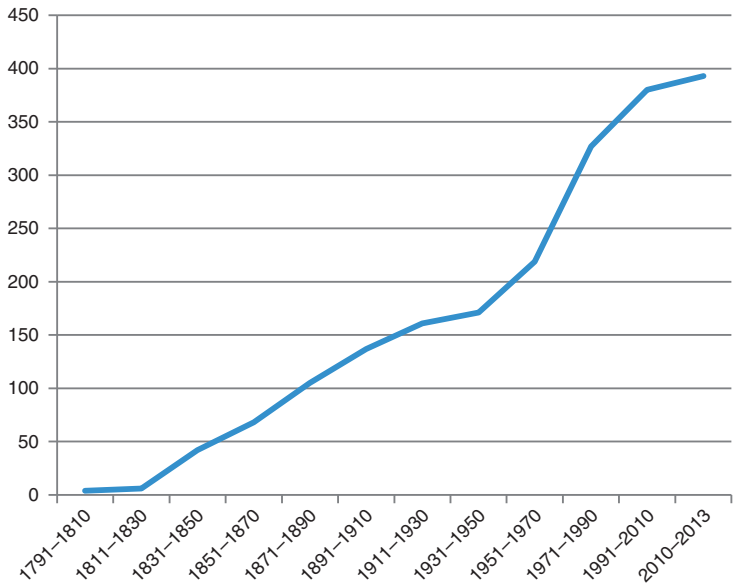

Figure 2. Cumulative number of species of reptiles recognised from the Australian deserts since the time of European settlement, in 20-year brackets.

The initial phase may be seen to come to its end in 1963 with the publication of Eric Worrell's *Reptiles of Australia*, the first book to deal comprehensively with the Australian reptile fauna.[3] Worrell summarised reptile taxonomy for the benefit of a general audience through the several editions of his book, as well as contributing to it through technical papers. His strongest interests were in snakes rather than lizards, with his Australian Wildlife Park supplying venom from Australian and foreign snakes for development of anti-venom over many years.[4] Nothing in his *Reptiles of Australia* drew particular attention to desert reptiles.

The second phase, from 1951 through to the present, exhibits acceleration. The mean rate of

description of new species per decade tripled from 11 between 1791 and 1950 to 35 between 1951 and 2010 (Fig. 1). Although Fig. 2 might be read to suggest a tapering off in new species in the most recent times, such a conclusion would be hasty because the final segment of the graph (13 species) represents three years only. Hence, there is as yet no objective evidence of approach to an asymptote in Fig. 2 that would represent full knowledge of all species in the assemblage: the number of species in the deserts is clearly destined to shoot well past 400. In parallel with expanding species-level taxonomy, numbers of new lizard genera were erected throughout this phase.

Curators and Collectors

What factors led to the dramatic increase in knowledge of reptilian diversity in the Australian deserts? Undoubtedly the most important was appointment of greater numbers of curators of reptiles in Australian museums, two of whom were principal architects of the explosion of knowledge. Harold Cogger, Curator at the Australian Museum in Sydney from 1960–75, and Deputy Director from 1976–95, set the stage by publishing a wonderful field-guide, *Reptiles and Amphibians of Australia*, in 1973.[5] The book was brought to life by colour photographs of virtually every species and, for the first time, it made available to non-specialists taxonomic keys for discriminating each species while in the bush. Cogger had undertaken ecological work on lizards inhabiting spinifex (*Triodia* spp.) and mallee (*Eucalyptus* spp.) in semi-arid New South Wales[6], and travelled widely in the deserts. His taxonomic descriptions did not happen to include desert species, but the various editions of his book were informed with personal knowledge of the diversity to be found in the outback. *Reptiles and Amphibians of Australia* inspired a multitude of naturalists and scientists to seek further and further afield and thereby to contribute specimens to the museums.

The various editions of Cogger's *Reptiles and Amphibians of Australia* expanded inexorably in size in response to the fact that the numbers of described species were increasing in wetter parts of Australia as well as in the arid zone. Among the biggest contributors to the enlargement of Cogger's book, and to the work evident in Fig. 1, was Glen Storr, Curator at the Western Australian Museum from 1963 until 1986.[7] Like Cogger, he was at the centre of a web of collectors and ecologists who spread across the outback of Western Australia, the Northern Territory and Queensland. During an extended and extraordinarily productive period from 1964 to the end of his life in 1990, Storr described 105 new species of desert lizards and eight of snakes. As Laurie Smith put it:

> In 1971, he suffered a serious illness and nearly died. Impaired lung function meant he could only walk a short distance before becoming short of breath. He convinced himself he was living on borrowed time, and no doubt this attitude affected his approach to his goals. His quiet retiring life-style (Glen never married) became positively monastic, with papers being produced at an even greater rate.[7]

Storr had an outstanding eye for discriminatory taxonomic features in the skinks *Ctenotus* and *Lerista*, genera of considerable and initially confusing diversity (the genus *Ctenotus* was erected by him in 1964). He described 49 (including 38 desert-dwellers) of the 103 currently recognized species of *Ctenotus* and 26 species (23 of them in the deserts) of the 91 in *Lerista*. His guidebooks to Western Australian lizards, written with colleagues at the Western Australian Museum, allowed naturalists access to his store of systematic knowledge.[8]

Two further individuals made notable contributions to the biology of lizards throughout this period, although their efforts were not focused on the deserts: in systematics, Allen Greer[9]; and in ecology, Harold Heatwole[10].

Technical Factors

The recent expansive phase of taxonomic knowledge is due also to technical advancements in molecular systematics. The increasing numbers of specimens flowing in to museums from the 1970s onwards was paralleled by developments in the use of DNA technologies for quantifying systematic distinctiveness and relatedness. This world-wide phenomenon has revolutionised systematics; in Australia its application led rapidly to further uncovering of the hidden evolutionary richness of the Australian reptiles (and among many other taxonomic groups too). Leaders of this field with Australian desert reptiles are Stephen Donnellan, Mark Hutchinson and Mark Adams at the South Australian Museum, and

Figure 3. *Diporiphora ameliae* from Valetta Station, Qld, a species newly described in 2012. Photograph: Angus Emmott.

Ken Aplin from the Western Australian and other Museums.[11] This aspect of phase two is still especially active, with many other contributors (Fig. 3).

A second technical development is so much in the background as to be easily overlooked—the increasing availability of reliable four-wheel-drive vehicles from the 1970s onward. Camel teams had hitherto been essential for travel into the western deserts, meaning practically that the country was mostly inaccessible to non-Indigenous people. The availability of tough yet comfortable vehicles allowed the network of field-survey workers and reptile collectors mentioned above to fan out across the country. Other groups relevant to this account took up the same opportunities, among them not just ecologists but also anthropologists.[12]

The Land of Lizards: the Spinifex Country

Tantalising hints of something out of the ordinary in desert lizards began emerging as soon as the spinifex country was opened up by developments in transport. The naturalist H. H. Finlayson travelled (with horses and camels still) many times into northern South Australia and the southern Northern Territory during the 1920s and 1930s. Although his attention was focused on mammals, his travels with Aboriginal people exposed him to the significance of reptiles and led him to coin an important phrase.

> To a very large extent it is a land of lizards … two species of monitors, the goannas of bush lore, are more often seen than any others, and scarcely a day goes by without encounters of some sort with these two great lizards, on account of the blacks' fondness for them as an article of diet.[13]

Donald Thomson led a small party by truck westward across the Northern Territory border into the Great Sandy Desert of Western Australia, north of Lake Mackay, in 1957.[14] Thomson was biologist-cum-anthropologist, and as well as reporting on matters Indigenous he published, with William Hosmer, a systematic account of the reptiles encountered.[15,16] The dietary importance of lizards was evident.

> … the ability of the aborigines … to utilize every part of these apparently insignificant lizards has been a factor in the survival of the Bindibu [Pintupi] in parts of the desert where the white man, strange to this environment, sees no game and can find nothing that appears to be edible.[16]

In 1963, the journalist Douglas Lockwood accompanied Jeremy Long on an expedition from Papunya, Northern Territory, into the Gibson Desert of Western Australia. Lockwood's account of their journey into Pintupi country, published the following year, was titled *The Lizard Eaters*.

> … a young girl, aged about six, was sitting alone in the desert … Two hours later the mother of the first girl and a sister aged about thirteen arrived. They had been hunting and had found several lizards. Later still, the father, Kuku, came in with a crown of lizards in his hair.[17]

Dick Kimber travelled widely in the deserts west of Alice Springs in the 1970s, often with Pintupi man Nosepeg Tjupurrula, the principal guide also for the journey recorded in *The Lizard Eaters*. Nosepeg was creative in English. In 1976, Kimber later recounted, Nosepeg mentioned that he and his Aboriginal compatriots were living in an 'enormous reptile "poultry run"'.

> Tjupurrula saw the fresh goanna track and immediately turned to follow it. He came to the

> goanna hole and instantly knew that it was 'at home' … He pushed the digging-stick through the sand … three times, always closely watching the slight mound of soil which had held the spinifex tussock. Each probe took him closer to the tussock. Suddenly the soil began to give way as a hole opened up immediately below the centre of the tussock-mound. As the lucky goanna poked his head up … Tjupurrula seized him by the neck.[18]

Many observers at the Aboriginal settlements created on the fringes of the western deserts from the 1950s onward also noticed the widespread use of reptiles for food and medicine. For example, Father Anthony Peile of the Balgo Mission, Western Australia, was impressed by the importance of reptiles to the Kukatja people of the northern Great Sandy Desert, and his publications included accounts of ethno-herpetology.[19]

The significance of these accounts to our story is the growing realisation that the lizard assemblages of the sandy deserts were not just diverse in species but also contained an extraordinary abundance of individuals. What appeared to white visitors as a wasteland was a 'reptile poultry run' to its Indigenous owners. Hence, major ecological questions begin to take on more concrete form: why are there so many species, and how is it that the animals are so abundant?

One ecologist stood out in shaping these questions, indeed in creating them. In 1966 Eric Pianka, a postdoctoral fellow at Princeton University, fulfilled a long-held dream of travelling to Australia. He had undertaken doctoral studies in North America and wished to compare the assemblages of lizards in major continental deserts world-wide, with Australia becoming the first comparison. After 18 months he returned to the USA, took up a position at the University of Texas, and from that base returned to the Great Victoria Desert in 1978 for a further year. Over the decades since Pianka has continued to visit Australia for long periods.

> I can't seem to get Australia out of my system; I keep coming back here, again and again. My first trip down under was a quarter of a century ago … I've been back several times since then and have lived nearly four years in the outback … I have been at this remote study site for almost two weeks and haven't seen another human being for nearly that long. I treasure my solitude, space, privacy, peace and tranquillity. I'm a desert rat in my element.[20]

Pianka's memoir explains his pronounced reclusiveness, stemming ultimately from a dreadful childhood accident. His hermit-like tendencies account for the fact that he seemed elusive and indistinct to many Australian ecologists. One of us (SRM) remembers news of Pianka's imminent arrival in the country being circulated, only for him to disappear into the Great Victoria Desert without contact and far from sight. It was a signal occasion when we tempted him finally, in 1991, to visit Alice Springs and to deliver a seminar. But there was nothing reserved or retiring about his powerful string of publications, beginning in 1968.[21]

Pianka was aware of the uncertain state of lizard taxonomy and so took his first collections to Glen Storr, who assiduously turned the specimens into more new species (including *Ctenotus piankai*). Laurie Smith has commented that corroboration of morphological analysis by Pianka's detailed ecological data gave Storr confidence in his early taxonomic work in this complex genus.[7] Pianka's wealth of hard-won data, together with comparisons among North American and southern African deserts, was summarised in *Ecology and Natural History of Desert Lizards*.[22] In his writings he expresses continuing astonishment that the Australian spinifex deserts contain the most diverse lizard communities on Earth (up to 11 species at a site in North America and 18 in the Kalahari, compared with 42 in Australia) (Fig. 4).[23]

Such questions led others into field and conceptual ecological work in the spinifex deserts. Steve Morton and Craig James were motivated by the excitement of understanding fundamental attributes of a vast area of the continent that hitherto had largely been overlooked by ecologists. They placed the diversity and abundance of the lizard assemblages into a broad context of the spinifex grassland biome, the least productive among all environments of arid Australia.[24] Because spinifex grows where soils are distinctly infertile most herbivores find the plant inedible and, consequently, considerable biomass accumulates. However, termites are capable of using poor forage thanks to the symbiotic microbes in their digestive systems, and so are exceedingly abundant. The hypothesis, therefore, is

Figure 4. Mike Gillam and Mike Fleming installing pit-traps for lizards in the Tanami Desert, Northern Territory, October 1985. Photograph: Steve Morton.

that lizards have radiated in spinifex and are so abundant there largely because of the particular suitability of termites as food for lizards. Those species whose abundance is supported by the ready supply of termites in turn provide a food-source for numerous lizard-eaters, such as goannas (*Varanus* spp.). The hypothesis simultaneously emphasised a web of related forces adding to the success of lizards. Notable among such forces was the erratic rainfall that produces a characteristic 'boom and bust' in food supplies, a pattern relatively readily accommodated to by the reptilian body-plan. Pianka's studies had revealed high proportions of termites in the diets of many lizards[22], and Craig James subsequently confirmed, in spinifex grassland south of Alice Springs, that termites were indeed finely partitioned in diets of sympatric *Ctenotus*, the different species eating different termites as the latter change in activity through time.[25]

Such an inter-connected hypothesis is almost certainly inadequate at certain junctures. Pianka pointed out that it does not account for the fact that southern Africa supports the highest diversity of termites yet only moderate lizard diversity compared to Australia.[26] Comparisons with semi-arid South American environments also cast doubt on the overall efficacy of the hypothesis.[27]

A further important element of ecosystem dynamics in spinifex country is intermittent burning. The fire regimes of the spinifex grasslands are the most globally distinctive of all Australian desert vegetation types. Because biomass does not break down to the same extent as in other vegetation formations it accumulates in relationship to aggregated rainfall. Hence, spinifex inevitably burns after some years—indeed, it is 'designed' to do so—and opens up the system to a flush of successional plant species before the spinifex gradually re-grows to dominance once more.[28] Fire thereby creates mosaics of different vegetational states at the landscape scale, leading to suggestions by Pianka that lizard diversity has been further favoured through evolutionary time by such succession.[26] It is unarguable that fire opens up early-successional habitats for species other than those closely associated with mature spinifex. However, virtually all such species are found in many habitats widely across the deserts, not just in the spinifex country. It seems unlikely, therefore, that these taxa speciated in response to regular presence of early successional phases following the burning of spinifex. Nevertheless,

it is true that fire allows them to take advantage of the dynamism introduced into spinifex grasslands by pyrrhic succession, and so to contribute to the large pool of species to be found there.

A decade after the ideas summarised above were advanced, Craig James and Rick Shine suggested that the size of the species pool in the spinifex deserts is indeed a fundamental element in creating high levels of coexistence at the site-scale.[29]

Their analysis was only of *Ctenotus* species, yet has wider implications. Most arid-zone species occur over vast areas, yet these distributions reveal occupation of similar ranges of 'climate space' to *Ctenotus* from all bioclimatic regions, so that a given amount of climatic space translates into a larger geographic distribution—hence, more potential overlap with other species—in the deserts than in other biomes. Hence, the high number of coexisting *Ctenotus* species in arid-zone habitats may simply reflect the facts that the deserts are large (so that many species have evolved therein) and climatically relatively homogeneous (so that any species evolving in that biome can disperse widely, and thus overlap with many other species). To a considerable extent the unusual species richness of lizards at study-sites in the spinifex grasslands may be more an epiphenomenon of continental biogeography, of the large pool of potential colonists at a site, than a result of local ecological interactions.

The interpretations advanced by James and Shine are convincing. Nevertheless, their narrative does leave aside the question as to why the environment is sufficiently congenial as to provide for ongoing persistence of so many species after they have been produced through evolutionary time. It seems that the characteristics of the food sources sustaining lizards will remain at least a partial contributor to an ultimate explanation of the phenomenon. Furthermore, debates about ecological causes of a rich assemblage of abundant lizards have had wider influence on accounts of the likely ecological forces dominant in the Australian deserts.[2,30]

Ecological questions have not been confined to the origins of high abundance and diversity, or to inter-continental comparisons of diversity. Fire pattern and its management implications have received attention[31], as well as ongoing investigations of autecology and coexistence through fine-scale habitat separation[32].

Beyond the Spinifex Country

Not everyone has been pre-occupied by the spinifex deserts. Elsewhere, just as in the spinifex country, the breadth of lizards available for study provides many areas for fruitful ecological research. Studies are gradually accumulating of lizard assemblages in other major desert biomes such as the mulga and chenopod shrublands.[33] Michael Bull's long-term studies of behaviour in large skinks, *Tiliqua* and *Egernia*, stand out.[34] Work begins to appear on conservation biology of particular species.[35] The wealth of species and potential questions here, too, seem certain to continue attracting attention from naturalists and scientists.

Of rapidly emerging potential, among naturalists particularly, is the phenomenon of social media, which is allowing a community of like-minded people to share knowledge of reptiles (both in and beyond the deserts). There are several on-line groups allowing discussion and debate in real time on different aspects of herpetology. These forums may be spurring people on to greater endeavour—they foster interest, especially among novices; provide inspiration to otherwise isolated individuals; and provide a large body of high-quality photographs, in turn allowing taxonomists quickly to observe significant variations across the continent. Smart phone 'apps' may accelerate this phenomenon.[36] In addition a website provides up-to-date information on current taxonomy for any interested observer.[37]

Conclusion

Appreciation of the extraordinary nature of the Australian desert lizards has come about through four developments: a cadre of dedicated systematists; explosive expansion in technologies for molecular analysis of species relationships; opening-up of the spinifex country; and the vigorous efforts of a few dedicated ecologists.

The significance of a staunch core of systematists is not likely to be unique to the lizard story. The uncovering, through time, of unusual aspects of the Australian biota has always depended on such aggregated effort and will continue to do so. Nor is the explosion of knowledge being

made available through DNA technologies particularly distinctive in Australian lizards, for such techniques are revolutionising systematics world-wide. In pointing out these wider generalities we are in no way downplaying their importance in the case of lizards.

The third force identified—four-wheel-drive transport into hitherto largely impenetrable country—is of special significance. Any view of the spinifex grasslands as a biome worthy of investigation seems to have taken some time to develop because it was widely seen in earlier times as a 'wasteland' unfit for pastoral use (or any other, for that matter). Growing interest in Aboriginal culture and knowledge led more people to regard the country as interesting in its own right, because traditional ways of life have persisted in the western deserts for longer than in most other regions of Australia. It also led to concerns about land management, as Aboriginal burning (or, more properly, its withdrawal) became a focus of natural resource managers. With the advent of effective vehicles such interests could now be satisfied, and so we see an ongoing transformation in perceptions of the spinifex deserts among scientists and naturalists.

Finally, growth in knowledge of the Australian desert lizards has been deeply influenced by the passion of some dedicated ecologists. The most prominent, Eric Pianka, has devoted a big part of his life to his Australian work. In turn, his prominence in ecology ensured that his favourite animals and their environment gained greater international exposure than otherwise might have been expected.[38] As time passes, several other scientists and naturalists are in the process of creating their own sustained records of investigation.

The contribution of individuals determined to follow their own passions is notable in the desert lizard story. This is particularly so because scientific investigation of the spinifex grasslands, where the full flowering of phenomenal diversity existed, was never propelled by wider economic forces, which so often act to throw up financial opportunities for research leading to growth in fundamental understanding. Without such financial incentives for basic research only the most determined investigators are likely to persist—and in this case to succeed in revealing some astonishing things about the ecology of the continent. To borrow the words of Douglas Lockwood[17], we now understand that Australia wears a crown of lizards in its hair.

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