Journal of the Royal Society of Western Australia, 80:113-122, 1997

Granite outcrops: A collective ecosystem

B York Main

Department of Zoology, University of Western Australia,
Nedlands Western Australia 6907
email: bymain@cyllene.uwa.edu.au

Abstract

Ecological systems of granite outcrops are posed as having arisen through one of two processes or through a combination of both processes; through colonisation of exposed and weathered rock surfaces and/or through retention of components of relict biotic assemblages surrounding such exposures. In the context of such evolved ecological systems, the inter-relationships of outcrop configuration, the geological and climatic history and associated changes from mesophytic to sclerophyll or xeric vegetation of surrounding landscapes is discussed with reference to selected outcrops.

Introduction

Ecosystem, like biodiversity, is an "in" word. But what does it mean? As an abbreviation of ecological system, it denotes some sort of interaction of life forms and dependence within a physical, non-biological framework on which the living forms in turn have some effect. As a system, an inherent cohesion is intimated; external limits are inferred. All this in turn suggests that an ecosystem has boundaries. A dictionary supports this concept in the definition "*The plants and animals of a particular habitat, together with the environment influenced by their presence*" (Onions 1978). Ecosystems, as nominated in common biological parlance, can be large or small, relatively open or near-closed. An ecosystem can range from the complexity of a tropical rainforest to an individual tussock grass on Beauchene Island in the Falkland Islands archipelago (Smith & Prince 1984).

How then to define a granite outcrop ecosystem? It must comprise some sort of cohesive biotic community supported by a physiographic matrix, which embraces both time and space components and be clearly demarcated from any adjacent, contiguous or surrounding ecosystems. Granite outcrops were referred to early as monadnocks or "island hills" (Jutson 1934) who recognized them as exposed residuals surrounded by more readily weathered components of the underlying bedrock. They are currently regarded popularly as "islands" (Anon, undated). In the context of "islands" many botanical studies have been undertaken in southwestern Western Australia (Ornduff 1987). Current understanding and interpretation of the peculiarites of the biota of the outcrops has been partially wrapped in island biogeography theory. The obvious refugial role of the rocks has also been noted in relation to isolates of former more widespread and continuous distributions of plants such as jarrah (Abbott 1984) and also of various animals. Recognition of both the refugial and insular nature of granite outcrops has underpinned much of the drive and justifcation for conservation and inclusion of particular rocks in the nature reserve system of Western Australia.

The "island" concept of outcrops has been generally stimulated by observation of their present biotic distinctiveness or biotic disjunction with their immediate surrounds, particularly in relation to vegetation and ephemeral aquatic fauna. While documentation of vegetation, vertebrates and aquatic invertebrates has already been undertaken on selected granite outcrops (see elsewhere in this issue), the terrestrial and/or lithic invertebrates are less well known. Few, if any, comprehensive studies have attempted to document the interactive relationships of the total biota of a granite outcrop although Main (1967) presented a simplistic naturalist's view of the ecology of a particular rock, Yorkrakine Rock, in the wheatbelt. McMillan & Pieroni (undated) have given a "primer" account of the life forms associated with granite outcrops.

To understand the representativeness and cohesion of the biota on any one outcrop and to be able to arrive at generalisations regarding the composition of the biota over the array of outcrops in any region or on a continental scale, I believe one needs to adopt an historical perspective. While documenting (a) the characteristics of the outcrops as they appear now and (b) the present biota, one needs at the same time to ask;

- How have these "ecosystems" come about ?
- What were the antecedent landscapes like?
- How has the biota responded to the sequential changes of the landscapes through to the present time?

I shall now attempt to show that by adopting this historical approach we can come to some understanding of

- the physiography of the outcrops,
- the distribution and restriction of dominant elements of the biota,
- "ecosystems" of selected rock configurations, and
- over a geographic span suggest that there are biotic patterns peculiar to granite outcrops which comprise a "collective ecosystem".

Granite Outcrops Symposium, 1996

From the outset, my discussion will be limited largely to the granite outcrops of southern Western Australia, south of approximately 26 degrees latitude, and hence those which occur in a predominantly winter rainfall region. In the more northern and eastern areas particularly, they are also affected by summer rainfall in the form of thunderstorms. Outcrops near the south coast experience the benefit of coastal precipitation either as light drizzle or fog induced by onshore winds associated with high pressure systems. The relevance of the overall discussion to outcrops elsewhere, particularly Eyre Peninsula, is implicit.

Distribution and Characteristics of Granite outcrops

The present scenario

Granite outcrops, as loosely defined, are scattered throughout southern Western Australia from north and west of the Nullarbor *i.e.* from the arid interior, through woodlands and forest country to the southwest coast. They appear as emergent protuberances of the basement rock over the Great Plateau or Archaean Shield (of the Yilgarn craton) and similarly as promonotories on the dissected edges of the western escarpments and across the southern landforms of the state. Jutson (1934) referred to these "island hills" as remains of the "old plateau". Clarke (1994) dated the "stripping" of the regolith of much of the Yilgarn craton (which would account for "granite" exposures) as between Middle Jurassic and early Eocene and associated such stripping with uplift and incision of the palaeodrainage system. It is outside the scope of this paper to discuss the petrology or origin of the rocks which aspects are dealt with elsewhere in this issue. It is only relevant here to discuss the physiographic configurations of the rocks as they affect the biota and its distribution.

Widely scattered as they are, the rocks fall within three major rainfall zones as defined by Hopper (1979) as the high, transitional and arid rainfall zones representing 800-1400, 300-800 and less than 300 mm per annum. Interestingly, rocks within these three zones can be more or less defined by their grey, brown or red colour respectively which reflects indirectly the response of living organisms *e.g.* types of predominant lichen growths, or conversely their absence, to the rainfall gradient. The composition of the ecosystems of particular rocks is determined partly by the present rainfall *i.e.* the zones as delimited above, by the geo-climatic history with the associated changes from a mesophytic to sclerophyll and xeric vegetation and the configuration and topography of the rocks.

Configuration and topography of rocks

Configuration of rocks ranges from high, sharply declivous domes to barely perceptible, flat exposures. Such configurations generally reflect the degree of erosion of the surrounding landscape which in turn has exposed the basement rock to varying degrees. A convenient characterisation of the predominant configurations adopted here (Fig 1) is as follows:

- Single or multiple domes, monadnocks or tors, as "islands" on the dissected Darling Plateau and in a landscape of low relief *e.g.* the predominant outcrops of the Great Plateau ("inselbergs" of Jutson (1934); Fairbridge & Finkl (1978); Finkl & Churchward (1974) and in part "bornhardts" of Campbell (1997).
- Flat, often disc-like pavements (Fig 1) which are also a frequent feature on the plateau.
- Subsurface basement highs, here referred to as "fugitive outcrops" (Fig 1).
- Asymmetric declivities or tors as exposures in mountain ranges *e.g.* the Porongurup Range and throughout the forested southwest of Western Australia (comparable to the domes of The Plateau).
- Coastal declivities and near-coastal knobs protruding through Pleistocene limestone deposits.
- Tumuli of boulders either around a central core or as rock "piles" (Fig 1; Plate 1) . The latter are sometimes adjacent to salt lake lineages where they may be erosional features of former domes which have weathered to blocks in association with the presence of salt. Such rock piles are comparable in part to "nubbins" and "castle koppies" of Cambell (1997).
- Scattered boulders (especially on escarpments or ridges), or clusters of small tors, or "haystacks" (Twidale & Campbell 1984).

It is the domes (monadnocks or tors) and the disc-like pavements which most closely fit the general concept of an "outcrop" *i.e.* as a sizable, isolated "intrusion" into the landscape (Ornduff 1987) and it is predominantly these configurations which will form the main focus of my discussion with reference to others as listed above for comparison. However, all types of configurations share some basic ecological elements while differing in structural and biotic detail. A combination of rock topography, which has been partly determined by past erosion and climatic patterns, and impacts of current weather conditions determines the level of complexity of the ecosystem of a particular outcrop.

Topographic features and associated biota of outcrops

The more subdued the profile of an outcrop the less complex the topography hence a "pavement" rock generally presents little sculpturing whereas a higher exposure exhibits a more varied topography (Fig 1). The main topographic features of an outcrop are associated with the sculptured surface and the surrounding "apron".

The sculptured surface. The sculptured surface may be relatively "smooth" or pitted and dimpled (Jutson 1921). As well as the rock crust having partially detached pieces, including "pop-ups" or "A-tents" (see Campbell 1997), the surface may also be littered with exfoliated plates, flakes or slabs. Both attached and loose rock plates provide habitat for invertebrates *e.g.* spiders, centipedes, scorpions, pseudoscorpions, opiliones, pupating insects, moths, beetles and also vertebrates particulary frogs and lizards such as geckoes and the agamid *Ctenophorus ornatus*.

The wave-like slopes ("flared slopes" of Campbell 1997) of some higher domes have been variously interpreted as the result of subsurface weathering in the presence of water (see Campbell 1997) or partly by

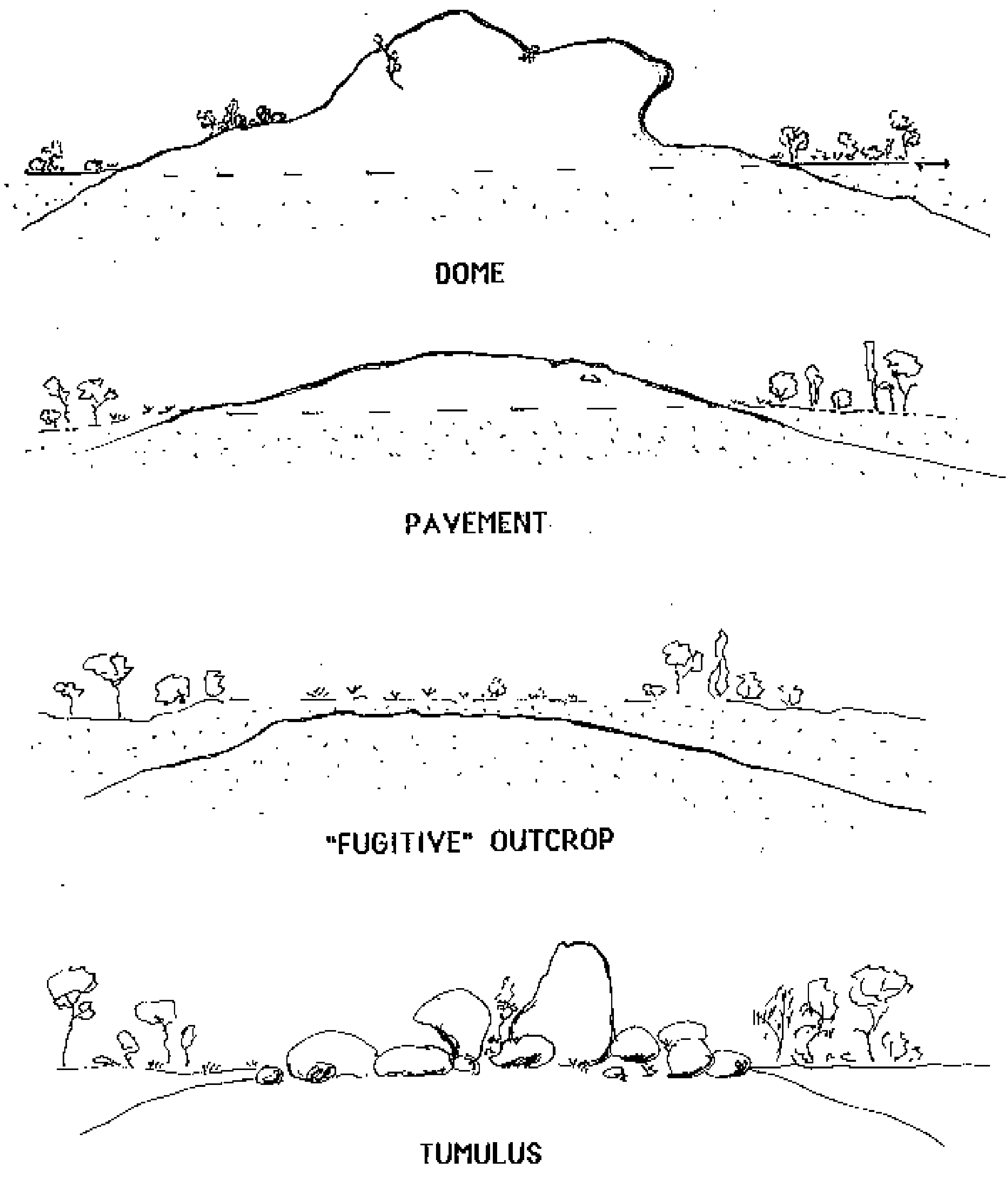

Figure 1. Examples of configurations and topography of granite outcrops.

sandblasting by wind. However some initial sculpturing may have been by the Permian ice sheet which is known to have covered much of southwestern Western Australia (McWhae *et al.* 1958). Earlier, Clarke (1919) had remarked on glacial deposits in inland southern Western Australia as have Fairbridge & Finkl (1978). However, Clarke (1994) doubts that any relicts of Permian landforms could be anything but minor and restricted today. The "waves" form dramatic drops and frequently direct rain onto either surrounding aprons or into flat bottomed gorges from which creeks may debouch. Both such sites provide moisture-holding habitats.

Certain outcrops weather into block formations (Jutson 1934) and have large boulders both on their profiles and scattered around the base (see "nubbins" of Campbell 1997). These boulders sometimes erode into cave-like shells (tafoni) or narrow-based pedestal shapes (see Campbell 1997). Runoff water from the boulders maintains a moister habitat than the general rock surface and where there are clusters of boulders, intervening soil supports ephemeral and perennial vegetation. The boulder piles or clusters (Plate 1) form habitats for animals ranging from invertebrates to vertebrates such as bats and marsupials (euros and rock wallabies) and snakes and varanid lizards.

"Fugitive" outcrops (Fig 1) of the basement rock often appear as open meadow-like spaces surrounded by higher shrubby vegetation, woodlands or forest. They are vegetated by the same fringe or meadow plants as occur on rocks in the same region. As summer-dry bogs they provide habitat for relict burrowing spiders *e.g.* the mygalomorph *Teyl* (Withers & Edward 1997, Fig 2) and various insects such as cicindellid beetles.

Algae and lichens occur on most rock surfaces. Lichens are renowned for being able to withstand extremes of temperature. Pertinent to growth and survival on granite outcrops is the fact that dry thalli of some genera have been demonstrated to resist temperatures as high as 70-101 °C. However, the tolerance of moist thalli does not exceed 46 °C (Lange cited by Hale 1967). Some lichens are very long lived but they are also colonisers *e.g. Parmelia* occurs abundantly on the rocks. Lichens have the capacity to fix nitrogen and in the presence of rain to leach minerals from the rock surface. In so doing, they gradually break down the rock surface forming soil particles. Thus their role in making granite outcrops suitable for colonisation by mosses and finally other plants is highly important (Plate 2). While no studies appear to have been conducted in southern Western Australia on the possible association of organisms such as invertebrates living in the thalli, certain moth larvae feed on lichens on the outcrops (*pers obs).*

In wet areas, considerable moss mats or swards occur where a little soil has accumulated. Larger rocks with higher profiles frequently have deep crevices which similarly support moss mats and rock ferns (the most common and widespread being *Cheilanthes*) and also the blind grass *Stypandra* and various shrubs *e.g. Baeckea, Beaufortia*, *Kunzea* or *Anthocercus* depending on the location. *Kunzea,* which is common on dryer rocks, characteristically also grows from deep narrow fissures and thus gives the appearance of hanging from the rock itself. In contrast *Anthocercus* which grows in higher rainfall areas grows in the moss mats or swards and consequently often suffers windthrow (Plate 3).

Higher rocks may also have shelves with an accumulation of soil where again moss mats, ferns and shrubs flourish. Newbey (1995) remarked on deposits of "skeletal soil" up to 30 cm deep on lowlying areas of granite exposures. These deposits may also provide habitat for perennial mygalomorph spiders. The interface of rock and soil of crevices and shelves is frequently fringed with the liliaceous pincushion plant *Borya* in dryer areas, and in wetter areas the heather-like *Andersonia. Borya,* as one of the "resurrection" plants (Gaff 1981) is able to withstand considerable desiccation during which times it assumes a striking orange colour (Plate 2), but reverts quickly to a bright green following water uptake after rain (see Plate 5, and Hopper *et al.* 1997). A variety of orchids, composites and other ephemerals intermix near these fringes. Various invertebrates such as insects and spiders live in any soil accumulations *e.g.* of crevices and shelves, which support plant life. The gorges, in the higher rocks, support the same sort of vegetation as the shelves with occasionally the addition of the Christmas tree (*Nuytsia floribunda*), *Allocasuarina huegeliana* and *Acacia rostrata* .

Large depressions ("dimples" of Jutson 1921; and in part "flat-floored pans" of Campbell 1997) occur on most outcrops which have at least some relatively flat areas. After rain these depressions fill with water to form ephemeral pools. The quillwort *Isoetes* frequently forms a dense lawn on the floor of such ponds. An array of invertebrates including the crustaceans Conchostraca (shield shrimp *Triops*), Cladocera, Ostracoda, Anostraca (brine shrimp), insect larvae, water mites, flat worms (Platyhelminthes), rotifers and also frog tadpoles are active seasonally in the ponds.

Rocks with higher topography encourage a cascading effect of runoff after rain. This runoff may erode the rock surface into tiers of pit-like depressions ("dimples"), of which the deeper ones are sometimes called "arm-chair basins", along drainage lines thus forming temporary waterfalls (Jutson 1921) which leave in their wake a series of longer lasting pools. A later seral stage of such stepped pools or water holes are soil-filled pockets which finally develop into "Babylonian gardens" (Plate 4).

Gnammas (rock holes) may be present on both dome and pavement configurations and are frequently permanent water reservoirs. As well as habitat for invertebrates, the pools and gnammas are an important source of water for vertebrates, both permanent habitat associates and transitory fauna *e.g.* birds and also bats (R How, *pers comm*; Dell & How 1984, p 69) and larger marsupials.

The meadows, formed over infilled ephemeral ponds, are a common feature on outcrops (Plate 5). Depending on the seral stage these are crusted with lichens or vegetated by moss mats, *Borya* or *Andersonia* heaths, blind grass and restionaceous tussocks and small shrubs such as may also occur on shelves or in crevices of the outcrop. In that these meadows form seasonal bogs, usually in winter but also during summer thunderstorms, they provide important habitats for moisture dependent organisms particularly invertebrates including species of the mygalomorph spider *Teyl*.

Fissures, crevices, shelf meadows and seral-pond meadows, boulder shadows where soil accumulates, lichen and moss around the lips of fixed rock plates, and even the soil spill around exfoliated slabs, all form to some degree relatively moist habitats when compared to the general rock surface. As such they form the principal habitats for smaller organisms, both invertebrates and vertebrates including frogs and lizards, while wallabies take advantage of larger boulder accumulations.

The apron. The descending edges of outcrops frequently fan out into soil covered aprons of varying width depending on the declivity of the rock. Soil depth varies from 1.5 to 2.0 m (Newbey 1984 p33, 1988 p11) and throughout the seasons are alternately waterlogged and dry, thereby constraining both the vegetation and soil living invertebrates. Shallow soils with little vegetation apart from moss mats and rock fern, and meadows of *Borya* and ephemerals or in wetter areas

Plate 1. A rock pile (tumulus) near Hyden, Western Australia, with surrounding *Allocasuarina* grove.

Plate 2. A meadow of *Borya* at edge of rock with adjacent lichen crusts on rock, Plover Rock, Western Australia. Note the "drought" mode of the brightly coloured *Borya*.

Plate 3. Wind-thrown *Anthocercus* plant on Torbay Hill, Western Australia.

Plate 4. "Babylonian Gardens" growing in the pockets of soil formed in the tiers of infilled rock holes (armchair basins) on Torbay Hill, Western Australia. This stepped sequence of soil pockets would formerly have been a seasonal waterfall.

Plate 5. A tiny *Borya* meadow formed in an infilled rock pool on a rock at Payne's Find, Western Australia. Such meadows provide habitat for the mygalomorph spider *Teyl* and other invertebrates.

Plate 6. The stem-flowering ("cauliflory") of *Hakea petiolaris*, a condition possibly relictual from an earlier climatic period when the plants grew under a canopy.

Andersonia, gradually blend into tussock and shrub thickets similar to the vegetation of the larger meadows and shelves on the rock proper or in the shallow gorges with the addition of sandal wood. In the semi-arid and arid region, the aprons may have an extension of indiginous grasses from park-like acacia groves. *Allocasuarina* shrubs and trees frequently fringe the outer extension of aprons or grow along creeks at the interface of rock edge and apron. Particularly on higher rocks which provide much runoff, the creeks at either the boundary of the apron or where they transect the apron are important seasonal habitats for invertebrates and frogs and in summer provide damp refuge areas. The apron meadows, like the meadows formed in infilled ponds and over "fugitive" outcrops, are sanctuary to relict burrowing spiders *e.g. Teyl* species which aestivate in sealed burrows, and insects whose larvae are dependent on a seasonally wet substrate.

Microclimate of outcrops and effects on biota

Outcrops, particularly in the semiarid and arid regions are subject to extremes of temperature and alternatively wet and dry seasonal conditions. Botanical studies and zoological works have both noted upper rock surface temperatures of over 50 °C (Marchant 1973; Bradshaw & Main, 1968). Bradshaw & Main (1968) also noted that air temperatures were at least ten degrees lower under the overhangs of attached rock plates and even under loose slabs. Animals such as the common ornate dragon lizard, *Ctenophorus ornatus*, take advantage of these retreats and also the shade cast by boulders. The latter also provide refuge from the heat for rock wallabies and euros. Presumably the large goannas also benefit from boulders and large semi-attached rock sheets.

Rocks and rock slopes of coastal hills, the southern mountains and southwest peaks *e.g.* Porongorups, Granite Peak, Mt Lindsay, Many Peaks and peaks in the Darling Ranges such as Mt Cooke, all benefit from the altitudinal self-generated cloud and fog mantles which increase the moisture content of vegetation, litter and soil thus providing microhabitats for invertebrates.

Conversely many rocks in regions of low rainfall while capturing isolated fog nevertheless do harvest moisture and thereby provide refuge for moisture dependent biota. It has been noted that even light rain generates run off from rocks. In winter 5 points (1.8 mm) of rain, in summer 7 to 9 points (2.5-3.2 mm) generates run off. More significantly it is recorded that "Kondinin Rock has been known to yield water .... from a light mist" (Fernie 1930). Such harvested water naturally channels into creeks at the rock/apron interface, around the base of boulders and into crevices and fissures and under overhangs and exfoliated slabs. It is also sufficient to wet dried beds of ponds and activate dormant insects and aestivating frogs. Thus, even minimal moisture catchment becomes of major importance for the survival of relict invertebrates.

Origin and Distribution of the Biota

Historical perspective and persistence

The outcrops appear as present day intrusions in the surrounding landscape (Ornduff 1987) but they would not in earlier geoclimatic periods have stood out in such isolation. Although their lithic core would have set them apart topographically, a much wetter climate and mesophytic vegetation containing southern rainforest elements including *Nothofagus* and associated plants (Balme & Churchill 1959) would have maintained more continuity in the vegetation and fauna. Biotic isolation focused around granite outcrops would have begun in the Tertiary along with the sclerophylly of the vegetation. Outlying botanical components of the forest region of southwestern Western Australia associated with granite outcrops in the dryer transitional rainfall zone, such as the jarrah (*Eucalyptus marginata*) stand at Jilakin Rock (Abbott 1984; Churchill 1968) indicate the contraction of species to refuges in the face of changing climatic conditions. Another possible relict of an earlier bio-climatic scenario is *Hakea petiolaris* . This species exhibits the peculiar habit of stem-flowering or "cauliflory" (Plate 6), which White (1986) describes as characteristic of certain plants growing under a closed canopy. Thus it is possible that *H. petiolaris* is a relict of an earlier, wetter, forested landscape.

With a continued trend towards a dryer, more seasonal climate, invertebrates dependent on a continuously moist habitat would have become concentrated in microhabitats such as already noted around granite rocks, while many (as with larger vertebrates) may have disappeared altogether. Some animals show definite adaptive responses through life history strategies to increased aridity and marked seasonal changes by retreating to permanently moist microhabitats at certain times of the year. Others, such as the aquatic invertebrates (Crustacea, insect larvae, platyhelminths, *etc*) are well suited through dormant life history stages to avoid severe summer drought. For example, many branchiopod crustaceans have resistant eggs and can remain viable in the dry soil of ponds for long periods.

There appear to be few animals tied completely to rock habitats throughout their entire life cycle. The rock wallaby, although dependent for shelter on rocks, is more widespread and forages away from rocks. In some places euros similarly make use of rocks for shelter. Many other vertebrates such as kangaroos, echidnas, bats and a whole suite of birds make transitory use of granite outcrops especially as a water source and thus are probably dependent on them during summer drought but are not confined to them. Many frogs live and breed around rocks, but are not soley restricted to granite outcrops as a habitat.

A notable vertebrate which is confined to granite outcrops is the widespread dragon lizard, *Ctenophorus ornatus*, which thus represents a collective of disjunct populations. Similarly a few plant species have a fragmented distribution with occurrences confined to granite rock habitats *e.g. Isotoma* (James 1982), *Eucalyptus caesia* (see Hopper *et al.* 1982), *E. crucis* (see Brooker & Kleinig 1990), *Kunzea pulchella*, and some orchids. Certain invertebrates likewise are tied to granite outcrops. The biogeographically-ancient midge *Archaeochlus*, whose larvae develop in seeps on granite rocks, is an example (Cranston *et al.* 1987). Nevertheless, over the range of the genus in southwestern Australia and extending to Central Australia (P Cranston, *pers comm*) three species are included. Most branchiopod crustaceans of the ephemeral rock pools occur on scattered outcrops. A well known example is the shield shrimp *Triops* which occurs not only on rocks but also along the edges of lakes and in temporary puddles in lowlying areas; there is no site specificity because of the wind-borne dispersal of the resistant eggs throughout the dry inland. The same probably holds for most aquatic invertebrates, except possibly for some water mites particulary in the forested south-west.

Various insects such as lichen-eating moth larvae and possibly some of the moisture-loving grasshoppers are possibly restricted to granite outcrops.

Amongst spiders, a *Rebilus* species (family Trochanteridae) occurs on many inland rocks where it lives under loose and attached slabs. Some other spiders with similarly flattened body form such as an unnamed lycosid, previously attributed to *Pardosa* (Main 1976, Plate 25) is confined to inland granite rocks while *Hemicloea* species occur under slabs on granites in southern forest areas but it is doubtful whether it or *Rebilus* are confined to rock habitats. *Selenops,* although a rock inhabiting genus, is not restricted to granite but is found also on sandstone formations. Other spiders frequently found on granites include wolf spiders such as *Lycosa leuckhartii*, *Miturga* species and the redback spider *Latrodectus hasselti*. All are readily dispersed and not confined to granites.

Site specificity

In contrast to this pattern, an interesting mygalomorph spider genus, *Teyl,* which is widespread in south-west Western Australia (and occurs in restricted areas of Eyre Peninsula and western Victoria), appears to be one of the few genera of animals which has at least some species restricted to particular granite outcrops *i.e.* species that are site specific. A striking confirmatory example is an undescribed species from Paynes Find Rock in which the spider exhibits an aberrant carapace modification (an everted fovea). This peculiarity does not occur in species of neighbouring rocks and indicates development of a morphological feature in isolation. The spiders are extremely sedentary, do not readily disperse and are active for only a very short period of the year. The spiders live in burrows in the meadows (Plates 2 & 5) and apron soils of the rocks and seal the burrows when the soil begins to dry out. At least one species of pseudoscorpion *Synsphyronus elegans*, which lives under rock slabs, appears to be site-specific to Yorkrakine Rock (north of Tammin).

While there are few data on either endemicity to granite outcrops and/or rock-site specificity of invertebrates there is apparently considerable botanical endemicity of particular rocks (see Hopper *et al.* 1997). The lack of invertebrate data may be giving a false impression of low endemicity.

Biogeographic patterns: relative ages

Those invertebrate species which are confined to particular rocks probably indicate an older biogeographic phenomenon than those species which have not speciated in response to habitat isolation. I suggest this speciation began with the change to sclerophylly and seasonality in the early and mid-tertiary which would have induced a concentration of moisture loving organisms around the granite rocks, not because of any special affinity for rocks *per se* but because of their capacity to provide wet microhabitats in an otherwise dry terrain. This moisture holding capacity of areas around substantial granite outcrops also holds good for “fugitive rocks”. Main (1996) noted the occurrence of Mesozoic genera of mygalomorphs such as *Teyl* in microhabitats over granitic “basement highs” on relictual parts of the old Tertiary plateau of the wheatbelt of southern Western Australia. The model she presented could explain the distribution of many archaic invertebrates associated with higher parts of the inland plateau which in turn embraces many granite outcrops.

A richer fauna of both vertebrates and invertebrates must have existed during the mid-to-late Tertiary and into the Pleistocene, similarly focused around granite outcrops, but some of which has become extinct along with increased aridity. Fossil deposits of diprotodonts and other vertebrates at Balladonia (Glauert 1912) from a dam excavation adjacent to granite domes indicates just such a concentration (even if only seasonal) as we now see for certain extant organisms. Such species may also have been associated with other granite rocks which did not provide the same extensive boggy conditions suitable for fossilisation.

At best, the granite outcrops currently preserve a partially relictual, but also a predominantly widespread although contracted and fragmented biota. Nevertheless, high botanical endemicity has been demonstrated for selected taxa which have been extensively studied. This suggests that the invertebrate fauna requires comparable in depth surveys, particularly of those forms with sedentary behaviour.

Aeolian reinforcement

The role of lichens and algae in both physically breaking down a “sterile” rock surface and also “capturing” atmospheric nutrients, primarily nitrogen, and thereby making a substrate or creating an environment for other organisms, has already been noted. An additional primary and continuous source of biological enhancement of granite outcrops is prevalent in what may be termed the aeolian medium. Swan (1992) defined an “aeolian zone” as “a region around and beyond the limits of the flowering plants”. He suggested that the combined aeolian zones of the world constitute an “aeolian biome”. An expanded definition of the “aeolian biome” could readily embrace granite outcrops both during the initial stages of their colonisation and later, even when a considerable associated biota has developed. The isolated granite outcrops of south-western Western Australia and/or other parts of southern Australia provide staging posts or scattered points in a biological lattice. Aerially-borne nutrients, and organic and inert debris as well as propagules of plants and animals (as spores, seeds and resistant eggs, and various other life history stages of invertebrates, including Collembola, aphids, thrips and large-winged insects) all combine to provide a continuous aeolian reinforcement of spatially isolated granite outcrops.

The seasonal behaviour and dormancy of some of the invertebrate fauna has already been mentioned. Spiders

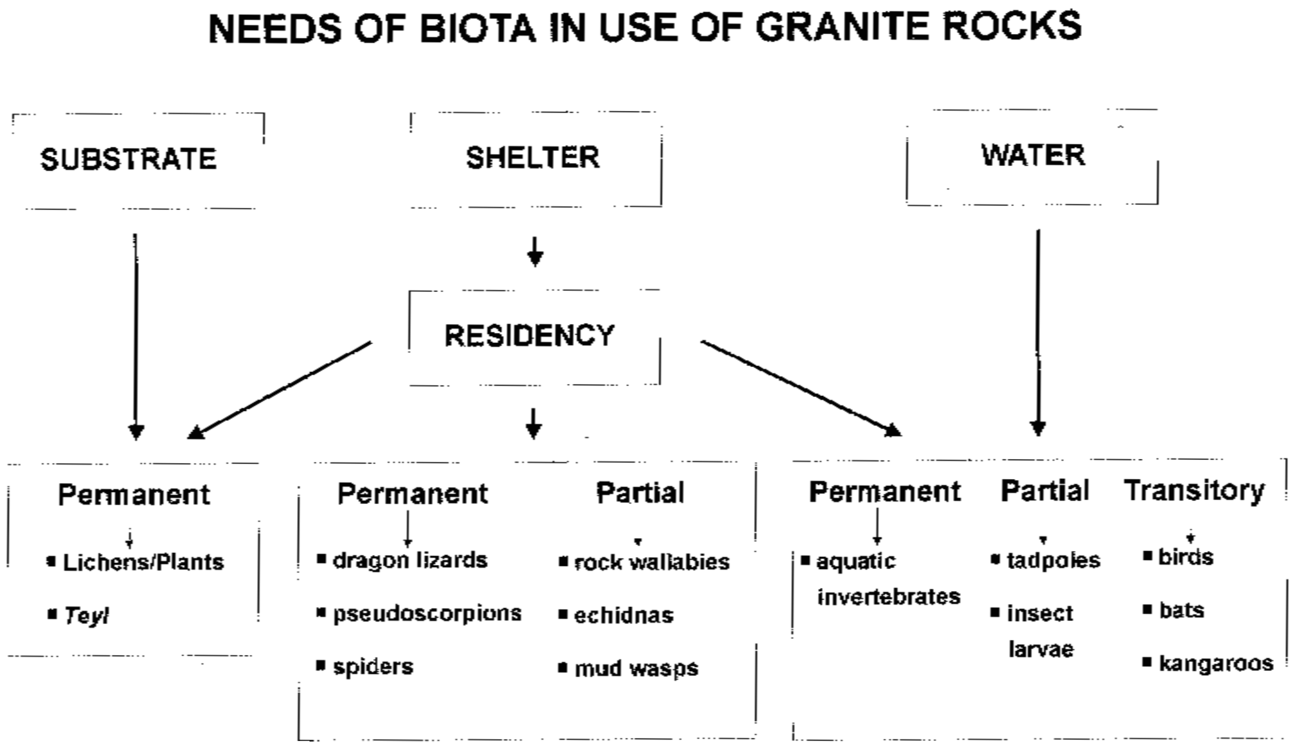

Figure 2. Selected examples illustrating the needs of the biota in their use of granite outcrops summarised according to their residency status in relation to provision by rocks of a substrate, shelter and water. Amongst the transitory fauna dependent on rocks for water, the present environment includes feral animals from rabbits and foxes to camels and donkeys.

such as the poor disperser *Teyl* are dormant for at least six months of the year secluded in sealed burrows, but other organisms deposit eggs or encysted dormant stages in the soil or dried out beds of ephemeral ponds. These latter organisms may be dispersed aerially, hence both reinforcing otherwise isolated populations and inhibitng allopatric speciation. Not only are propagules of plants and invertebrates aerially dispersed but also adult insects may form part of the aeolian fauna thereby accounting for the general lack of rock specificity.

Irregular but recurrent weather events such as cyclonic winds, tornadoes, dust storms and local "cock-eyed bobs" (Hunt 1929) each with their propensity for lifting, distributing and dumping fine biotic material, all reinforce the aeolian element of granite rocks.

Thus, finally, although from present knowledge the biota (especially of the fauna) associated with granite outcrops appears to have a distinctiveness, it represents predominantly a collective of "refugees" rather than an array of separate biotas tied to particular sites. Nevertheless I believe the relict mygalomorph genus *Teyl* may be representative of many other invertebrates of which we are not aware. This example indicates the need for thorough comprehensive surveys of invertebrates on selected outcrops over a wide geographic range.

Geographic replacements

In spite of the taxonomic commonality over a wide range of rocks, especially at the generic level and in many cases the lack of species endemicity, there are some noticeable geographic replacements by ecological "equivalents" of certain rock adapted organisms, both plants and animals, or organisms centred around outcrops. For example *Anthocercus* of the southern forests is replaced by *Kunzea pulchella* in the wheatbelt, which in turn is replaced by a *Beaufortia* in the eastern Goldfields. Amongst spiders over the same geographic span, *Hemicloea* is replaced by *Rebilus* and a lycosid. Trapdoor spiders of the Aganippini similarly replace one another in the apron meadows and fringing vegetation of disjunct rocks. Although superficially such replacements may be loosely regarded as "equivalents", a better term might be "behavioural counterparts" since the replacements are clearly associated with the rainfall zones and as such, physiological and interactive differences must be associated with the taxonomic shifts.

Further study of this phenomenon as demonstrated by a selection of taxa over a geographic span of rocks could well prove worthwhile.

Conclusions

The ecology of the biota can be summed up in the concept of the needs of the respective taxa in relation to what the rocks offer towards their livelihood (see Fig 2). The use of granite outcrops in satisfying the needs of their resident biota are primarily related to the functions offered by (a) the substrate *i.e.* the rock surface as a "home base" or attachment plane, (b) the rocks as shelter, and (c) the rocks as a water source. The biota can be grouped into permanent, partial or transitory residents according to the degree of association throughout the organisms' life histories.

No one rock maintains a "closed" ecosystem. Although some rocks with complex configurations and diverse biota with a high degree of interaction as measured by botanic richness, habitat availability for fauna, and food chains, may tend towards self-containment they are in fact still "open" in the same sense that a cave ecosystem is. Cave ecosystems are dependent on residents (such as bats) which live partly outside the cave to bring in some nutrients and also on the accidental deposition, such as by floods, of detrital matter. Granite rocks similarly are dependent on the partial and transitory residents to enrich the ecosystem. In addition the propagules and non-biotic detritus supplied by the aeolian medium continuously enhance the viability of a rock ecosystem. Thus even those elements which have permanent residency have some dependence beyond the margins or physical boundaries demarcating a particular rock. Figure 2 summarises the relationship of a granite outcrop biota to the outcrop and the surrounding environment.

In essence it can be stated that granite outcrops support a characteristic assemblage of plants and animals comprised of isolated populations of relictual genera and/or species, and widespread examples from the surrounding environment. There are many examples of granite outcrops, as isolates, retaining components of a once more widely distributed biota, for example the stand of jarrah trees at Jilakin Rock (Abbott 1984). With increasing sclerophylly of the vegetation associated with a drying of the climate since the mid-late Tertiary, the granite outcrops because of their water harvesting/ retention capacity have become the foci around which moisture-dependent organisms have concentrated. Nevertheless they support both sedentary isolates and mobile, wide ranging organisms as well as wind-borne biota.

It is notable that apart from the more sedentary organisms and particularly elements of an older evolutionary radiation, such as the Mesozoic mygalomorph spider genus *Teyl* , most animal genera have not speciated in association with particular outcrops in spite of population fragmentation. Few organisms are endemic to particular rocks. However, there is evidence that there is a high level of genetic difference between populations of particular species from different rocks. Endemicity *i.e.* rock-specificity amongst plants, appears to be more pronounced, on present evidence, than amongst the fauna. In contrast to the taxonomic conservatism of much of the outcrop biota there are some interesting examples of geographic replacement of behavioural counterparts represented by unrelated taxa particularly over the rainfall gradient.

Also of interest, many organisms although now confined to granite outcrops either entirely or for a greater part of their life history do not exhibit adaptations peculiar to "rock- living" (the agamid lizard *Ctenophorus ornatus* and certain spiders *e.g.* a lycosid are exceptions) but rather are confined now to rocks because of their refugial role in maintaining cool, moist habitats on which such species are dependent as a legacy from their earlier historical environmental association.

In summary, a granite outcrop at the individual level maintains a co-operative of refugees, but on a broad scale granite outcrops represent a collective ecosystem.

References

Abbott I 1984 Ecological features of an outlying stand of jarrah (*Eucalyptus marginata*) at Jilakin Rock, Western Australia. Journal of the Royal Society of Western Australia 66:107-110.

Anon undated Granite Outcrops: Living Rocks. Department of Conservation and Land Management, Perth.

Balme B E & Churchill D M 1959 Tertiary sediments at Coolgardie, Western Australia. Journal of the Royal Society of Western Australia. 42:37-43.

Bradshaw S D & Main A R 1968 Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. Journal of Zoology 154:193-221.

Brooker M I H & Kleinig D A 1990 A field guide to Eucalypts Vol 2. Southwestern and Southern Australia. Inkata Press, Melbourne & Sydney.

Campbell E M 1997 Granitic landforms. Journal of the Royal Society of Western Australia 80:101-112.

Churchill D M 1968 The distribution and prehistory of *Eucalyptus diversicolor* F. Muell., *E. marginata* Donn. ex Sm., and *E. calophylla* R. Br. in relation to rainfall. Australian Journal of Botany 16:125-151.

Clarke E de C 1919 Notes on the occurrence of boulders, possibly glaciated, near Leonora and Laverton. Journal of the Royal Society of Western Australia 6:27-32.

Clarke J D A 1994 Geomorphology of the Kambalda region, Western Australia. Australian Journal of Earth Sciences 41:229-239.

Cranston P S, Edward D H D & Colless D H 1987 *Archaeochlus* Brundin: a midge out of time (Diptera: Chironomidae). Systematic Entomology 12:313-334.

Dell J & How R A 1984 Vertbrate Fauna. In: Biological Survey of the Eastern Goldfields of Western Australia. 2. Widgiemooltha-Zanthus area. Records of the Western Australian Museum. Supp 18:57-69.

Fairbridge R W & Finkl C W 1978 Geomorphic analysis of the rifted cratonic margins of Western Australia. Zeitschrift für Geomorphologie 22:369-389.

Fernie N 1930 Water supplies from rock catchments in the Western Australian wheat belt. Journal of the Institution of Engineers of Australia 2:198-208.

Finkl C W & Churchward H M 1974 The etched surfaces of southwestern Australia. Journal of the Geological Society of Australia 20:295-307.

Gaff D F 1981 The biology of resurrection plants. In: The Biology of Australian Plants (eds J S Pate & A J McComb). University of Western Australia Press, Perth, 114-146.

Glauert L 1912 Fossil marsupial remains from Balladonia in the Eucla Division. Records of the Western Australian Museum 1: 47- 65.

Hale M E 1967 The Biology of Lichens. Edward Arnold, London.

Hopper S D 1979 Biogeographical aspects of speciation in the southwest Australian flora. Annual Review of Ecology and Systematics. 10:399-422.

Hopper S D, Campbell N A & Moran G F 1982 *Eucalyptus caesia*, a rare mallee of granite rocks from south-western Australia. In: Species at risk: research in Australia. (eds R H Groves & W D L Ride). Australian Academy of Science, Canberra, 46-61.

Hopper S D, Brown A P & Marchant N G 1997 Plants of Western Australian granite outcrops. Journal of the Royal Society of Western Australia 80:141-158.

Hunt H A 1929 Record of notable meteorological events in Western Australia: windstorms, (hurricanes, cyclones, heavy gales, duststorms *etc*). In: Results of rainfall observations made in Western Australia. Commonweath of Australia Bureau of Meteorology, Melbourne, 162-187.

James S H 1982 The relevance of genetic systems in *Isotoma petraea* to conservation practice. In: Species at Risk: Research in Australia (eds R H Groves and W D L Ride). Australian Academy of Science, Canberra, 63-72.

Jutson J T 1921 Note on the "dimpling" of granite hills in sub-arid Western Australia. Proceedings of the Royal Society of Victoria 33:108-111.

Jutson J T 1934 The physiography (geomorphology) of Western Australia. Geological Survey of Western Australia, Bulletin 95:1-365.

Main B Y 1967 Between Wodjil and Tor. Jacaranda & Landfall, Brisbane & Perth.

Main B Y 1976 Spiders. Collins, Sydney.

Main B Y 1996 Microcosmic biogeography: trapdoor spiders in a time warp at Durokoppin. In: Gondwanan Heritage, Past Present and Future of the Western Australian Biota (eds S D Hopper, J A Chappill, M S Harvey & A S George). Surrey Beatty & Sons, Chipping Norton, NSW.

Marchant N G 1973 Granite Outcrops. In: Flowers and Plants of Western Australia (eds R Erickson, A S George, N G Marchant & M K Morcombe). A H & A W Reed, Sydney, 199-202.

McMillan P & Pieroni M undated Exploring Granite Outcrops. Department of Conservation and Land Management, Perth.

McWhae J R H, Playford P E, Lindner A W, Glenister B F & Balme B E 1958 The stratigraphy of Western Australia. Journal of the Geological Society of Australia 4:1-161.

Newbey K R 1984 Physical environment. In: Biological Survey of the eastern Goldfields of Western Australia. 2. Widgiemooltha-Zanthus area. Records of the Western Australian Museum, Supp 18:29-40.

Newbey K R 1988 Physical environment. In: The Biological Survey of the Eastern Goldfields of Western Australia. 4. Lake Johnston-Hyden. Records of the Western Australian Museum, Supp 30:7-16.

Newbey K R 1995 Physical environment. In: The Biological Survey of the Eastern Goldfields of Western Australia. 11. Boorabbin-Southern Cross area (eds Keighery G J, McKenzie N L & Hall N J) . Records of the Western Australian Museum, Suppl 49:6-15.

Onions C T 1978 The Shorter Oxford English Dictionary. Clarendon, Oxford.

Ornduff R 1987 Islands on Islands: Plant Life on the Granite Outcrops of Western Australia. University of Hawaii Press, Honolulu.

Smith R I L and Prince P A 1984 The natural history of Beauchene Island. Biological Journal of the Linnaean Society 24:233-283.

Swan L W 1992 The aeolian biome ecosystems of the earth's extremes. Bioscience 42:262-270.

Twidale C R & Campbell E M 1984 Murphy Haystacks, Eyre Peninsula, South Australia. Transactions of the Royal Society of South Australia 108:175-183.

White M E 1986 The Greening of Gondwana. Reed, Frenchs Forest.

Withers P C & Edward D H D 1997 Terrestrial fauna of granite outcrops in Western Australia. Journal of the Royal Society of Western Australia 80:159-166.