Understanding arid Australia

It's a land of extremes — unlike, in many important ways, most of the world's driest areas

Peter Canty

Arid Australia is truly a land 'where the creeks run dry or ten foot high': its normal state is one of severe drought. Water-holding frogs (*Cyclorana platycephalus*) lie buried for months or even years, awaiting the sudden flush of food provided by flooding rains.

As the first European explorers of this continent discovered (to their cost, more often than not), Australia's vast deserts and arid lands differ fundamentally from similar environments in the Northern Hemisphere.

Different rules apply here — for plants and animals as well as for humans. There may be superficial similarities, but they are mirages — baffling images that conceal the profound differences.

The paradox is that while Australia's arid zone (which covers about 70% of the continent) has attracted considerable research, surprisingly little effort has been devoted to attempting to understand how it works on a broad scale. Researchers have usually accepted an ecological framework based on Northern Hemisphere research, despite obvious contrasts.

For example, while theoretical models of arid zone ecology ignore the role of fire in shaping the interaction of land, plants and animals, we now know that fire is among the most important forces in Australia's arid zone, profoundly modifying habitats on which whole communities depend.

Second, an average annual rainfall of fewer than 250 mm has long been regarded as one of the definitions of an arid zone; yet between 1870 and 1980 the annual rainfall in

Alice Springs ranged from 60 to about 900 mm, with an average of 270 mm. Alice Springs is indisputably located in the arid zone. What is most significant is the extremes of rainfall rather than the mean: as the bush song has it, this is a land 'where the creeks run dry or ten foot high, and it's either drought or plenty'.

Third, a historical bias towards certain groups of species — for example, the dominant mammals of African, Asian and North American deserts — has ignored the fact that mammals have become major players in those environments only because water and nutrients, although in short supply, are reliable enough to sustain warm-blooded vertebrates such as birds and mammals.

The dominant predators in much of Australia's arid lands, however, are reptiles, whose physiology makes them better able to cope with extremes of drought and sudden, short-lived abundance.

At a more subtle level, the apparently uniform topography of Australia's arid regions has confounded ecologists expecting to find the sort of relationships between soil type (which, in Australia's case, is mostly leached and nutrient-poor), rainfall and vegetation that have structured patterns of animal distribution in their Northern Hemisphere counterparts. Here, distribution and abundance are likely to be driven more by micro-topographical factors such as highly localised sources of water and nutrients.

All these factors have made it difficult for ecologists to compare what they have found in arid Australia with similar environments in other parts of the world. They lacked a theoretical framework that can not only help them understand and explain the differences, but also help manage human impacts, including pastoral production and tourism, on essentially fragile ecosystems.

Now Dr Mark Stafford Smith and Dr Stephen Morton, of the CSIRO Division of Wildlife and Ecology's Centre for Arid Zone Research in Alice Springs, have developed a theoretical framework — set out in a series of propositions, paraphrased below — that has been hailed by arid zone ecologists as a major contribution to our appreciation of the uniqueness of arid Australia, as a model that places the relationships that characterise it into the context of arid zone ecology as a whole and as a basis for the conservation and management of Australia's arid environments.

Their framework looks at arid Australia from three perspectives: the physical environment; the consequences of those physical features for plant life; and the consequences of both physical and botanical features for animals.

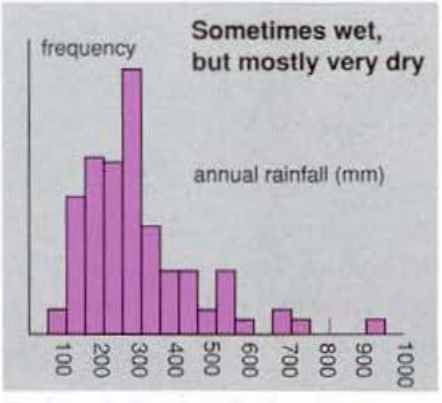
1. Rainfall is unpredictable

Water in the form of rain is the engine that drives the arid zone, but it is impossible to predict when and where it will fall and how long it will last. (Alice Springs, for example, receives more than 20 rainfall events of less than 1 mm for every fall of 200 mm.) Most falls are too small, too scattered and too infrequent to have any immediate effect on plant growth.

Infrequent, heavy rains caused by southerly incursions of cyclonic and monsoonal depressions are responsible for shaping, maintaining and altering the most important patterns in the environment. These falls also inspire spectacular — if relatively brief — abundances of plant life and hence support a greater mass of both plants and animals than would be expected of an environment where water is generally scarce.

2. Big rains structure the environment

Heavy rainfall establishes patterns of fertile alluvial soils in run-on zones — areas where rain, carrying with it suspended minerals and organic nutrients, collects after flowing from run-off zones around hills, monoliths, sand dunes and so on (see 'Looking after the land at Uluru', *Ecos* 71). To



The irregularity of rain in the arid zone shows up in this chart of how often annual rainfalls of different sizes have occurred over a 113-year period at Alice Springs. The most common yearly rainfall is between 250 mm and 300 mm — just enough to keep the environment ticking over, but not enough to inspire major changes in the distribution and abundance of plants and animals.

paraphrase American geologist Jerome Wyckoff, 'relief is the elixir of life': accidents of topography have created run-on zones that receive more water more often, and hence are more productive, than most of arid Australia's generally flat landscapes. Heavy rains also recharge water tables and create flows in subsurface drainage systems, making water and nutrients available to long-lived perennial plants.

3. An ancient, infertile landscape

By definition, ecosystems consist of networks of interdependent relationships, so every element in an ecosystem relates in some way to all other elements. Rainfall is no exception: not only does it provide water in run-on zones, it also carries nutrients to those zones.

That process is important because arid Australia's soils are ancient and highly weathered, and are therefore very low in minerals and nutrients (phosphorus and nitrogen levels, for example, are less than half the average found in arid zones on other continents). The least fertile habitats are the vast spinifex dunefields and the broad swaths of mulga shrubland. Throughout much of arid Australia nutrients are concentrated in the top 5–10 cm of the soil profile, so they are easily picked up by wind or rainfall and transported, together with water, to run-on zones.

4. Survival of the wettest

Just as occasional heavy rain drives changes in arid ecosystems, so the concentration of water and nutrients created by such rain drives localised changes in soil fertility, with inevitable significance for plant and animal communities.

The arid zone is a mosaic of several components: 'hot spots', characterised by constant and reliable water supplies and relatively high nutrient levels; areas with reliable but intermittent water supplies and relatively fertile soils; and land with unreliable and intermittent water supplies and infertile soils. River channels are not necessarily fertile, but they have a reliable supply of underground water that raises soil moisture levels to the point where perennial plants can survive periods of low or no rainfall, thus becoming foci for animal life.

5. A diversity of survival strategies

With rainfall so irregular, plant communities have become highly diverse because no one suite of survival strategies will remain the most successful over long periods of time. The 'best' strategy at one time may be ineffective at another.

Slow-growing, deep-rooted plants are better able to survive long droughts and to make the best use of water than fast-growing, shallow-rooted ones, but they are less competitive as seedlings (when they run the risk of being overshadowed by faster-growing plants) and grow more slowly as adults (when they run the risk of being denied scarce soil nutrients by more opportunistic ones).

Short-lived plants grow faster, invest less energy in producing roots and use nutrients more quickly, but are less drought-tolerant than slow-growing species.

Where water and nutrient supplies are predictable, plants can fairly easily achieve a balance between drought tolerance and fast growth; as conditions become less regular, however, the range of strategies must broaden.

This is the situation in arid Australia, where areas with poor water supplies tend to be dominated by long-lived perennials such as mulga: richer areas, such as floodplains, have the widest variety of plant species and survival strategies, with ephemerals as well as perennials using different aspects of the water-availability cycle and tolerating different degrees of drought. In river channels and similar places with continuous water, deep-rooting perennials dominate through competition and by tying up nutrients.

The wide variety of survival strategies explains some of the hitherto puzzling features of arid Australia. Succulents that store water in their stems — cacti, for example — require regular rain; the absence of regular

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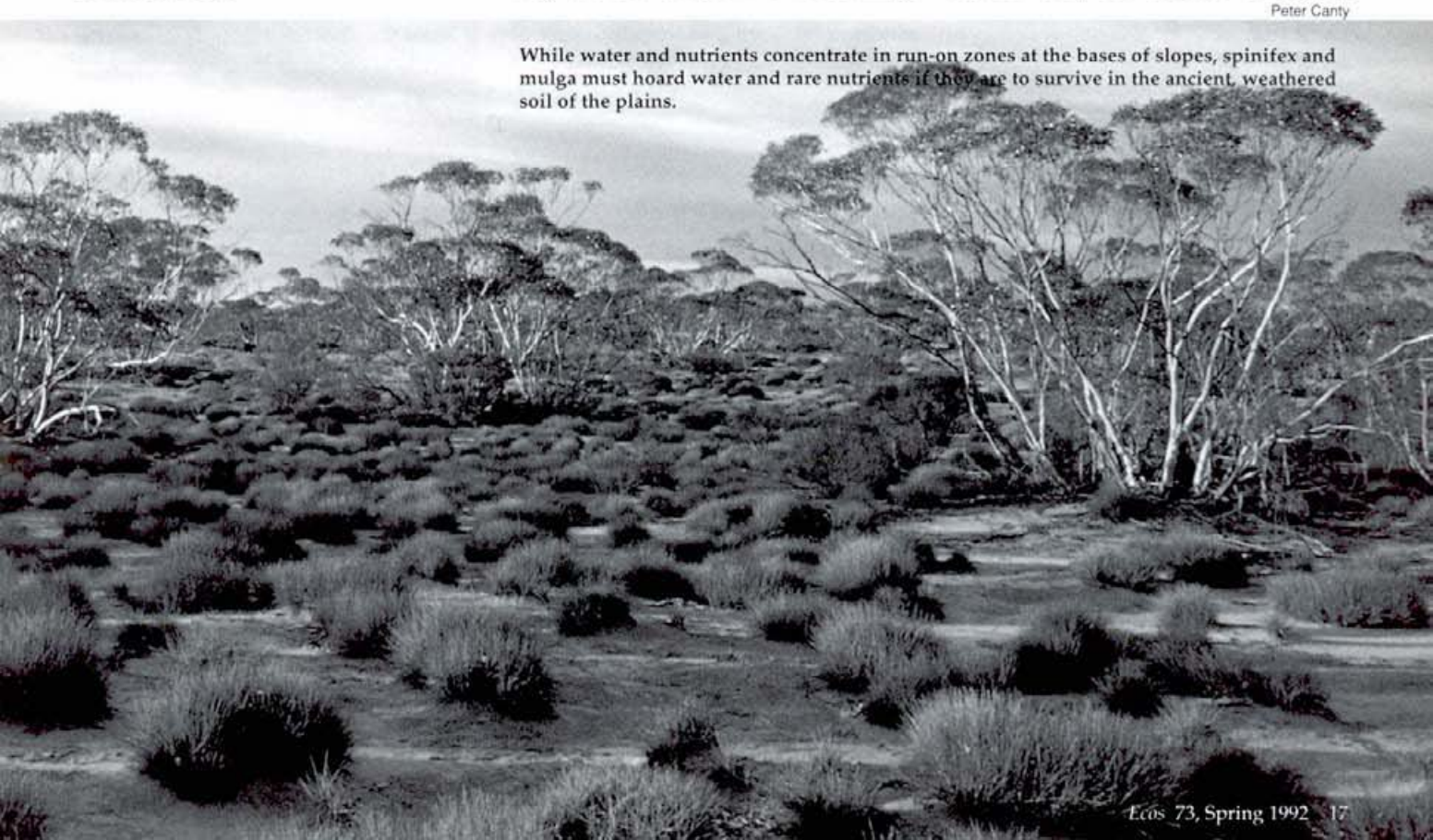
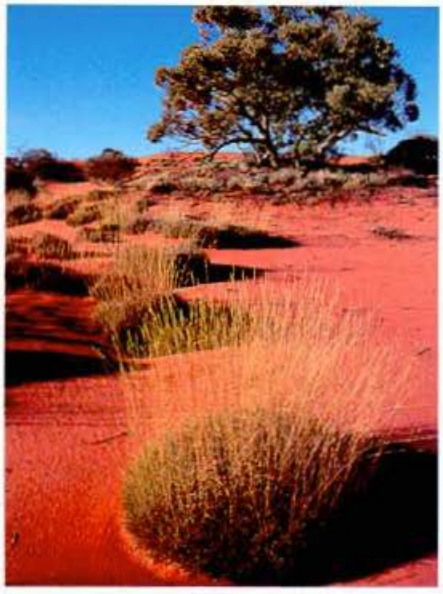


While water and nutrients concentrate in run-on zones at the bases of slopes, spinifex and mulga must hoard water and rare nutrients if they are to survive in the ancient, weathered soil of the plains.



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Fierce competition for nutrients has created a landscape dominated by plants, such as spinifex and the marblegum (*Eucalyptus gongylocarpa*), that employ chemical defences against each other as well as against predators.

rainfall explains the absence of such stem succulents. Long-lived perennials grow only where water supplies are reliable, so they do not need to time their flowering according to rain; this has important implications for insects and birds, which can rely on a reasonably regular, if not always abundant, food supply.

6. Fertility controls digestibility

Perennial plants growing in infertile soil and nourished by irregular rainfall tend to be difficult to digest, since they protect themselves from dehydration and predators with carbon-based chemical defences such as tannins and lignin — the production of which diverts energy from growth. Spiny plants are uncommon, perhaps because tannins and lignin make them unnecessary. Sclerophyll, or hard-leaved, plants are distinctive features of arid Australia, as is a general absence of deciduous plants (the term 'evergreen' hardly applies in this environment).

Another feature of the widespread use of carbon-based compounds is that the large amount of carbon in leaf litter inhibits microbial breakdown, so nutrients locked up in plant material are recycled only slowly... further reducing already low amounts of nutrients in the soil.

7. Carbohydrate is plentiful

The arid zone is rich in carbon dioxide and sunlight, if not nutrients, so plants are not limited by their ability to produce carbohydrates through photosynthesis. Carbohydrate-based products — woody seed cases, sweet fruits, winged seeds, flowering spikes, nectar and so on — are therefore cheap to manufacture, since they require relatively little energy.

As long as water is available, perennial plants can maintain continuous production of carbohydrate, producing sugar-rich nectar or fruits that enhance their chances of seed dispersal. Some trees tolerate high numbers of sap-sucking insects; these in turn attract ants, which deter other herbivorous animals.

8. Fire is important

Large numbers of perennial plants, slow decomposition of litter and plentiful carbohydrate-based tissue, as well as resin- or oil-rich leaves, provide abundant fuel for fires, which arise from lightning strikes, Aboriginal fire-stick-farming practices or deliberate burning to promote the growth of pasture plants.

In extremely infertile environments such as spinifex grasslands, fires play a major role in nutrient recycling, with many species surviving only as dormant root-stock or seeds between them. Fires also create space for seedlings between established plants. In fertile environments that are dominated by perennial plants, fire allows re-invasion by shorter-lived ephemerals.

9. Food rather than water governs animal life

The availability of water is, of course, central to all animal life in the arid zone, but it is not water that determines whether or not an individual animal will survive. Invertebrates and vertebrates alike minimise their dependence on water by avoiding extremes of temperature, by burrowing, by foraging at the least stressful times and through physiological mechanisms such as torpor or aestivation during very hot weather. Only four or so of the 95 species of mammals, 25 of 230 species of birds, none of the 210 reptiles and none of many thousands of invertebrates depend on 'free' water (water from rivers, waterholes and so on).

Because they avoid heat stress, animals can obtain almost all the water they need from their food, which has the advantage that water, energy and nutrients are usually found in the same package.

The problem is reduced to finding enough packages of food: the generally low food value of Australian arid zone plants flows on to consumers, so they 'define' food quality in terms of nutrient content. Animals thus have a choice between a relatively small number of food, water and nutrient packages with high value or widespread food of little quality.

10. Feast or famine

Unreliable rainfall combined with low soil fertility in the arid zone promotes

the formation of islands of relatively fertile soil in a vast sea of soil containing little or no nutrients. In turn, long-lived deep-rooting perennial plants tend to dominate regions with intermittent water and low nutrient levels, while highly competitive fast-growing ephemerals are more common in well-watered areas with fertile soils.

That pattern has a profound influence on the distribution of animal

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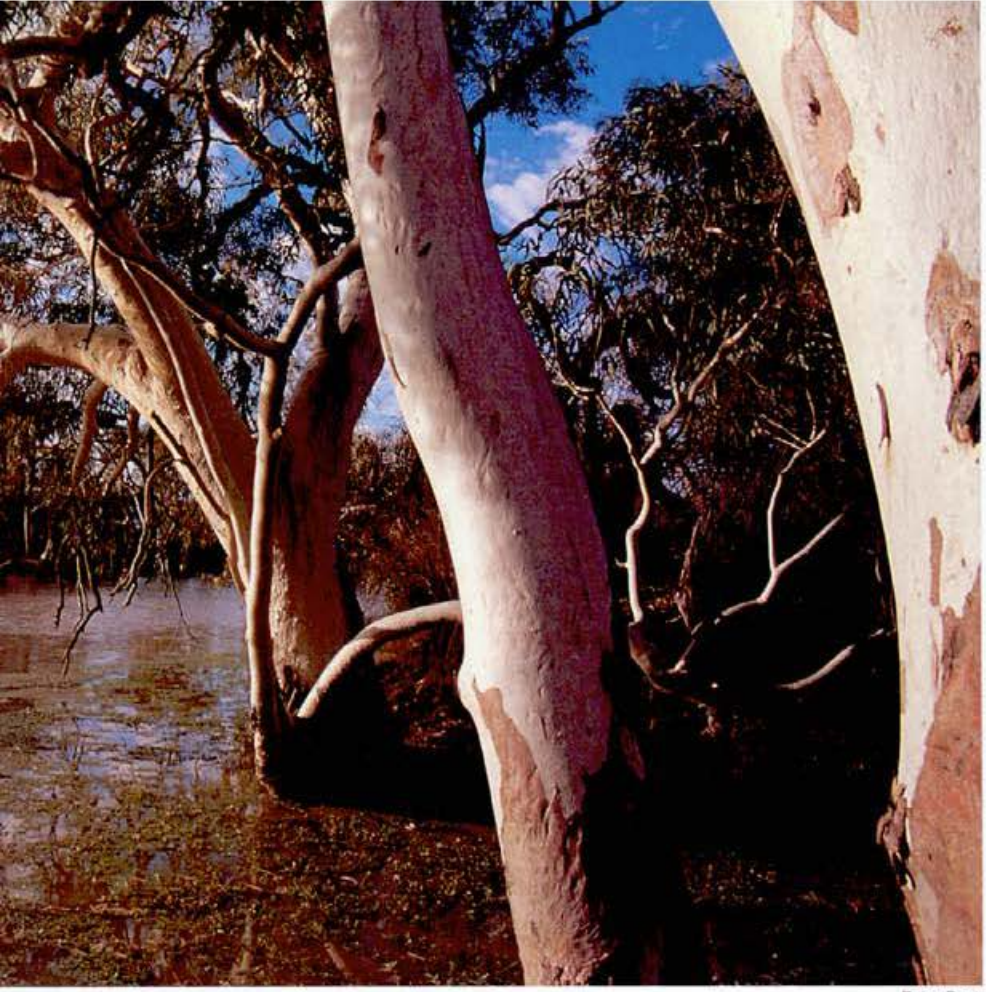
The seeds of short-lived plants such as cattlebush (*Trichodezma zeylanicum*) germinate quickly after rain, providing a rich source of food for insects and, in turn, their predators.



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Big rains not only provide abundant water; they also carry nutrients over vast areas. Nutrients are captured by ephemeral plants (below), then become available to animals and to long-lived perennials.

life. Persistent plants tend to be associated with low fertility, so persistent herbivores must cope with a lack of free water, little shelter and food that has a daunting combination of defences (such as tannins, lignin or woody spiky growth) and low digestibility.

To persist in these harsh conditions, herbivores must specialise: for example, sap-sucking and root-eating invertebrates are common throughout arid Australia, and tend to remain active for months or even years after rain.

Other herbivores can be present only ephemerally, since they rely on high-quality, ephemeral plants that are relatively free of anti-herbivore defences. And since ephemeral plants are available for limited periods, herbivores that rely on them must 'hop through time', usually by laying drought-resistant eggs or by becoming inactive during long droughts. Grasshoppers and beetles provide classic examples of both these strategies.

11. Termites rule, O.K.

Vast areas of arid Australia support plants that are too poor for even the hardiest persistent herbivore, so most plant material remains untouched until it dies. Despite its low nitrogen content, dead plant material supports a rich and diverse array of detritivores... a group so dominated by termites that it would be fair to say they themselves dominate the entire arid zone.

Termites are extraordinarily abundant throughout the infertile regions of arid Australia, especially in spinifex and mulga landscapes; their mounds are distinctive features of the northern part of the arid zone, where occasional heavy rain requires them to raise their colonies above regularly waterlogged ground.

12. Producers and consumers

In comparison with dry and infertile or intermittently rich environments, areas with reliable water supplies, and hence relatively high soil fertility, support permanent production of plant material. This in turn supports more or less permanent and stable populations of persistent consumers.

Because they cannot digest the sort of fodder available to termites, and because their physiological requirements bar them from infertile environments except during brief periods when (easily digestible) ephemeral plants are abundant, mammalian herbivores are effectively restricted to richer areas such as run-on zones and river channels.

Invertebrate herbivores such as grasshoppers, moth and butterfly larvae and sap-sucking insects prefer these areas, too, providing a stable food resource for insectivorous reptiles, birds and mammals... which in their turn support a relatively stable population of carnivores and scavengers.

However, introduced animals such as rabbits, cats and foxes — not to mention cattle, horses, goats and donkeys — also prefer reliable water and food supplies, placing these always vulnerable oases under even greater pressure from predation and degradation.

13. Perennial plants, persistent insects

Ants and termites are especially prominent in infertile environments, since they have evolved social systems that enable them to make the best use of very limited food and water resources. Their colonies store energy for

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the future, providing a buffer during pulses of high or extremely low production.

It is no coincidence that highly perennial plants such as mulga and spinifex support highly persistent insect colonies. Both have taken the strategy of persistence to its greatest extent, being able to harvest and store intermittent supplies of food and water.

Ants and termites decline in diversity and ecological importance as conditions improve, with relatively few species living in richer environments.

14. You are what you eat

The kinds of predators found in various parts of the arid zone reflect variations in water and nutrient availability. In infertile regions, dominance by termites combined with the unreliability of rainfall (and hence food production) means that predators must be able to adapt to sudden surges in production followed by long periods of low productivity.

As expected, invertebrate predators such as spiders and king crickets or vertebrate ones with low metabolic rates and an ability to escape extremes of temperature — lizards, for example — predominate here, while mammals and birds are less able to survive such a regime as residents and tend to move in and out according to surges in populations of invertebrates.

Invertebrate and reptilian predators are also found in richer environments, although they play a much less dominant role, relying more on leaf-eating insects such as grasshoppers and butterfly and moth larvae. However, these environments support a much larger array of insectivorous and nectar-feeding birds, and carnivorous and scavenging reptiles and mammals.

15. An absence of booms and busts

Despite arid Australia's uncertain and unreliable climate, the populations of many ecologically important animals do not fluctuate in a straightforward manner according to rainfall. Indeed, there's such a diverse sequence of foods available after rain that a complementary sequence of animals increases in numbers or moves into areas of high productivity to take advantage of food supplies. Food supplies overlap in time, so consumers persist for long periods.

Long-lived perennial plants, because they aren't wholly dependent on rainfall, can keep growing for long periods after groundwater recharge and can therefore provide a stable (and often carbohydrate-rich) source of production for consumers such as herbivores and sap-sucking insects.

Likewise, populations of root-feeding insects are extremely stable despite wide fluctuations in rainfall intensity and reliability. They provide a stable source of food for predators, especially since they are more active during warmer months when rain is more likely — ideal conditions for supporting a population of predators.

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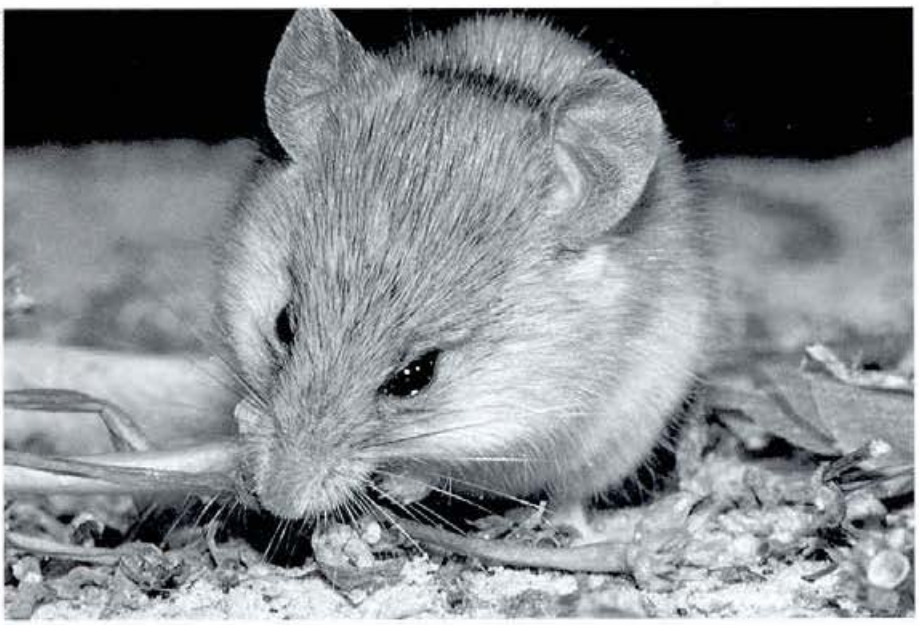

Arid zone residents such as the sandy inland mouse (*Pseudomys hermannsburgensis*) feast on the insects that follow the desert's brief bloom, replenishing their energy reserves for a burst of reproduction.

Dr Morton and Dr Stafford Smith stress that many of the features of arid Australia are also found in other arid zones. The Kalahari of southern Africa, for example, doubtless encompasses areas of equal infertility... albeit — and this is the important distinction — not to the same geographic extent. In one sense, arid Australia is different simply because it is so big.

Arid Australia's infertile soils have also shaped plant communities and hence animal communities into a distinctive combination of survival strategies, to the extent where broad judgments cannot be made about a particular ecosystem without referring directly to what part of the landscape is under consideration.

Most importantly, however, arid Australia's ecological relationships are affected by extremes of long droughts and short periods of high moisture. No other arid zone experiences this unpredictability on such a huge scale, so the forces shaping the distribution, diversity and life histories of the plants and animals in arid Australia are different from those in other arid zones.

Carson Creagh

More about the topic

A framework for the ecology of arid Australia. D. M. Stafford Smith and S. R. Morton. *Journal of Arid Environments*, 1990, **18**, 255–78.

Where the creeks run dry or ten feet high: pastoral management in arid Australia. M. H. Friedel, B. D. Foran and D. M. Stafford Smith. *Proceedings of the Ecological Society of Australia*, 1990, **16**, 185–94.

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