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The Royal Society of Western Australia

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The journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

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The Royal Society of Western Australia Medallist, 2001

Dr Phillip Playford

Geological Survey of Western Australia

Born in Guildford, Western Australia in 1931, Phillip Playford graduated in 1952 from the University of Western Australia with First Class Honours in Geology. He found employment as a field geologist with the Bureau of Mineral Resources but soon transferred to a similar position with West Australian Petroleum who were searching for oil near Exmouth Gulf. Over the next eight years he rose to become Staff Stratigrapher. His work concentrated initially on unravelling the stratigraphy of the southern Carnarvon Basin and the lower Murchison area. Later he moved to the Perth Basin, his research leading to the discovery of the Dongara gas field. While with WAPET, Phillip also began research on the Devonian Reefs of the Canning Basin; this became a life-long interest.

In 1960 Phillip went to the USA and Stanford University, gaining a PhD in geology in 1962. In that year he returned to the Public Service, as Supervising Geologist of the Sedimentary (Oil) Division with the Geological Survey. He supported the drilling program that led to the discovery of the Barrow Island oil field. After a short time as Exploration and then General Manager with Abrolhos Oil, in 1970/71 he continued his career with the Geological Survey, becoming Deputy Director in 1980. From this position he was promoted to Assistant Director General of Mines and finally transferred sideways to become Director of the Geological Survey. Since retiring in 1992, he has spent several months each year with Survey staff in the Canning Basin and at Shark Bay, continuing to make new discoveries. In all he has published 95 scientific papers.

While all this was happening, Phillip had another life, in history. Since seeing the remains of an old sailing ship at the foot of the rugged cliffs north of the Murchison River he has studied wrecks on the Western Australian coast and the history of voyages by the Dutch East India Company. His book on the Zuytdorp (Carpet of Silver) won its category in the WA Premier's Book Awards for 1996. It was followed by an account of Willem de Vlamingh's voyage to the Swan River in 1697.

Phillip joined the Royal Society in 1952 and served on Council for 25 years. He was President in 1969/70 and was awarded Honorary life Membership in 1999.

Other honours that he has received include; Gibb Maitland Medal of the Geological Society of Australia, Lewis G Weeks Gold medal of the Australian Petroleum Exploration Association, Special Commendation Award of the American Association of Petroleum Geologists, Distinguished Membership Award of the Petroleum Exploration Association of Australia, Honorary Life Member of the National Trust (WA), Honorary Doctor of Science of The University of Western Australia, and Member of the Order of Australia (AM).

The Permo-Carboniferous Glaciation of Gondwana: its legacy in Western Australia (Medal Address March 2001)

It has long been known that large areas of the Gondwana Supercontinent, comprising Australia, Antarctica, Africa, India, and South America, were subject to repeated glaciations during the Early Permian and Late Carboniferous (about 270 to 320 million years ago), but there has been no general agreement on the form and magnitude of those glaciations. In Western Australia, the best evidence of glaciation is displayed in Early Permian strata and landforms, but some authorities have claimed that this does not point to the existence of major ice sheets in the area at that time.

That view is now challenged by new evidence, mainly derived from glacial landforms, which indicate that a succession of major wet-based ice sheets, several kilometres thick, probably extended across all or most of the Australian continent and other parts of Gondwana during the Early Permian. The ice, moving away from the south pole, generally travelled north-northwest over Western Australia and South Australia and north-northeast over Victoria and Tasmania, as shown by striations in glaciated pavements formed below the ice.

In the northern Canning Basin, the uppermost surface of the Devonian limestone ranges is sub-horizontal, essentially marking the level of the Early Permian unconformity. The unconformity surface, where freshly exposed, is a striated glacial pavement, indicating movement of the ice to the north and north-northwest, directly towards the mountainous area of the Kimberley Block, which at that time was probably entirely covered by ice. Extensive karst features and glacial valleys were formed in limestones in the

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subglacial environment, and are now exposed where the overlying Grant Group has been removed by Cainozoic erosion. The exhumed Early Permian geomorphic features consist of extensive cave systems, canyons, dry valleys, tunnels, and dolines, notable examples including Mimbi Caves, Windjana Gorge, Menyous Gap, and Tunnel Creek.

Early Permian glacial landforms are widely developed in Precambrian rocks along the northern margin of the Pilbara Block. They comprise ice-scoured channels, U-shaped valleys, rock drumlins, and polished striated pavements, conspicuous examples including the valley of Shay Gap, a drumlin field near Carawine Pool, and a major linear channel north of Pearana Rockhole. These features of the modem landscape were originally formed below the base of a thick continental ice sheet during the final culmination of the ice age.

The Permo-Carboniferous ice age was one of the most momentous events in the geological evolution of Western Australia, with far-reaching geomorphological effects that are still evident in modem landscapes. Relict glacial landforms are widespread, and show that extensive areas of the Great Plateau, covering the Yilgarn Block and parts of the Pilbara and Kimberley Blocks, were planed down below the ice, forming a level surface above which a few remaining hills and mountains projected. The glaciated surface was dissected by a network of rivers during pluvial periods of the Mesozoic and Early Tertiary. Remnants of those river systems are preserved today as shallow palaeochannels crossing the otherwise level surface of the Great Plateau, a surface that basically is inherited from the Permo- Carboniferous glaciation of this part of Gondwana.

The Royal Society of Western Australia
Medal Recipients
1924-2001

The Medal of The Royal Society of Western Australia was instituted in 1924 to mark the centenary of the birth of Lord Kelvin (26 June, 1825). The Royal Society Medal (originally referred to as the "Gold Medal" and then subsequently sometimes as the "Kelvin Medal' due to the association of the inaugural award with the centennial Kelvin celebration and because the medal bears in relief on its obverse side the head of Kelvin) is awarded approximately every four years for distinguished work in science connected with Western Australia.

The original dye for the medal, first struck in 1924, remains in the safe-keeping of The Society. The first three medals were struck in gold, and all subsequent medals in silver.

The first medallist of The Royal Society was Dr William J. Hancock, Government Electrical Engineer and Honorary Medical Radiographer at Perth Hospital, who in 1924 was the recipient of the Medal of The Royal Society of Western Australia, in recognition of his pioneering work in the medical application of X-rays.

The most recent medallist Dr Phillip Playford was presented with the Medal of The Royal Society of Western Australia, in recognition of his contributions to geology and history of discovery in Western Australia.

Recipients of the Medal of The Royal Society of Western Australia:

(reference to Journal of the Royal Society notice of medal award in parentheses)

1924	Dr W J Hancock: radiography; medical application of x-rays (10:xvii)
1929	Dr E S Simpson: mineralogy and geology of Western Australia (15:iv)
1933	Mr W M Carne: plant pathology; the bitter pit of apples (19:xi)
1937	Mr A Gibb Maitland: Pilbara survey and artesian water supplies (23:xi)
1941	Prof E de C Clarke: geology of Western Australia (27:v)
1945	Mr L Glauert: natural sciences (31:vi)
1949	Mr C A Gardner: botany, the flora of Western Australia (35:v)
1955	Dr H W Bennetts: veterinary science; live stock diseases (40:1)
1959	Prof E J Underwood: animal nutrition and husbandry (43:67)
1966	Mr C F H Jenkins: agricultural entomology and natural history (49:91)
1970	Prof R T Prider: geology; petrology and mineralogy (53:95)
1979	Prof R M Berndt: anthropology; aboriginal studies (63:29)
1979	Prof B J Grieve: botany; ecophysiology and the flora of WA (63:29)
1979	Dr D L Serventy: zoology; ornithology and nature conservation
1983	Dr J S Beard: botany; vegetation classification and mapping (65:93)
1986	Prof C A Parker: soil biology
1993	Prof J R de Laeter: geophysics and geochronology (77:4)
1995	Prof A R Main: zoology; ecology and nature conservation (78:89)
1997	Prof Ernest Hodgkin: estuarine studies (80:287)
1997	Prof Arthur McComb: plant growth and ecology (80:287)
2001	Dr Phillip Playford: geology and history of discovery in Western Australia (84:1)

Journal of the Royal Society of Western Australia, 84: 5-11, 2001

Calamoecia trilobata n sp (Copepoda: Calanoida) from salt lakes in south-western Australia

S A Halse & J M McRae

Department of Conservation and Land Management, CALM Science Division, PO Box 51 Wanneroo WA 6946
stuarth@calm.wa.gov.au janem@calm.wa.gov.au

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Abstract

A new species of calanoid copepod, *Calamoecia trilobata* n sp, is described from saline lakes in the central and southern Wheatbelt of south-west Western Australia. *Calamoecia trilobata* appears to occur in comparatively few lakes and to be restricted to south-west Western Australia. It is unusual in that the size ratio between sexes, as well as female size, varies significantly among lakes. The genus *Calamoecia* now contains three saline-water species, all of which occur in Western Australia. *Calamoecia salina* and *C. clitellata* are also found in eastern Australia.

Keywords: *Calamoecia trilobata*, Copepoda, salt lakes, sexual dimorphism, Western Australia

Introduction

Most calanoid copepods in inland waters of Western Australia belong to the genera *Calamoecia*, *Boeckella* and *Hemiboeckella* in the family Centropagidae (Maly & Bayly 1991; Maly *et al.* 1997). With the recent description of *Calamoecia halsei* (Bayly 1998), ten described species of *Calamoecia* have been recorded in Western Australia. Two additional taxa that are probably distinct species await description: *Calamoecia* cf *lucasi* (Bayly 1998) and *Calamoecia tasmanica* sl (Bayly 1992), which was wrongly referred to as *Calamoecia tasmanica tasmanica* by Maly *et al.* (1997).

Most species of *Calamoecia* are restricted to fresh water, with the only described species in saline water bodies being *Calamoecia salina* and *Calamoecia clitellata* (Bayly 1992). A third species of *Calamoecia* from saline lakes in the central and southern Wheatbelt regions of south-west Western Australia is described below.

Methods

Specimens were collected using pondnets with 50 µm or 250 µm mesh and preserved in 1-2 % phosphate-buffered formaldehyde or 70 % alcohol. Lake salinities were measured *in situ* with a WTW Multiline P4 meter. Specimens were measured under a Leica MZ12 stereomicroscope fitted with an eyepiece micrometer and dissected with entomological pins in polyvinyl lactophenol mountant on a microslide under the same microscope. Dissected specimens and appendages were examined with differential interference contrast illumination using a Zeiss Axioskop 2 microscope and drawn under bright field illumination using a Zeiss Jenamed microscope and *camera lucida*. The system of abbreviations given by Bayly (1992) was used in the description of the legs; the system of Huys & Boxshall (1991) was used for mouthparts.

Statistical significance of variation among lakes in size and size ratio between sexes was tested using 1-way analysis of variance and Duncan's multiple range test (SAS statistical package, SAS Institute 1989). Prosomal and overall length ratios were tested separately. Prosomal length was measured along the midline, overall length excluded the caudal setae.

Taxonomy

Family Centropagidae Giesbrecht
Genus *Calamoecia* Brady
Calamoecia trilobata n sp

Type material

Holotype: male, dissected on microslide, Western Australian Museum of Natural Science WAM C 24446, Ardath Lake (32° 05' 52" S 118° 09' 21" E), 10.xi.1998, S A Halse & D J Cale. Allotype: female, dissected on microslide, WAM C 24447, same location and collecting details. Paratypes: male, dissected on microslide, WAM C 24448; female, dissected on microslide, WAM C 24449; 15 males and 15 females undissected in vial, WAM C 24450, same location and collecting details.

Additional material

Male, dissected on microslide, WAM C 24451; female dissected on microslide, WAM C 24452; 10 males and 10 females undissected in vial, WAM C 24453, Shackleton Lake (31° 56' 36" S 117° 53' 41" E), 21.x.1997, A M Pinder & J M McRae. Male, dissected on microslide, WAM C 24454; female dissected on microslide, WAM C 24455, Baandee Lake (31° 35' 28" S 117° 57' 21" E), 21.x.1997, A M Pinder & J M McRae. 10 males and 10 females, WAM C 24521, un-named wetland in Frank Hahn National Park (32° 57' 50" S 120° 21' 41" E), 20.viii.1998, A M Pinder & J M McRae. 5 males and 5 females, WAM C 24522, Lake Campion (31° 8' 28" S 118° 20' 17" E), 10.xi.1998, S A Halse & D J Cale.

Description of female

Size: Length of prosome of 10 females from type locality 0.73 - 1.06 mm (mean 0.83 mm); length to end of caudal rami (excluding caudal setae) 1.01 - 1.38 mm (mean 1.15 mm).

Whole animal (Fig 1A): Body of typical *Calamoecia* form, without obvious distinguishing features on 4th prosomal segment.

Antennule (Fig 1A): Antennule of 25 segments.

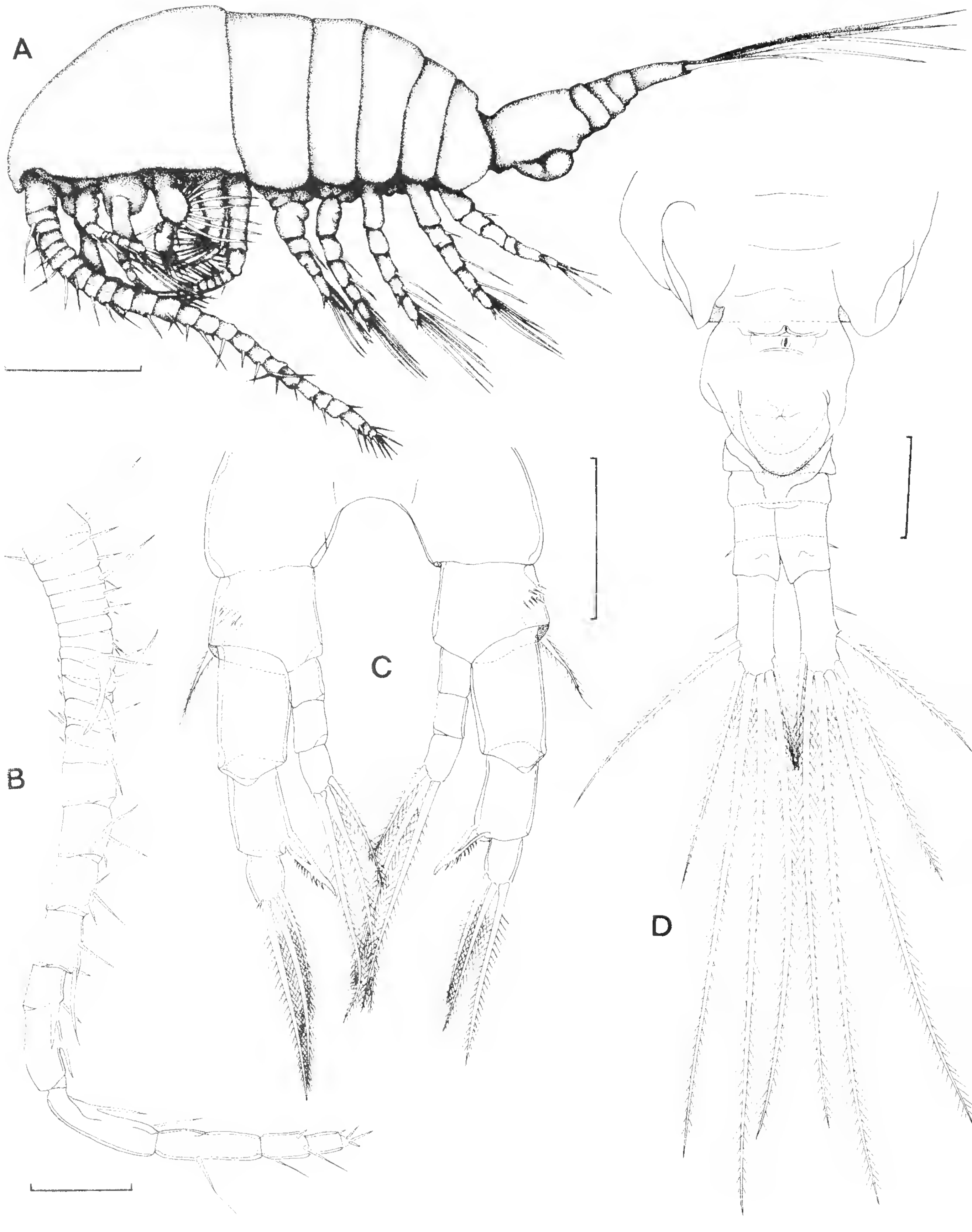

Figure 1. *Calamoecia trilobata* n sp; **A**, whole animal, lateral view of female; **B**, right antennule of male holotype (WAM C 24446); **C**, fifth leg of female allotype (WAM C 24447); **D**, ventral view of female genital segment. Scale: A = 0.5, B-D = 0.1 mm.

Antenna (Fig. 2B): Coxa with 1 seta, basis with 2 distal setae. Exopod with 7 segments and setation 1.3.1.1.1.2.3, distal segment small. Endopod with 3 segments; 2 setae on proximal segment, row of 6-9 lateral setae usually increasing in size distally on penultimate segment, 6 large terminal and 1 smaller offset seta on ultimate segment.

Mandible (Fig. 2D): Cutting edge with 8 teeth, ventral tooth low and intercusp depression between it and second tooth small. Basis with 3 setae, exopod with 5 segments and setation 1.1.1.1.2. Endopod with 2 segments, proximal segment with 3 setae, distal with 11.

Maxillule (Fig. 2C): Praecoxa with 9 spine-like setae and 3+1 finer setae on arthrite, coxal epipodite with 9 large plumose setae, coxal endite with 4 setae. Proximal basal endite with 4 setae, distal with 6, basal exite with 1, exopod with 8. Endopod with 9 setae but poorly differentiated from basis and segmentation unclear.

Maxilla (Fig. 2A): Proximal praecoxal endite with 3 large and 2 small setae and small spine on inner distal corner, distal endite with 2 large and 1 small setae. Coxal endites with 2 large and 1 small setae. Allobasis with 2 large plumose setae and 1 spine-like seta, endopod 3-segmented with setation 2.1.2.

Maxilliped (Fig. 2E): Praecoxa with 1 seta (not obviously differentiated from coxa). Coxal edites with 2, 3 and 4 setae, and tufts of spinules that become more pronounced distally. Basis with 3-4 setae and proximal row of spinules. Endopod 6-segmented with setation 2.4.4.3.3+1.4.

First leg (Fig 3A): Re2 and Re3 sometimes poorly differentiated. Outer Re spine formula 0.0.1, secondary spinules on spine not unusually large (see Bayly 1998). Re3 with 3 terminal and 1 inner setae, Re2 sometimes with 1 seta on inner edge. Re1 with 1 seta on inner edge. Ri1 with 3 distal and 1-2 inner setae. Seta on inner distal corner of B1 reaching distal edge of B2.

Fourth leg (Fig 3B): Outer Re spine formula 0.1.1 or 0.1.2. Re3 with 3 terminal and 2 inner setae, Re2 with 1 seta near inner distal corner, Re1 with 1 seta near inner distal corner. Ri2 with 1 outer, 3 terminal and 2 inner setae, Ri1 with 1 (Fig 3B) or 2 seta on inner distal third.

Fifth leg (Fig 1C): Outgrowth from inner distal corner of Re2, with obvious secondary spinules on distal side, extending approximately to distal end of Re3, which has 3 terminal setae, the inner slightly shorter than the outer 2. Ri with 3 clearly differentiated segments and not extending past Re2. Ri3 with 3 terminal seta, inner of which slightly shorter than outer 2.

Urosome (Fig 1D): Genital segment about as wide as long, viewed ventrally, with pronounced bulge on right side midway along segment and an indentation posterior to the bulge.

Description of male

Size: Length of prosome of 10 males from type locality 0.56 – 0.65 mm (mean 0.60 mm); length to end of caudal rami 0.79 – 0.93 mm (mean 0.86 mm).

Mouthparts: Antennule (Fig. 1B) of 22 segments with hinge between 18 and 19. Other mouthparts similar to those of female.

Fifth leg (Fig 3C-E): Right Re claw curved with small protuberance at inner distal corner of Re3 and seta on distal anterior face of Re2. Stout spine on distal inner corner of right Re1. Right Ri delicate, 3-segmented and without setae; often distorted during preservation (Ri3 bends over and all segments shrivel - *e.g.* Fig 3C); Ri3 conically shaped. Left Re 2-segmented; Re1 with ridge on outer edge of anterior face that continues into Re2 (Fig 3C); Re2 with stout terminal seta. Left Ri 1-segmented, broad and plate-like with distal portion divided into 3 lobes (Fig 3E). Left Ri often closely adpressed to left Re1 with outer lobes of Ri wrapped around inner face of Re. The 3 lobes of Ri difficult to distinguish and often distort during fixation; anterior lobe largest and posterior lobe notched (Fig 3C,E). Left B2 with small mesially directed projection or spine on inner surface.

Derivation of name

The name *trilobata* is derived from the Latin *lobus* for lobe or rounded protuberance, referring to the three lobes of the male fifth left Ri, which are one of the unique features of the species.

Remarks

Both sexes of *C. trilobata* are readily distinguished from the other 2 salt-lake *Calamoecia* species, *C. salina* and *C. clitellata*, on characters of the fifth leg. Female *C. trilobata* have 3-segmented Ri that are much shorter than on *C. clitellata* (Bayly 1962) and slightly shorter than on *C. salina* (Bayly 1961). Ri of *C. trilobata* and *C. salina* can be distinguished by the 3 long setae on the former and 2 short setae on the latter. Re3 of *C. salina* have only 2 setae, those of *C. clitellata* have 1 long and 2 very short setae, whereas *C. trilobata* have 2 long and 1 shorter setae. Another distinctive feature of female *C. clitellata* is the dorsal prominent saddle on the 4th prosomal segment (Bayly 1962). Males of the salt-lake *Calamoecia* species are even more easily separated using morphology of the fifth leg: *C. clitellata* males have 2-segmented right Ri with a lobe on Ri2, *C. salina* 3-segmented Ri with 2 small distal setae and *C. trilobata* 3-segmented Ri without setae. Left Ri of *C. clitellata* are 1-segmented and conical in shape, Ri of *C. salina* are 3-segmented with 2 terminal setae and *C. trilobata* are 1-segmented, plate-like and lobed. *Calamoecia salina* can also be distinguished by the long processes arising from B2 (Bayly 1961) and *C. trilobata* by the stout spine on the inner distal corner of right Re1.

If one attempts to key out *C. trilobata* using the dichotomous key in Bayly (1992), the following key numbers apply: 1, 2, 8, 9, 11. Dichotomy 11 contains *C. gibbosa* and *C. lucasi*, both of which have distinctly different male and female fifth legs from *C. trilobata* and are restricted to fresh water (Bayly 1961, 1979).

Most previous descriptions of species of *Calamoecia*, other than *C. t. subattenuata* (Fairbridge 1945b), place little emphasis on mouthparts or legs 1-4 because fifth legs, particularly of males, are such a reliable taxonomic character (Bayly 1961, 1962, 1992). Mouthparts and legs 1 and 4 of *C. trilobata* have been described to provide information about characteristics of the genus *Calamoecia* and in case, at a later

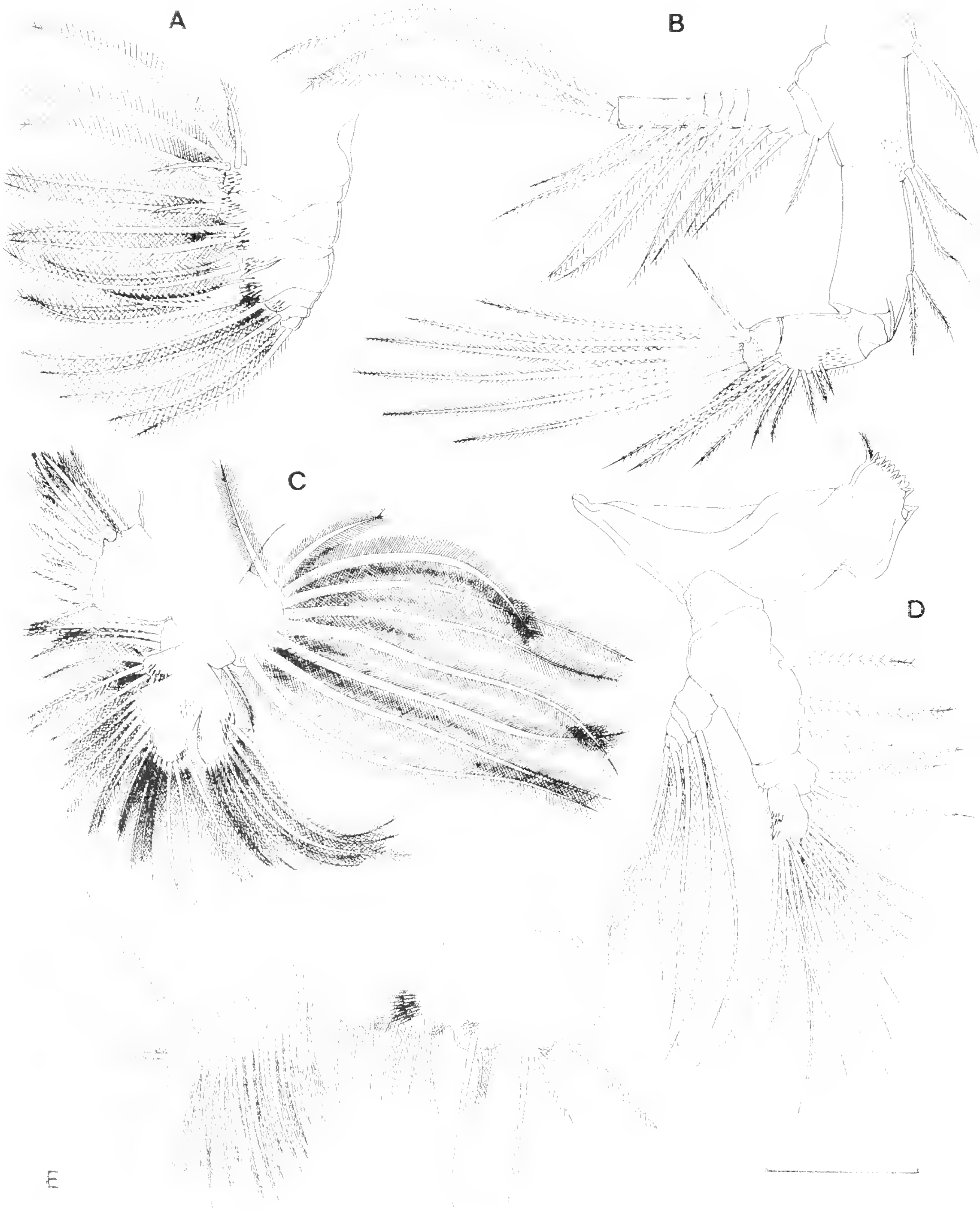

Figure 2. *Calamoecia trilobata* n sp, female paratype (WAM C 24449); **A**, maxilla; **B**, antenna; **C**, maxillule; **D**, mandibule; **E** maxilliped. Scale: 0.1 mm.

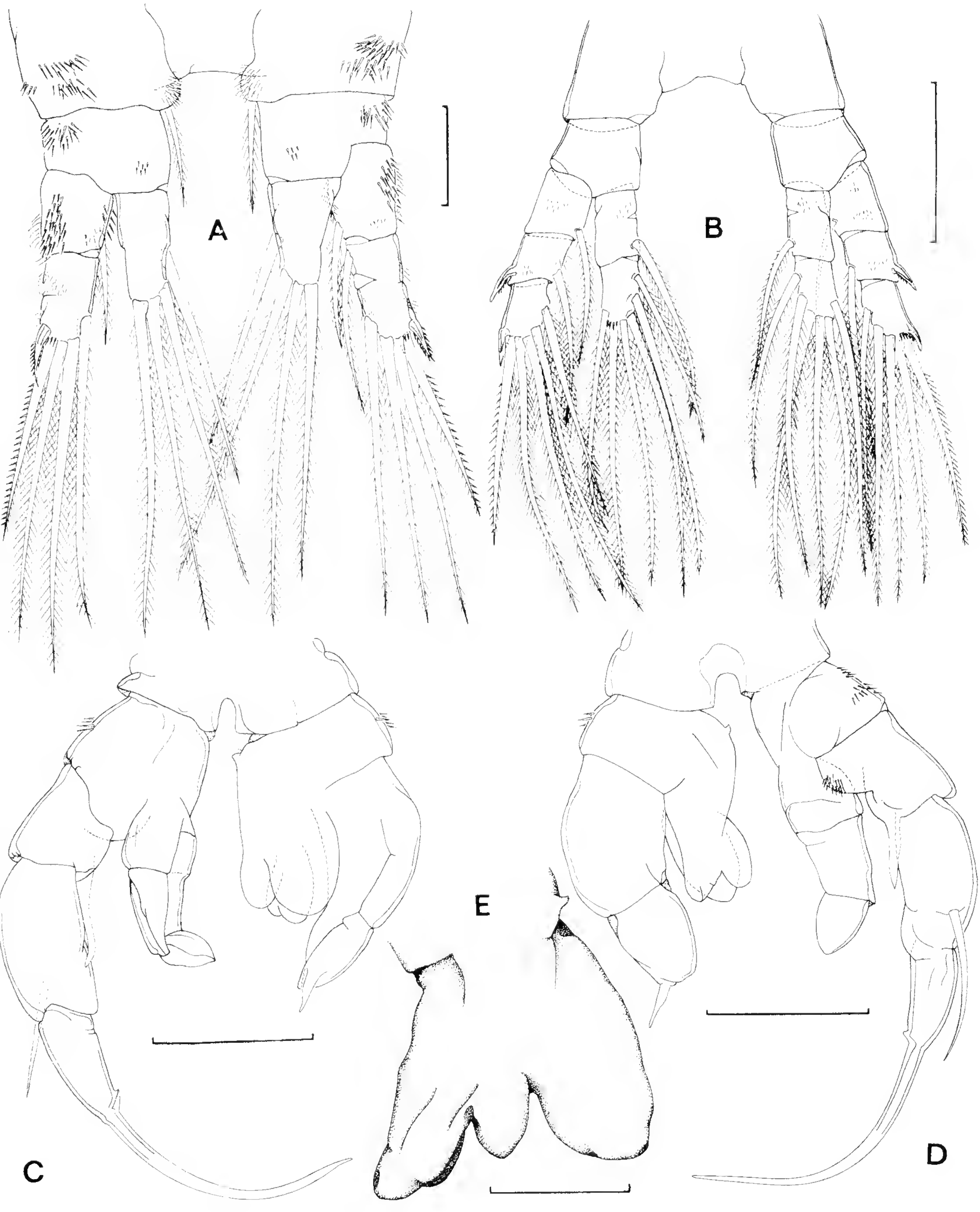

Figure 3. *Calamoecia trilobata* n sp; **A**, first leg of female allotype (WAM C 24447); **B**, fourth leg of female allotype; **C**, anterior view of fifth leg of male holotype (WAM C 24446); **D**, posterior view of fifth leg of male paratype (WAM C 24448); **E**, medial view of left endopod of male fifth leg, flattened to show the 3 lobes that characterize the species. Scales: 0.1 mm.

Table 1. Mean (± se) prosomal and overall lengths in mm, and ratio between sexes, for randomly selected adult male and female *Calamoecia trilobota* from 4 water bodies in south-western Australia. Female lengths and ratios of male:female length varied significantly between sites ($P<0.001$, means with different superscripts differed with $P<0.05$).

Site	Depth (m)	Salinity (g L^{-1})	Measure	Male	Female	Ratio ♀/♂	*n*
Ardath	ca 0.5	60	Prosome	0.60 ± 0.01	0.83 ± 0.01^{A}	1.38 ± 0.06^{A,B}	10
			Overall	0.86 ± 0.02	1.15 ± 0.02^{A}	1.34 ± 0.05^{A,B}	10
Campion	ca 2.0	160*	Prosome	0.61 ± 0.02	0.77 ± 0.03^{A}	1.26 ± 0.04^{A}	5
			Overall	0.86 ± 0.03	1.08 ± 0.04^{A}	1.25 ± 0.04^{A}	5
Frank Hahn	0.15	33	Prosome	0.59 ± 0.01	1.06 ± 0.02^{C}	1.79 ± 0.04^{C}	10
			Overall	0.91 ± 0.02	1.47 ± 0.01^{C}	1.62 ± 0.04^{C}	10
Shackleton	0.1	240*	Prosome	0.64 ± 0.02	0.94 ± 0.02^{B}	1.49 ± 0.05^{B}	10
			Overall	0.93 ± 0.02	1.30 ± 0.03^{B}	1.40 ± 0.04^{B}	10

* probably all dead at this salinity

date, more subtle taxonomic characters are used to resolve species complexes within the genus, as happened with the cyclopoid genus *Mesocyclops* (*e.g.* Dussart & Fernando 1988). While the ancestral calanoid condition of a 3-segmented endopod on legs 1-4 (Huys & Boxshall 1991) is present in centropagids such as *Boeckella* (Fairbridge 1945a; Green & Shiel 1999), segmentation is reduced in *Calamoecia* with a 1-segmented endopod on leg 1 and 2-segmented endopod on legs 2-4 (Bayly 1961). The separation between Re2 and Re3 of leg 1 is frequently indistinct in *C. trilobata* and some other species of *Calamoecia* (*e.g. C. t. subattenuata*, Fairbridge 1945b).

Some reduction of segments from the ancestral condition also occurs in mouthparts of *Calamoecia trilobata* and *C. t. subattenuata* (Fairbridge 1945b). This is most noticeable in the exopod of the antenna and the endopod of the maxillule (*cf* Huys & Boxshall 1991; Green & Shiel 1999). There are pronounced differences in the cutting edge of the mandibular coxae in *C. trilobata* and *C. t. subattenuata*, with the latter having a proportionally larger ventral tooth and greater intercusp distance between the ventral and second tooth. Such differences have been shown to be related to diet (Itoh 1970; Green & Shiel 1999).

Some species of Centropagidae, although rarely *Calamoecia*, show considerable overall variation in size, owing to a combination of sexual dimorphism and differences between season in absolute size of both sexes. Bayly (1978) suggested size ratios between sexes of the same species are usually stable, however, with species typical of temporary water bodies having greater dimorphism than those of permanent waters. *Calamoecia trilobata* differs from this pattern and displayed a variable amount of dimorphism, which was the result of changes in female size while male size remained constant (Table 1). Bayly (1978) related large size differences to low competition and predation pressure and, in agreement with this hypothesis, dimorphism in *C. trilobata* was most strongly expressed in ephemeral pools where species richness was low and few predators and competing planktivores were present. Contrary to Bayly's suggestion that dimorphism is under genetic control, it appeared to be environmentally induced in *C. trilobata*.

Ecology and biogeography

Calamoecia trilobata has been recorded from Frank Hahn National Park at a salinity of 33 g L^{-1} TDS, Ardath Lake at 56 g L^{-1} on 9.x.1997 and 60 g L^{-1} on 10.xi.1998, Baandee Lake at 63 g L^{-1}, Campion Lake at 160 g L^{-1} and Shackleton Lake at 240 g L^{-1}. Populations of the species in Ardath Lake in 1998 and in Shackleton Lake were extremely large, although it is probable that animals in Campion and Shackleton Lakes were dead (and preserved in brine) at the time of collection. Four of the lakes where *C. trilobata* has been collected are within 90 km of each other in the central Wheatbelt region of south-west Western Australia but the other (Frank Hahn National Park) is 300 km away. Given that *C. trilobata* has been collected from only 5 lakes, despite widespread collecting (Maly *et al.* 1997; S A Halse unpublished data), it is likely the species is a halobiont restricted to a comparatively small number of naturally saline lakes. *Calamoecia salina* also occurs at comparatively few lakes in Western Australia (Maly *et al.* 1997; S A Halse, unpublished data) and appears restricted to naturally saline water bodies. *Calamoecia clitellata* occurs in both naturally and secondarily saline lakes throughout the south-west and is by far the most commonly encountered of the 3 species in Western Australia.

Why more salt-adapted species of *Calamoecia* occur in Western Australia than other parts of Australia is not fully understood but is probably the result of Western Australia being an old and geologically stable landscape with a relatively long history of natural salinity. The current distribution of lakes and rivers in Western Australia reflects palaeodrainage systems that have existed since the late Cretaceous or early Tertiary. Most of these ceased to flow by the mid-Miocene (Graaff *et al.* 1977) and subsequently became saline, meaning that salt lakes have been present in the landscape since at least the beginning of the Quaternary (Salama *et al.* 1992). Many salt lakes in the Wheatbelt and Goldfields regions are 100,000s of years old (Commander *et al.* 1994) and a highly diversified salt-adapted crustacean fauna has become established, and has evolved, over this time (see De Deckker 1983; Bayly 1993). *Parartemia*, the endemic Australian anostracan genus, provides the most extreme example of radiation with 7 of the 9 described species occurring in, and 6 restricted to, the south-west (Geddes

1981). Undescribed, and presumably endemic, salt-lake species of ostracods belonging to the genera *Australocypris*, *Diacypris*, *Reticypris* and *Heterocypris* occur in the same area (S A Halse, unpublished data) and the discovery of *C. trilobata* provides further evidence that extensive radiation has occurred within several crustacean groups in saline habitats in south-west Western Australia.

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The effects of reducing bird predation on canopy arthropods of marri (*Eucalyptus calophylla*) saplings on the Swan Coastal Plain, Western Australia

N C P Evelegh[1], J D Majer[1] & H F Recher[2]

[1] Department of Environmental Biology, Curtin University of Technology,
GPO Box U1987, Perth, WA 6845. email: *imajerj@info.curtin.edu.au*

[2] School of Natural Sciences, Edith Cowan University,
Joondalup, WA 6027. email: *hrecher@eagle.fste.ac.cowan.edu.au*

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Abstract

The effect of bird predation on canopy arthropods inhabiting Marri (*Eucalyptus calophylla*) saplings was examined in *Banksia* woodland on the Swan Coastal Plain of Western Australia. Twenty pairs of saplings were selected and one of each pair was enclosed in bird-proof mesh to exclude foraging birds. Saplings were sampled in April 1998, prior to bird exclusion, and in August 1997, October 1997 and May 1998 after exclusion. Abundance, species richness and size of some arthropods increased on meshed saplings in certain months following bird exclusion. Spiders (Araneae) were most different between meshed and open saplings, with their abundance increasing on the saplings from which birds were excluded and remaining significantly more abundant after one year. The abundance of larger arthropods (in particular, spiders) increased and smaller animals decreased following bird exclusion, suggesting an interaction with birds on spiders as prey, and between spiders and their prey.

Additional evidence of an effect of bird predation on the arthropod fauna was found in the amount of arthropod-related damage to leaves on meshed and open saplings. Damage to leaves, recorded over an 8-week period in spring, on meshed saplings was 21% of total leaf area, compared with 6% on open saplings. These differences indicate that damage to canopy foliage is reduced by bird predation of herbivorous arthropods, and are consistent with trends in arthropod abundances between open and meshed saplings. We conclude that predation by birds affects the composition and size structure of canopy arthropod communities on eucalypts, and there is merit in initiating longer and more extensive studies.

Keywords: bird, predation, arthropods, Marri, Swan Coastal Plain

Introduction

Birds are arguably the most important visually-hunting predators of arthropod herbivores (Strong *et al.* 1983). Otvos (1979) and Holmes (1990a) suggest that birds suppress and delay the build-up of arthropod populations, thereby increasing the interval between arthropod outbreaks. Predation by birds may also accelerate the decline of arthropod populations after epidemics. Thus, the greatest influence of avian predation on arthropod populations may be exerted at endemic rather than epidemic levels (Holmes 1990a; Stephen *et al.* 1990).

Although there have been few studies on the interactions between birds and their prey, experimental and observational studies alike indicate a complex set of interactions affecting the abundances and community composition of both forest arthropods and forest birds (*e.g.* Holmes *et al.* 1979; Holmes 1990a;b; Loyn *et al.* 1983; Recher *et al.* 1996a). As well as affecting the population dynamics of individual species, birds may affect the taxonomic composition of the arthropod fauna and the size distribution of forest arthropods. In turn, the effects of avian predation on forest arthropods and the behaviour of birds may affect the species composition and abundance of both the forest avifauna and of other predators on forest arthropods. Such interactions may have important consequences for the health and sustainability of forest ecosystems (Loyn 1983; Loyn *et al.* 1983). Loyn *et al.* (1983) demonstrated that colonial Bell Miners (*Manorina melanophrys*) excluded other passerines from eucalypt forest occupied by the colony. The consequence was an increase in insects, and the progressive degradation of the forest within the colony as a consequence of increased insect herbivory. When the miners were removed, other passerines returned and insect abundances were reduced. Marquis & Whelan (1994) found that the exclusion of birds from White Oak (*Quercus alba*) saplings increased numbers of arthropods and increased damage to foliage by grazing insects. They predicted that observed declines in North American populations of insectivorous birds could reduce forest productivity through increased abundance of arthropod herbivores and their subsequent impact on plant growth.

Despite the potential importance of birds as regulators of forest arthropod populations and of the composition of arthropod communities, few workers have attempted to measure the scale of avian predation on forest arthropods. Almost all such attempts have investigated bird predation on one or a few pest arthropods (*e.g.* Campbell *et al.* 1983; Kroll & Fleet 1979; Morrison *et al.* 1989; Solomon *et al.* 1976; Torgersen *et al.* 1990). Studies such as those of Loyn *et al.* (1983) and Marquis & Whelan (1994) are exceptional. Given the importance of forest arthropods as 'rate regulators' of ecological processes within forest ecosystems (Springett 1978), the richness of arthropod faunas in eucalypt forest canopies (Majer *et al.* 1994; Recher *et al.* 1996a), and the importance of arthropods as food for eucalypt forest birds (Loyn *et al.* 1983; Recher *et al.* 1991, 1996a), we measured the impact of bird predation on the abundance, taxonomic composition and size structure of eucalypt canopy arthropods and the interactions of these variables with the amount of arthropod damage to canopy foliage. We report here the results of a one-year study on the exclosure of birds from Marri (*Eucalyptus calophylla*) saplings on the Swan Coastal Plain near Perth, Western Australia.

Site description and methodology

Study site

The study was conducted at Lowlands, a private property located 50 km south of Perth on the Swan Coastal Plain of Western Australia. Lowlands is a mosaic of fallow pasture and bushland that, unlike much of the bushland on the Swan Coastal Plain, has not been subject to periodic logging and fires (Keighery *et al.* 1995). A significant portion of the native vegetation on the property was never cleared and a core of native vegetation, broadly defined as *Banksia* woodland, dominates the property (Keighery *et al.* 1995; D van Gool, Agriculture WA, personal communication).

Experimental design

On the basis of similarities in location, height and canopy volume, 40 Marri saplings were selected and paired, giving two treatments with 20 replicates in each. Selected saplings were under 3 m in height. No flowering was recorded for saplings during the study.

Birds were excluded from one sapling of each pair by construction of a triangular cage around the sapling, using stakes and 25 x 25 mm polyethylene bird control mesh. No section of the canopy protruded outside the triangle. Cages were constructed in early May 1997. In the following, we refer to caged saplings as 'meshed' and to the uncaged saplings as 'open'. Prior to bird-exclusion, all 40 saplings were sampled for arthropods using the foliage beating and branchlet shaking method described by Majer *et al.* (1996).

A circular calico sheet, 100 cm in diameter with a single slit cut from the centre to the edge, was placed around the trunk of each sapling, giving a standard collection area for all saplings. Saplings were then shaken and beaten using a wooden pole to dislodge any arthropods from the canopy. Fast moving arthropods were collected immediately using forceps. The remainder of the collection was emptied from the sheet on to a piece of white cardboard and brushed into a collecting vial containing preserving fluid. The first sample was taken in April 1997. Post-exclusion samples were taken in August and October 1997, and in May 1998. All material was sorted and scored to the ordinal level.

Following log-normal transformation to stabilise variance and validate normality assumptions, a paired t-test was used to compare each ordinal taxa between saplings from open and meshed categories for each of the four sampling periods. The two-tailed probability was used. In order to summarise the influence of bird exclusion on the arthropod fauna as a whole, each taxon was categorised in each sampling period on whether numbers were more abundant (+), less abundant (-) or equally abundant (=) on meshed as opposed to open saplings. The numbers of taxa in the '+' and '-' category were then compared with the expected score using a 'sign test' based on the binomial distribution. On the null hypothesis that bird exclusion had no effect on the fauna, each taxon was assumed to have an equal chance of being more or less abundant on the meshed trees. The '=' category was excluded from the analysis.

Material collected in April, August and October 1997, but not May 1998, was also sorted to morpho-species. Due to small size (generally less than 1.5 mm in length) and difficulties with identification, Psocoptera, Collembola, Acarina, Thysanoptera, Diptera adults (<3.0 mm) and larvae, early-instar Blattodea nymphs, Lepidoptera larvae, Coleoptera larvae, and Hymenoptera larvae and wasps were not assigned to morpho-species.

The diversity of a community comprises two characteristics; the total number of species (richness) and the relative abundance of individuals of each species (evenness). Arthropod species richness (*S*) was obtained by summing the number of morpho-species collected in a particular time and treatment. The cumulative number of morpho-species was also plotted against sapling numbers for both open and meshed categories. The diversity of arthropods was further investigated using the Shannon & Weaver (1949) H^1 index, which attempts to give a combined measure of richness and evenness. This was calculated by the following formula:

$$H^1(decits) = \frac{N \log N - \sum_i n_i \log n_i}{N}$$

where N = total number of individuals, and n_i the importance value of the *i*th morpho-species. This was then used to derive the evenness index (J^1), which was calculated as

$$J^1 = \frac{H^1(decits)}{\log S}$$

The greater the value of J^1, the more even is the relative abundance of individuals of each morpho-species.

Each arthropod was assigned to a length size-class; 1 is <0.5 mm; 2 is 0.51-1.0 mm; 3 is 1.01-2.0 mm; 4 is 2.01-3.0 mm; 5 is 3.01-4.0 mm; 6 is 4.01-5.0 mm; 7 is 5.01-10.0 mm; and 8 is >10.01 mm long. Differences in numbers of arthropods within each size class between meshed and open saplings for the pre-exclusion and post-exclusion samples were analysed using the Mann-Whitney U-test. This was used in preference to the t-test in view of the large number of zeros in the data. The two-tailed probability was used.

Foliage damage

Total height, mean crown diameter taken along two planes (east-west and north-south), and vertical depth of crown were measured for each sapling to outline its shape and size. Canopy measurements were repeated in October

1997. Differences in growth measurements between meshed and open saplings for the pre-exclusion and post-exclusion samples were analysed using the Mann-Whitney U-test. A non-parametric test was used because the data included negative values, which arose because canopies of some saplings had shrunk during the period between measurements. The two-tailed probability was used.

To quantify leaf damage caused by herbivorous arthropods, during August five undamaged leaves emerging from newly opened shoots were selected at random on each of a subset of paired saplings and a plastic coated wire band was used to secure a numbered 2.5 x 2.5 cm aluminium tag around the petiole of each leaf. All 40 saplings were inspected. Of these, 17 had experienced new leaf flush. This included six paired replicates (12 saplings, giving 60 leaves) which were used for the analysis. The subset represented a cross section of the different heights, canopy volumes, locations, surrounding vegetation types and bird exposure status of the saplings.

Damage to leaves was assessed by tracing tagged leaves from each sapling onto separate transparent plastic sheets. The extent of leaf damage was traced on two occasions over an 8-week period between August and October 1997. In October, individual leaves, together with any damage present, were outlined and damage was assigned to one of two categories as follows; leaf chewers (portions of the leaf lamina had been removed, either along the margins or within the lamina) and leaf miners (irregular shaped areas of raised necrotic leaf epidermis, also evident as narrow trails of damage). Where extensive damage had occurred to actively expanding leaves (generally by leaf chewing arthropods), estimation of an entire mature leaf was undertaken, as this was required for the estimation of total leaf damage. The method of estimation for entire leaf areas of chewed leaves was that described by Abbott *et al.* (1993), who concluded that their technique of tracing leaf outlines and damaged parts onto transparent plastic was accurate and reliable.

Leaf area and categorical damage to individual leaves were measured using a Delta-TO digital scanner (DIAS II). Damage in each category was measured using the DIAS II scanner for each leaf and then tabulated. Individual leaf damage by miners and chewers was totalled separately for each cohort of leaves and then expressed as a percentage of total leaf area for the sapling. Incidences of leaf abscission were removed from damage estimates, as factors other than arthropod damage may be involved. Differences in leaf damage between meshed and open saplings for the pre-exclusion and post-exclusion samples were analysed using the Mann-Whitney U-test. A parametric test was considered to be inappropriate because the data were percentage values. The two-tailed probability was used.

Results

Numbers of arthropods

Ordinal invertebrate means for open and meshed saplings for each sampling period are summarised in Table 1. Numbers of arthropods collected across all taxa were generally low and variance in means was high for both pre-exclusion and post-exclusion samples. The total number of arthropods on saplings was highest in the April 1997, lower during August and October 1997, and lowest in May 1998 (Table 1).

The low numbers of arthropods collected and high numbers of zeros in the data resulted in few statistical differences. In April 1997, differences in numbers of individuals between saplings that were to be meshed and those that were to remain open were not significant. For the first post-exclusion sampling period in August 1997, a significantly larger number of spiders (Araneae) was found on meshed saplings than on open saplings (t_{14} = 3.55, *P* <0.005), but no significant differences were found in numbers of other arthropods. Mean numbers of spiders had increased on both open and meshed saplings between the August and October sampling periods (Table 1), and spider abundance was again significantly higher on meshed saplings (t_{14} = 3.73, *P* <0.005). No significant difference was observed between open and meshed saplings in October for other taxa. This pattern was repeated in the May sample, with spiders once again being significantly (t_{10} = 4.71, *P* <0.001) more abundant on the meshed than open saplings. There were no differences in abundance for the other taxa.

The signs of differences between mean invertebrate numbers in ordinal taxa for open and meshed categories in the pre-exclusion and post-exclusion samples are shown in Table 2, together with sign total summaries. Prior to bird exclusion in April, the distribution of sign scores between taxa did not differ from that expected using a two-tailed signs test. The post-exclusion August sample showed an increase, although not significant, in the number of taxa that were most abundant on meshed saplings. This shift continued through to the October sample (Table 2), where the number of taxa that were more abundant on the meshed saplings was significantly greater (*P*<0.005) than on the open saplings. The trend of abundance persisted in the May sample, with a greater number of taxa being more abundant on the meshed than open saplings. However, the difference was not significant.

Species richness

For the April pre-exclusion period, 42 morpho-species were collected from meshed saplings and 51 from open saplings (Table 3). The species accumulation curve for arthropods collected over this period (Fig 1a) shows that, in most paired replicates, cumulative numbers of morpho-species on open saplings were greater than, or equal to, those of meshed saplings. The diversity (*H'*) value and species richness of open saplings was also higher than that for meshed saplings in April, prior to bird exclusion (Table 3). Evenness (*J'*) values were almost identical for open and meshed saplings. This indicates a similar evenness of species abundance patterns between the two exclusion categories prior to experimental manipulation.

In August, 69 and 73 morpho-species were identified on open and meshed saplings respectively (Table 3). Species diversity and richness increased for both categories between the April and August, while evenness remained the same for open saplings. In contrast, meshed saplings displayed an increase in evenness of spread of

Table 1. Ordinal means (± se, n = 20) for invertebrates collected from open and meshed *E. calophylla* saplings during April, August and October, 1997 and May, 1998.

		April-97		Aug-97		Oct-97		May-98	
	Order	Open	Meshed	Open	Meshed	Open	Meshed	Open	Meshed
Arachnida	Pseudoscorpionida	-	0.10	-	0.05	-	-	-	-
	Acarina	42.60 ± 18.50	18.85 ± 4.15	13.95 ± 2.09	12.50 ± 2.30	10.85 ± 1.50	12.50 ± 2.36	1.80 ± 0.65	12.10 ± 98.70
	Araneae	2.30 ± 0.33	2.10 ± 0.42	2.45 ± 0.35	5.75 ± 0.81	3.50 ± 0.45	8.75 ± 1.19	1.90 ± 0.36	7.10 ± 1.62
Diplopoda	Polyxenida	-	-	0.10	0.25 ± 0.47	-	0.05	-	0.10 ± 0.07
Collembola		2.65 ± 0.46	3.55 ± 0.73	27.35 ± 7.96	18.10 ± 3.36	6.95 ± 1.69	8.50 ± 2.04	8.65 ± 6.28	3.30 ± 1.14
Insecta	Thysanura	-	0.05	-	-	-	-	-	-
	Ephemeroptera	-	-	0.05	-	-	-	-	-
	Blattodea-adults	-	-	-	-	0.05	0.30 ± 0.22	0.15 ± 0.08	0.10 ± 0.05
	Blattodea-nymphs	0.10	0.35 ± 0.21	0.10	0.50 ± 0.27	-	-	-	-
	Mantodea	-	0.05	0.05	-	-	-	0.10 ± 0.07	0.10 ± 0.07
	Demaptera	-	0.15	-	0.05	-	0.05	0.05 ± 0.05	0.20 ± 0.09
	Orthoptera	0.05	-	0.15	0.10	0.40 ± 0.12	-	-	0.10 ± 0.07
	Psocoptera	26.70 ± 7.04	50.15 ± 17.13	7.80 ± 2.05	6.85 ± 1.86	4.50 ± 1.20	5.70 ± 2.15	10.30 ± 3.59	10.45 ± 2.98
	Hemiptera	5.90 ± 1.25	2.95 ± 0.65	4.25 ± 0.96	4.90 ± 0.80	13.40 ± 2.80	10.00 ± 1.18	5.65 ± 2.27	3.20 ± 0.86
	Thysanoptera	5.85 ± 1.49	4.10 ± 0.79	0.45 ± 0.11	0.60 ± 0.34	12.20 ± 4.35	8.20 ± 2.41	0.80 ± 0.21	1.30 ± 0.40
	Neuroptera-adults	-	-	0.10 ± 0.05	-	-	-	-	-
	Neuroptera-larvae	-	-	-	-	0.05	0.05	-	-
	Coleoptera-adults	0.90 ± 0.15	0.70 ± 0.23	1.65 ± 0.72	1.85 ± 0.57	0.80 ± 0.22	1.10 ± 0.28	1.30 ± 0.34	1.30 ± 0.33
	Coleoptera-larvae	0.30 ± 0.39	0.25 ± 0.11	0.45 ± 0.19	0.25 ± 0.11	0.40 ± 0.12	0.35 ± 0.20	-	-
	Mecoptera	-	-	-	-	-	0.05	-	-
	Diptera-adults	0.20	0.05	0.40 ± 0.08	0.80 ± 0.31	0.25 ± 0.11	0.75 ± 0.21	0.10 ± 0.10	0.15 ± 0.08
	Diptera-larvae	0.10	-	0.45 ± 0.77	-	-	0.40	-	-
	Leidoptera-adults	-	-	-	0.10	-	0.05	0.05 ± 0.05	-
	Lepidoptera-larvae	0.60 ± 0.16	0.80 ± 0.29	0.95 ± 0.37	1.35 ± 0.41	1.85 ± 0.55	2.55 ± 0.68	0.50 ± 0.21	0.50 ± 0.22
	Hymenoptera-ants	4.62 ± 1.23	6.15 ± 1.82	5.60 ± 1.97	7.45 ± 1.45	4.70 ± 1.56	5.30 ± 1.70	9.75 ± 3.97	6.30 ± 1.85
	Hymenoptera-others	0.70 ± 0.14	0.25 ± 0.13	0.75 ± 0.14	0.95 ± 1.23	0.90 ± 0.45	0.95 ± 0.25	0.10 ± 0.07	-
	Total	93.57	90.60	66.90	62.45	60.50	66.00	41.20	46.3

Table 2. Breakdown of ordinal taxa sampled during April, August and October, 1997 and May, 1998 from open and meshed *E. calophylla* saplings; showing whether each taxon was less abundant (-), more abundant (+) or equally abundant (=) in the meshed than open saplings. Blank entries denote absence of the taxon in that sampling period.

Class	Order	Apr-97	Aug-97	Oct-97	May-98
Arachnida	Pseudoscorpionida	+	+		
	Acarina	-	-	+	+
	Araneae	-	+	+	+
Diplopoda	Polyxenida		+	+	+
Collembola		+	-	+	-
Insecta	Thysanura	+			
	Ephemeroptera		-		
	Blattodea-adults			+	-
	Blattodea-nymphs	+	+		
	Mantodea	+	-		=
	Dermaptera	+	+	+	+
	Orthoptera	-	+	+	+
	Psocoptera	+	-	+	+
	Hemiptera	-	+	-	-
	Thysanoptera	-	+	-	+
	Neuroptera-adults		-		
	Neuroptera-larvae			=	
	Coleoptera-adults	-	+	+	=
	Coleoptera-larvae	-	-	-	
	Mecoptera			+	
	Diptera-adults	-	+	+	+
	Diptera-larvae	-	-	+	
	Lepidoptera-adults		+	+	-
	Lepidoptera-larvae	+	+	+	=
	Hymenoptera-ants	+	+	+	-
	Hymenoptera-others	-	+	+	-
Number of taxa which:					
are most abundant on meshed saplings		9	14	16	8
are less abundant on meshed saplings		10	8	3	6
equally abundant between categories		0	0	1	3
significance of deviation of signs from random distributon		NS	NS	*	NS

* $p<0.005$; NS not significant

individuals among morpho-species. The higher evenness in the meshed sapling fauna reflects an increase in abundance of several rare species and a decrease in the two most abundant morpho-species. A comparison of numbers of morpho-species accumulated over the 20 paired replicates between April and August (Fig 1a,b) reveals a partial inversion of the open and meshed sapling curves, with a number of meshed saplings supporting higher total numbers of morpho-species than their open counterparts.

The increase in numbers of morpho-species observed in meshed saplings for the August sampling period continued until October, with 106 morpho-species identified from meshed saplings, but only 76 from open saplings (Table 3). Fig 1c shows the cumulative numbers of morpho-species collected over the 20 paired replicates for October. Here, differences in total morpho-species found within each of the 20 paired saplings have increased, with all 20 meshed saplings displaying higher total numbers of morpho-species. This indicates a proportionately larger increase in numbers of morpho-species collected from meshed saplings. Differences in the Shannon-Weaver diversity indices between exclusion categories for the October data support this trend, with a higher species richness and H' value for the meshed than open saplings, relative to April and August (Table 3). The highest species richness, species diversity and evenness values were recorded for meshed saplings in October. The elevated evenness index reflects an increase in abundance of several rare morpho-species and a substantial decrease in the most abundant morpho-species on meshed saplings. Species diversity and evenness was lower for open saplings in the October sample than for August (Table 3). Species richness, however, was slightly higher in the October sample than in August for open saplings. As morpho-species were not sorted in the May 1998 sample, diversity, richness and evenness values cannot be calculated for that period.

Arthropod size-classes

Numbers of arthropods recorded in each size-class for open and meshed saplings are presented in Fig 2. Variance in the means was generally high, and numbers of arthropods were low in all four of the larger size-classes in all sampling periods. Numbers of arthropods in size-class 2 were significantly greater on open saplings ($U = 124$, $N_1 = N_2 = 20$, $P<0.05$) than on saplings designated for meshing during the pre-exclusion sampling period. This was asso-

Table 3. Total numbers of morphospecies identified within ordinal taxa between 20 pairs of open and meshed *E. calophylla* saplings, for April, August and October, 1997. The species richness, Shannon Wiener diversity index (H^1) and eveness (J^1) values for these sampling periods are also shown.

		Pre-exclusion Apr-97		Post Exclusion Aug-97		Post-exclusion Oct-97	
Class	**Order**	**Open**	**Meshed**	**Open**	**Meshed**	**Open**	**Meshed**
Arachnida	Pseudoscorpionida	-	2	-	1	-	-
	Araneae	17	12	21	29	18	38
Diplopoda	Polyxenida	-	-	1	1	-	1
Insecta	Thysanura	-	1	-	-	-	-
	Ephemeroptera	-	-	1	1	-	-
	Blattodea-adults	-	-	1	-	1	4
	Mantodea	1	1	1	-	-	-
	Dermaptera	-	1	-	1	-	1
	Orthoptera	1	-	-	3	1	6
	Hemiptera	12	10	14	11	26	29
	Neuroptera	-	-	1	-	-	-
	Coleoptera-adults	9	6	13	12	14	15
	Mecoptera	-	-	-	-	-	1
	Diptera-adults	-	-	5	2	1	3
	Lepidoptera-adults (>3mm)	1	-	-	2	-	1
	Hymenoptera-ants	10	9	11	10	15	7
Species richness		51	42	69	73	76	106
Diversity (H^1)		1.18	1.15	1.27	1.37	1.16	1.51
Evenness (J^1)		0.69	0.71	0.69	0.74	0.62	0.75

ciated with abnormally high numbers of Thysanoptera in the open category saplings. All remaining size-classes had no significant difference between open and meshed saplings prior to exclosure (Fig 2a).

No significant differences in mean invertebrate numbers were observed between open and meshed saplings for any size-class in August, although numbers in the four largest size-classes were greater on the meshed saplings and three of the four smaller classes were greater on the open saplings (Fig 2b). In October, seven of the eight size-classes were more abundant on meshed saplings than on those to which birds had access (Fig 2c), with two of the four largest size-classes (4 and 8) being significantly more abundant (U = 126 and 118 respectively for $N_1 = N_2 = 20$, $P<0.05$). In May, members of size-class 2 were significantly ($U = 110$, $N_1 = N_2 = 20$, $P<0.05$) less abundant on the meshed than open saplings, while differences between the other sizes were not significant (Fig 2d).

Canopy size and arthropod damage to foliage

No significant difference was found in total height, crown diameter and crown depth between paired saplings prior to bird exclusion in April. An increase in mean crown diameter was recorded for all saplings after the final set of canopy measurements were taken in October. This increase was significantly greater on the open than on the meshed saplings ($U = 118$, $N_1 = N_2 = 20$, $P<0.05$) and was not caused by restrictions of the mesh; this was designed to allow plenty of growth. No differences in total height increase or foliage height were recorded between open and meshed saplings from pre-exclusion to October.

Cumulative damage between August and October to individual leaves by leaf chewers and leaf miners for each

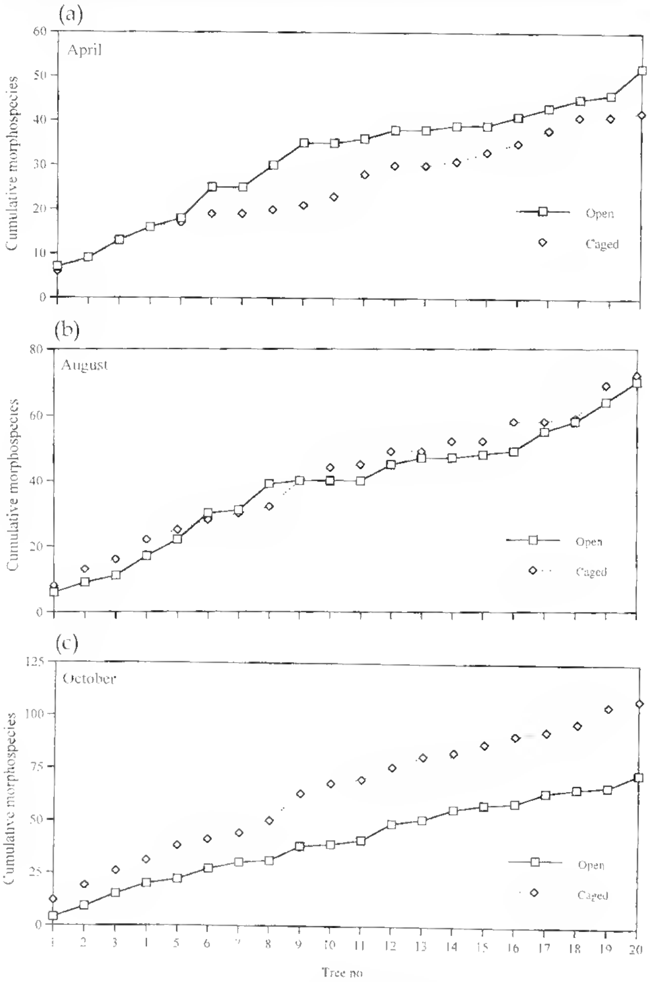

Figure 1. Accumulation of morpho-species from 20 paired *E. calophylla* saplings in two bird-exclusion categories for April, August and October, 1997.

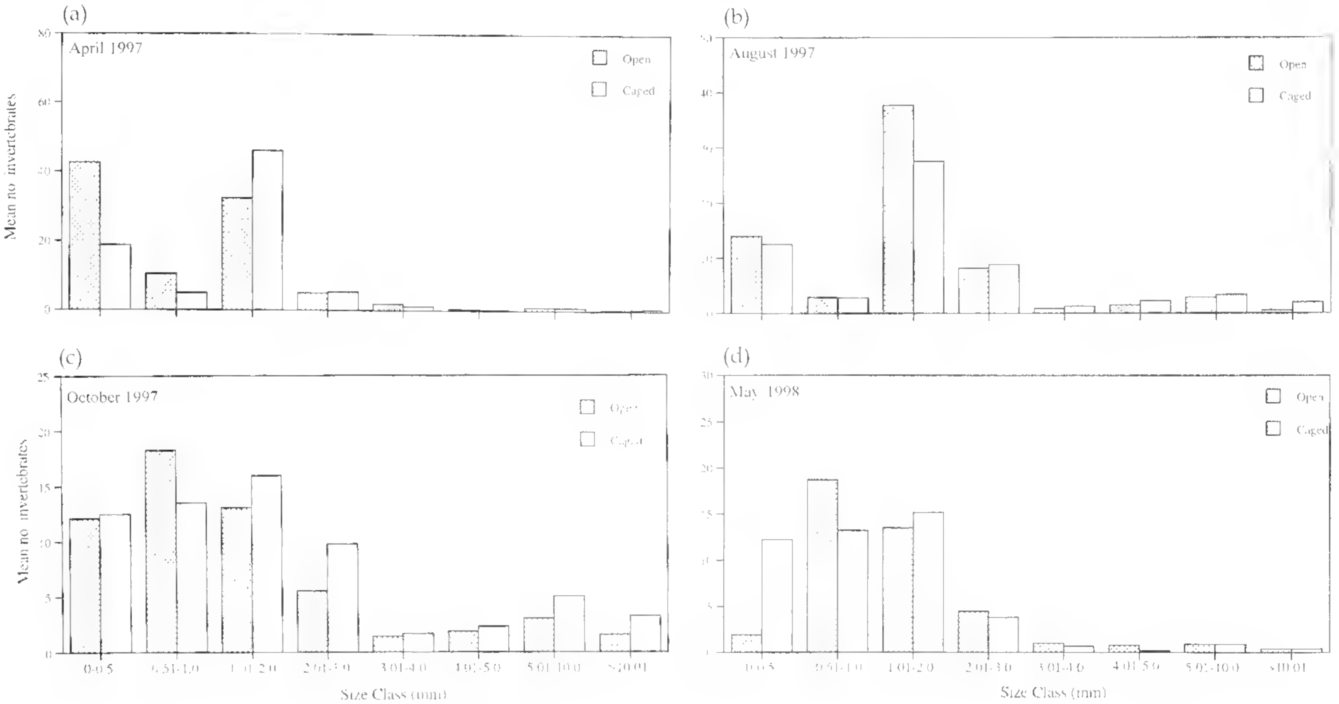

Figure 2. Mean number (n=20) of invertebrates in each size class collected from open and meshed *E. calophylla* saplings during April, August and October, 1997 and also May 1998.

paired replicate is shown in Fig 3. No significant difference in the leaf area damaged by leaf miners and chewers per sapling was found between exclusion categories, even though mean damage in both categories was higher on the meshed saplings. Total damage (*i.e.* chewers and miners), however, was significantly greater ($U = 5$, $N_1 = N_2 = 6$, $P<0.05$) on the saplings from which birds had been excluded.

Discussion

The pre- and post-exclusion sampling of the canopy fauna from Marri saplings revealed changes in the abundance, richness, diversity and size of arthropods between open and meshed saplings, suggesting that predation by birds affects arthropod abundance and community structure in these woodlands. However, many of the differences between exclusion categories were not significant, owing to the generally low numbers and high variances of arthropods collected from saplings.

The removal of the fauna during each sampling contributed to the reduced abundances recorded after the initial sample. However, Recher *et al.* (1996a,b) have shown significant differences in eucalypt canopy arthropod abundances seasonally and between years, and we do not consider it likely that the removal of the fauna appreciably affected differences between open and meshed saplings. Other studies have consistently shown that birds reduce the abundance of arthropod prey (Gunnarsson 1996; Holmes *et al.* 1979; Loyn *et al.* 1983; Marquis & Whelan 1994; Moore & Young 1991; Solomon *et al.* 1976;). Wiens *et al.* (1991) failed to find an effect of bird predation on arthropod abundances, but low primary productivity in the shrublands where they worked appeared to limit arthropod numbers. As the *Banksia* woodlands where we worked grow on nutrient-poor sands, and primary productivity is probably low, it is likely that the small number of arthropods on individual saplings and the low population densities of insectivorous birds in this habitat (Bamford 1986) are a consequence of low plant productivity (Recher *et al.* 1996a). Demonstrating a significant effect of predation by birds on arthropods under these conditions probably requires a long exclosure period and a larger number of samples than we obtained before patterns can unequivocally be detected.

Despite these limitations, species richness, numbers, and size of arthropods were significantly greater on meshed Marri saplings than on open saplings during spring (October), which is the period when we expect both the

Figure 3. Percentages of leaf area damaged by leaf miners and chewers on open and meshed *E. calophylla* saplings between August and October 1997 post-exclusion sampling periods.

abundances of arthropods and bird predation to be greatest (Recher *et al.* 1996a,b). Spiders showed the greatest response to exclusion of birds; they had increased abundance and more large individuals on meshed than open Marri saplings during all post-exclusion sample periods, including May when total arthropod numbers were lowest. Gunnarsson (1983) also found reduced mortality of spiders when birds were excluded from spruce (*Picea abies*) foliage. He suggested that large spiders seem more vulnerable to predation by birds than small spiders. As predators, spiders probably respond to the removal of bird predation in two ways. First, numbers and size of spiders increase as a result of reduced predation by birds. Second, if the numbers of other arthropods increase in the absence of birds, then the prey base for spiders is increased, allowing more and larger spiders to survive. We expect spiders to show the greatest response to removing bird predation for the reasons given but, as Marquis & Whelan (1994) point out, reduced predation by wasps on meshed saplings could also enhance spider productivity. This could happen either by the unintended exclusion of wasps by the mesh or through the mesh providing better cover for spiders.

Nonetheless, removal of bird predators appears to affect arthropod community structure by allowing another group of predators, the spiders, to increase (for comparable results, see Gunnarsson 1983, 1996; Halaj 1996; Halaj *et al.* 1997). The manipulation also appeared to allow rarer and smaller species to increase in abundance, as shown by the greater evenness of distribution of morpho-species abundance patterns observed in meshed saplings. These results indicate that bird predation is a major force affecting arthropod and spider abundance, size and species richness, as well as community trophic structure. This interaction is an example of a top down, trophic cascade of the type discussed by Letourneau & Dyer (1998).

Our results also indicate that predation by birds reduces the amount of arthropod damage to eucalypt foliage. Total arthropod damage on meshed saplings was significantly higher than on saplings exposed to bird predation. Moreover, damage estimates in this study were based on an 8-week recording period and as a result, probably underestimate effects. Abbott *et al.* (1993) reported that arthropod damage to leaves of Marri occurs mainly in the first 3 months of a leaf's development. Total arthropod damage estimates of 6.2% for Marri (Abbott *et al.* 1993) are comparable to those obtained here for open saplings (6.1%). Marquis & Whelan (1994) noted that differences in arthropod numbers resulted in differences in leaf area missing at the end of the season. Meshed plants produced approximately one-third less leaf biomass and total biomass compared to the controls. These findings are similar to ours, where meshed saplings exhibited approximately three times more leaf area damage than open saplings (21% of total leaf area damaged compared to 6%).

The short duration of the experiment (1-year), the small sample sizes, and high levels of variance, meant that the results were not always significantly different. By contrast, avian predation of grassland arthropods is better demonstrated and understood due to the existence of a range of comprehensive studies (*e.g.* Bock *et al.* 1992; Fowler *et al.* 1991; Joern 1986, 1992). We conclude that predation by birds affects the composition and size structure of canopy arthropod communities on eucalypts, and there is merit in initiating longer and more extensive studies in forest ecosystems such as the one studied here.

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Intestinal helminths of seven species of gekkonid lizards (Sauria: Gekkonidae) from Western Australia

S R Goldberg[1] & C R Bursey[2]

[1]Department of Biology, Whittier College, Whittier, CA 90608 USA
sgoldberg@whittier.edu

[2]Department of Biology, Pennsylvania State University,
Shenango Campus, Sharon, PA 16146 USA
cxb13@psu.edu

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Abstract

Two hundred specimens of seven species of geckos collected in Australia were examined for helminths: *Diplodactylus ciliaris, Diplodactylus conspicillatus, Diplodactylus elderi, Diplodactylus pulcher, Diplodactylus strophurus, Gehyra variegata*, and *Rhynchoedura ornata*. One species of Cestoda (*Oochoristica australiensis*), nine species of Nematoda (*Abbreviata tumidocapitis, Maxvachonia brygooi, Maxvachonia chabaudi, Parapharyngodon kartana, Skrjabinelazia machidai, Skrjabinodon parasmythi, Spauligodon ovifilus, Abbreviata* sp (larvae in cysts), *Physaloptera* sp (larvae in cysts), and a cystacanth of one species of Acanthocephala were found. Eighteen new host records are reported. *Skrjabinelazia machidai* is reported from Australia for the first time.

Keywords: intestinal helminth, gecko, Western Australia

Introduction

The lizard family Gekkonidae is well represented in Australia; 17 genera with about 102 known species (Cogger 2000). This paper reports helminths from seven species of Australian gekkonid lizards; *Diplodactylus ciliaris* Boulenger 1885, *Diplodactylus conspicillatus* Lucas & Frost 1897, *Diplodactylus elderi* Stirling & Zietz 1893, *Diplodactylus pulcher* (Steindachner 1870), *Diplodactylus strophurus* (Duméril & Bibron 1836), *Gehyra variegata* (Duméril & Bibron 1836) and *Rhynchoedura ornata* Günther 1867. These data are compared with previous reports of helminths harboured by Australian gekkonid lizards.

Methods

Two hundred geckos from the herpetology collection of the Natural History Museum of Los Angeles County (LACM) were examined for helminths. These specimens had been collected between 1966 and 1968 for an ecological study (Pianka 1972). Because the ecological study included stomach analysis, only small and large intestines remained with the carcasses. Numbers of lizards, mean snout-vent length (SVL), museum accession numbers and collection sites (latitudes, longitudes) are given for each species in the Appendix. Additional collection data are found in Pianka (1972). A helminth species richness analysis (excluding larval helminths) for Australian gekkonid lizards is presented. Lizard taxonomy is according to Cogger (2000).

Diplodactylus ciliaris is found in the interior of all mainland Australian states except Victoria; *D. conspicillatus* occurs in coastal and interior regions of Western Australia and the Northern Territory but is confined to interior regions of Queensland, New South Wales and South Australia; *D. elderi* is known from central and southern Western Australia; *D. pulcher* is found in central and southern Western Australia; *D. strophurus* occurs on the central coast and in the interior of Western Australia; *Gehyra variegata* is found throughout inland eastern and south-eastern Australia and has a separate population in southern Western Australia; *R. ornata* is known from all Australian states (Cogger 2000).

The intestines, body cavity and liver of each lizard were examined for helminths using a dissecting microscope. Each helminth was placed on a glass slide in a drop of undiluted glycerol and examined with a compound microscope. Nematodes were identified from these preparations. Cestodes and acanthocephalans were stained with hematoxylin and mounted in balsam for identification.

Results

Gravid individuals of one species of Cestoda, *Oochoristica australiensis* Spasskii, 1951 and seven species of Nematoda, *Abbreviata tumidocapitis* Jones 1983; *Maxvachonia brygooi* Mawson 1972; *Maxvachonia chabaudi* Mawson 1972; *Parapharyngodon kartana* (Johnston & Mawson 1941); *Skrjabinelazia machidai* Hasegawa 1984; *Skrjabinodon parasmythi* Mawson 1971; *Spauligodon ovifilus* Bursey & Goldberg 1999 were found. In addition, larvae (in cysts) of *Abbreviata* sp and *Physaloptera* sp as well as a cystacanth of an unidentified species of Acanthocephala were found. Eighteen new host records are noted (Table 1). Prevalence, mean intensity, and range of helminth infection by host are also presented in Table 1. Because physalopterid nematodes normally mature in the stomach (Anderson 2000), and because cysts containing larval physalopterids occasionally occur on stomach walls (Jones 1995a), *Abbreviata tumidocapitis* and larvae of *Abbreviata* sp and *Physaloptera* sp may be under-reported in Table 1.

Discussion

Helminth records now exist for 17 species of Australian gekkonid lizards and are summarized in Table 2. One species of Trematoda, *Paradistomum crucifer* (Nicoll 1914) Travassos 1919 has been reported to infect the gekkonid

Table 1. Prevalence (%), mean intensity (± se and range in parentheses) for intestinal helminths from seven species of gekkonid lizards from Western Australia, with sample size (n) in parentheses.

	Diplodactylus ciliaris		*Diplodactylus conspicillatus*		*Diplodactylus elderi*		*Diplodactylus pulcher*		*Diplodactylus strophurus*		*Gehyra variegata*		*Rhynchoedura ornata*	
		(n = 31)		(n = 32)		(n = 17)		(n = 20)		(n = 32)		(n = 25)		(n = 43)
Helminth	%	$\bar{x}$ ± se	%	$\bar{x}$ ± se	%	$\bar{x}$ ± se	%	$\bar{x}$ ± se	%	$\bar{x}$ ± se	%	$\bar{x}$ ± se	%	$\bar{x}$ ± se
Oochoristica australiensis	--	--	*3	2	*6	1	*15	1.7±0.6 (1-3)	--	--	*8	1	*47	2.6±0.4 (1-7)
Abbreviata tumidocapitis	--	--	--	--	--	--	*5	1	--	--	--	--	--	--
Maxvachonia brygooi	--	--	--	--	--	--	--	--	--	--	*12	1.3±0.3 (1-2)	--	--
Maxvachonia chabaudi	*3	1	--	--	*6	11	--	--	*63	4.7±1.1 (1-20)	--	--	--	--
Parapharyngodon kartana	*6	1	--	--	--	--	--	--	--	--	*8	(1-4)	--	--
Skrjabinelazia machidai	*3	4	--	--	--	--	--	--	--	--	--	--	--	--
Skrjabinodon parasmythi	--	--	--	--	*12	11±1 (10-12)	--	--	--	--	*8	1	--	--
Spauligodon ovifilus	--	--	*28	6.8±3 (1-29)	--	--	*30	5±1.8 (1-12)	--	--	--	--	*7	2.7±0.3 (2-3)
Abbreviata sp (larvae)	3	2	9	1.3±0.3 (1-2)	--	--	5	6	--	--	8	1	5	1
Physaloptera sp (larvae)	--	--	16	1	--	--	--	--	--	--	--	--	--	--
acanthocephalan cystacanth	--	--	3	1	--	--	--	--	--	--	--	--	--	--

* new host record

Christinus marmoratus as well as the scincids *Hemiergis peronii, Lerista bougainvillii, Trachydosaurus rugosus* and *Tiliqua scincoides*, the pygopodid *Delma fraseri*, and the varanid *Varanus varius* (Nicoll 1914; Angel & Mawson 1968; Mawson 1971).

Three species of cestodes have been reported from Australian geckos: *Cylindrotaenia allisonae* (Schmidt 1980) Jones 1987 from *Heteronotia binoei; Oochoristica australiensis* Spasskii 1951 from *Diplodactylus conspicillatus, D. elderi, D. pulcher*, and *Rhynchoedura ornata; Oochoristica piankai* Bursey, Goldberg & Woolery 1996 from *Nephrurus laevissimus* (see Pichelin *et al.* 1999 for localities). These three cestode species are known to occur in other lizard families. Angel & Mawson (1968) reported *C. allisonae* to also occur in the scincids *Hemiergis peronii* and *Lerista bougainvillii*; Spasskii (1951) described *Oochoristica australiensis* from the scincid *Trachydosaurus rugosus*; and Bursey *et al.* (1996) described *Oochoristica piankai* from the agamid *Moloch horridus*. In addition, there is a report by Angel & Mawson (1968) of an unidentified species of *Oochoristica* from the gekkonid *Christinus marmoratus*.

Two species of acanthocephalans have been reported from Australian lizards: *Porrorchis hylae* (Johnston 1914) Schmidt & Kuntz 1967 from the pygopodid *Lialis burtonis* and *Sphaerechinorhynchus rotundocapitatus* (Johnston 1912) Johnston & Deland 1929 from the scincids *Eulamprus quoyii, Hemiergis decresiensis, Lampropholis guichenoti* and the varanid *Varanus varius* (see Pichelin *et al.* 1999 for localities). Acanthocephalan cystacanths (unidentified as to species) have also been reported from the scincid *Hemiergis peronii*, collected in South Australia by Angel and Mawson (1968). This is the first report of a cystacanth in an Australian gekkonid. Because this larva does not mature in lizards, we have excluded it from Table 2.

Seventeen species of nematodes have now been re-

Table 2. Helmith parasites recorded for gekkonid lizards from Australia.

Helminth	*Paradistomum crucifer*	*Cylindrotaenia allisonae*	*Oochoristica australiensis*	*Oochoristica piankai*	*Oochoristica* sp	*Abbreviata bancrofti*	*Abbreviata tumidocapitis*	*Maxvachonia brygooi*	*Maxvachonia chabaudi*	*Parapharyngodon kartana*	*Pharyngodon kartana*	*Pharyngodon tiliquae*	*Physalopteroides filicauda*	*Skrjabinelazia machidai*	*Skrjabinelazia* sp	*Skrjabinodon oedurae*	*Skrjabinodon parasmythi*	*Skrjabinodon piankai*	*Skrjabinodon smythi*	*Skrjabinoptera goldmanae*	*Spauligodon ovifilus*	*Wanaristonglyus ctenoti*	*Wanaristongylus papangawurpae*
Host																							
Christinus guentheri	-	-	-	-	-	-	-	-	-	-	1,2	-	-	-	-	-	-	-	-	-	-	-	-
Christinus marmoratus	2	-	-	-	3	-	-	-	-	3	-	-	-	-	2,3	-	2	-	3	-	-	-	-
Diplodactylus ciliaris	-	-	-	-	-	-	-	-	4	4	-	-	5	4	-	-	-	-	-	-	-	-	-
Diplodactylus conspicillatus	-	-	4	-	-	-	5	-	-	-	-	-	5	-	-	-	-	-	-	-	4	-	5
Diplodactylus elderi	-	-	4	-	-	-	-	-	4	-	-	-	5	-	-	-	4	-	-	-	-	-	-
Diplodactylus pulcher	-	-	4	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-
Diplodactylus stenodactylus	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	6	-	6
Diplodactylus strophurus	-	-	-	-	-	-	-	-	4	-	-	-	5	-	-	-	-	-	-	-	-	-	-
Gehyra variegata	-	-	4	-	-	-	-	4	-	4	-	1	5	-	-	-	4	-	-	5	-	-	-
Heteronotia binoei	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nephrurus laevissimus	-	-	-	8	-	-	-	-	-	-	-	-	5,8	-	-	-	-	8	-	-	-	-	5,9
Nephrurus levis	-	-	-	-	-	-	-	8	-	-	-	-	8	-	-	-	-	8	-	-	-	5,8	-
Nephrurus vertebralis	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	8	-	-	-	-	-
Oedura robusta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
Phyllurus platurus	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhynchoedura ornata	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-
Underwoodisaurus milii	-	-	-	-	-	-	-	-	12	-	2	-	-	-	-	-	-	-	2	-	-	-	-

1, Johnston & Mawson 1943; 2, Mawson 1971; 3, Angel & Mawson 1968; 4, this paper; 5, H Jones 1995b; 6, Bursey & Goldberg 1999b; 7, M Jones 1987; 8, Bursey & Goldberg, 1999a; 9, H Jones 1987; 10, Johnston & Mawson 1947; 11, Irwin-Smith 1922; 12, Mawson 1972.

ported from Australian geckos (Table 2). Of these, eleven species: *Abbreviata bancrofti*, *Abbreviata tumidocapitis*, *Maxvachonia brygooi*, *Maxvachonia chabaudi*, *Parapharyngodon kartana*, *Pharyngodon kartana*, *Pharyngodon tiliquae*, *Physalopteroides filicauda*, *Skrjabinoptera goldmanae*, *Wanaristrongylus ctenoti*, *Wanaristrongylus papangawurpae* are generalists that have previously been reported from various lizard and snake families (Pichelin *et al.* 1999). Five species are known only from Australian geckos (*Skrjabinodon oedurae*, *S. parasmythi*, *S. piankai*, *S. smythi*, *Spauligodon ovifilus*). The remaining species, *Skrjabinelazia machidai*, was known only from non-Australian geckos: *Gekko japonicus* in Okinawa (Hasegawa 1984); *Lepidodactylus lugubris* in Hawaii (Goldberg & Bursey 1997). Australia is a new locality record for *Skrjabinelazia machidai*. It should be noted that female nematodes assigned to *Skrjabinelazia* sp. have previously been reported from the gekkonid *Christinus guentheri* by Angel & Mawson (1968) and Mawson (1971) and the scincid *Ctenotus schomburgkii* by Goldberg & Bursey (1995). Male and female specimens in the current study were consistent with those described by Hasegawa (1984) as *S. machidai*. The female specimens examined here are indistinguishable from those found in *C. schomburgkii* by Goldberg & Bursey (1995).

Encysted larvae assigned to the genera *Abbreviata* and *Physaloptera* as well as encysted larvae assigned to the family Physalopteridae have also been reported from Australian gekkonids, *Christinus marmoratus*, *Diplodactylus ciliaris*, *D. conspicillatus*, *D. elderi*, *D. stenodactylus*, *D. strophurus*, *Gehyra variegata*, *Nephrurus laevissimus*, *N. levis*, *Oedura robusta* and *Rhynchoedura ornata* (Jones 1992, 1995a, 1995b; Bursey & Goldberg 1999a). Physalopterid larvae have been reported from agamid, pygopodid, scincid and varanid lizards (Jones 1995a). Mature individuals of fifteen species of *Abbreviata* have been found in Australian reptiles (Pichelin *et al.* 1999). However, adults of species of *Physaloptera* are not known as parasites of Australian reptiles although adults of seven species are known from Australian mammals, five from marsupials and two from native rodents (Norman & Beveridge 1999). Roca (1993) suggested that prevalence of encysted larval nematodes in a lizard population indicates their degree of importance as prey because lizards can serve as intermediate hosts. Species of *Physaloptera* require an insect intermediate host (Anderson 2000). Further study will be necessary to determine whether geckos serve as intermediate hosts or accidentally acquire physalopterid larvae as a consequence of diet. Because these larvae were in cysts, we have excluded them from Table 2.

The species richness of helminth parasites for seven species of Australian geckos, 2.57 ± 0.37 se (range 1-4) is not significantly different (ANOVA, $F_{1,12} = 0.22$, $P > 0.05$) from the 2.29 ± 0.47 (range 1-4) reported for seven species of Australian agamids (Goldberg *et al.* 2000). These values are greater than the 2.06 ± 0.13 se, range 0-5) for lizards in general (Aho 1990), but they fall within the 95% confidence interval calculated for these lizards. Helminth records now exist for 17 of 102 (17%) Australian geckos. Subsequent examination of additional species will be needed before the helminth diversity of Australian geckos can be determined.

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Appendix

Gekkonid lizards examined from Natural History Museum of Los Angeles County (LACM), with longitude and latitude and helminths deposited in the US National Parasite Collection (USNPC).

- ***Diplodactylus ciliaris*** (N = 31, Mean (snout-vent length) SVL = 71 mm ± 1.0 se, range = 59-82 mm) collected 1966-1968, Western Australia, LACM (56800-56802, 56804, 28°09′S, 123°56′E), (56811, 56813, 56814, 56816-56818, 56822, 56825, 56826, 56828, 56829, 56831, 56833, 56838, 56840-56842, 56845, 26°17′S, 121°00′E), (56849, 26°27′S, 119°24′E) (56854, 56856, 56857, 56859, 56860, 27°05′S, 119°37′E) (56861-56862, 27°05′S, 119°37′E); Northern Territory (56847, 21°26′S, 130°54′E). USNPC # 89440 *Maxvachonia chabaudi;* USNPC # 89441, *Parapharyngodon kartana;* USNPC # 89442; *Skrjabinelazia machidai;* USNPC # 89443 *Abbreviata* sp (larvae).

- ***Diplodactylus conspicillatus*** (N = 32, Mean SVL = 59 mm ± 1.1 se, range = 48-70 mm) collected 1966-1968, Western Australia, LACM (56880, 28°30′S, 112°47′E), (56881, 56883-56885, 56889, 56890, 28°30′S, 125°50′E),(56891-56894, 56896-56901, 56903-56914, 25°20′S, 131°04′E); Northern Territory (56915, 25°20′S, 131°04′E), (56916, 22°49′S, 133°23′E),(56917, 25°12′S, 132°06′E). USNPC # 89447 *Oochoristica australiensis;* USNPC # 89448 *Spauligodon ovofilus;* USNPC # 89449 *Abbreviata* sp (larvae); USNPC # 89450 *Physaloptera* sp (larvae); USNPC # 89451 acanthocephalan cystacanth.

- ***Diplodactylus elderi*** (N = 17, Mean SVL = 43 mm ± 0.7 se, range = 38-47 mm) collected 1967-1968, Western Australia LACM (56762, 28°09′S, 123°056′E),(56763-56765, 26°14′S, 121°13′E), (56769, 56770, 56772-56774, 56777-56779, 56781, 28°27′S, 119°05′E) (56784-56787, 28°43′S, 118°38′E). USNPC # 89444 *Oochoristica australiensis;* USNPC # 89445 *Maxvachonia chabaudi;* USNPC # 89446 *Skrjabinodon parasmythi.*

- ***Diplodactylus pulcher*** (N = 20, Mean SVL = 54 mm ± 0.9 se, range = 48-62 mm) collected 1967-1968, Western Australia, LACM (56930-56932, 56935-56941, 56943, 28°27′S, 119°05′E), (56944, 30°55′S, 125°37′E), (56945, 56946, 29°05′S, 121°22′E), (56947-56950, 27°5′S, 119°37′E), (56951, 56952, 28°43′S, 118°38′E). USNPC # 89452 *Oochoristica australiensis;* USNPC # 89454 *Abbreviata tumidocapitis;* USNPC # 89455 *Spauligodon ovifilus;* USNPC # 89456 *Abbreviata* sp (larvae).

- ***Diplodactylus strophurus*** (N = 32, Mean SVL = 65 mm ± 1.5 se, range = 47-85 mm) collected 1967-1968, Western Australia, LACM (56671, 28°23′S, 119°05′E), (56676, 56677, 28°00′S, 120°19′E), (56678-57780, 28°27′S, 119°05′E), (56681, 56683-56685, 56689, 26°14′S, 121°13′E), (56990, 28°08′S, 123°55′E), (56991, 28°09′S, 123°56′E), (56992, 28°05′S, 124°15′E), (56993, 56694, 56696-56699, 56703-56711, 28°27′S, 119°05′E), (56713, 56715, 26°14′S, 121°13′E) (56718, 28°43′S, 118°38′E). USNPC # 89457, *Maxvachonia chabaudi.*

- ***Gehyra variegata*** (N = 25, Mean SVL = 44 mm ± 1.1 se, range = 35-58 mm) collected 1966-1968, Western Australia, LACM (57603, 57604, 25°47′S, 117°20′E), (57605, 30°05′S, 125°37′E), (57608, 57609, 57611, 28°19′S, 123°27′E); Northern Territory, LACM (57593, 57594, 25°59′S, 113°10′E), (57596, 57597, 22°49′S, 113°23′E), (57598-57599, 22°07′S, 131°21′E), (57613, 23°21′S, 129°22′E), (57614, 21°24′S, 130°53′E), (57615, 20°38′S, 130°25′E), (57622, 57626-57632, 57635, 27°05′S, 119°37′E), (57642, 28°47′S, 118°27′E). USNPC # 89458, *Oochoristica australiensis;* USNPC # 89159, *Maxvachonia brygooi;* USNPC # 89460, *Parapharyngodon kartana;* USNPC # 89461, *Skrjabinodon parasmythi;* USNPC # 89462 *Abbreviata* sp (larvae).

- ***Rhynchoedura ornata*** (N = 43, Mean SVL = 48 mm ± 0.8 se, range = 23-55 mm) collected 1967-1968, Western Australia, LACM (57661, 57674, 57675, 57679, 57681, 57684, 57685, 57702, 57712, 57721-57723, 57728, 57738, 57740, 57756. 57768, 28°27′S, 119°05′E), (57773, 57789, 57792, 28°28′S, 122°50′E), (57814, 28°31′S, 122°45′E), (57819, 57821, 57824, 57835, 57840, 57843, 28°30′S, 125°50′E), (57855, 57858, 57860, 26°17′S, 121°00′E), (57865, 57871, 57872, 57875, 28°17′S, 125°40′E), (57884, 57887, 28°08′S, 123°55′E), (57894, 26°14′S, 121°13′E), (57905, 57907, 57909, 57911, 57915, 57917, 29°05′S, 121°22′E) USNPC # 89463, *Oochoristica australiensis;* USNPC # 89465, *Spauligodon ovifilus;* USNPC # 89466, *Abbreviata* sp (larvae).

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Invertebrate occurrence and succession after episodic flooding of a central Australian rock-hole

I A E Bayly

Department of Biological Sciences, Monash University, Clayton VIC 3168*
*Address for correspondence: 501 Killiecrankie Road, Flinders Island TAS 7255
iaebayly@bigpond.com.au

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Abstract

A small rock-hole, located near Australia's point of inaccessibility, was sampled 10 times between its flooding on 20-21 April, 1998, and 16 June, 1998, when little water remained. Nine species were collected. Notable in occurrence was *Streptocephalus* (Crustacea: Anostraca) – a taxon long believed not to occur in Australia. New species of *Ilyocypris* (Crustacea: Ostracoda) and *Dorylaimus* (Nematoda: Dorylaimida) were discovered. The composition of the species assemblage differed markedly from that recorded from the relatively well studied granite gnammas in south-western Australia.

Keywords: rock hole, gnamma, flooding, crustaceans, central Australia

Introduction

Rock-holes capable of holding water are widely distributed throughout the arid regions of Australia. Despite the often cryptic and ephemeral nature of rock-hole waters, they have been of key importance for the survival of indigenous people in desert regions for thousands of years (Bayly 1999a). Studies of aquatic invertebrates associated with Australian rock-holes have been largely neglected until recently (Bayly 1997). Bishop (1974) studied a series of shallow pools in sandstone at North Head, Sydney, and Kanangra Walls, Blue Mountains, and recorded 18 taxa of invertebrates. Bayly (1982, 1997) studied the invertebrates of 55 gnammas on granite outcrops in southern Western Australia and found just over 100 invertebrate taxa including about 10 new species.

In central Australia, some invertebrates collected from quasi-permanent waters in large rock-holes (not gnammas) associated with gaps or gorges in the Macdonnell Ranges have been studied and identified. For example, Bayly (1964) recorded *Boeckella triarticulata* (Copepoda: Calanoida) from Simpson's Gap, Hugh Gorge and Glen Helen Gorge. However, the invertebrates living in temporary waters in the small rock-holes of central Australia have hitherto been neglected. The aim of this paper is to make a contribution to the filling of this gap.

Study site

The study site (Fig 1) was a rock-hole on Warumpi Hill situated about 4 km east of the Northern Territory community of Papunya (23°15′ S,131°54′ E), and only about 50 km from Australia's point of (mean maximum) inaccessibility from the coastline which is just south of Lake Lewis. The rock-hole (Fig 2) was located near the middle of a bare patch of rock positioned about three-quarters of the distance up the northern face of the highest portion of the hill. The summit has an altitude of 738 m above sea level and stands 120 m above the surrounding plain. Rock samples taken from the immediate vicinity of the rock-hole consisted of granitic gneiss of Lower Proterozoic age.

In plan, the rock-hole is shaped like an irregular biconvex lens with a maximum length of 225 cm and a maximum width of 43 cm. The maximum depth was 90 cm and the maximum volume of the rock-hole was about 400-500 L. From each of the two pointed extremities on either side of the lens-shaped rock-hole, a line or fracture-trace, indicating a joint plane, extended outwards on the surface of the rock for a distance of 2-3 m. This rock-hole, though not corresponding exactly, may be compared with the landform described as a "canoe" by Twidale & Corbin (1963). This form is sometimes referred to as a "water-eye"

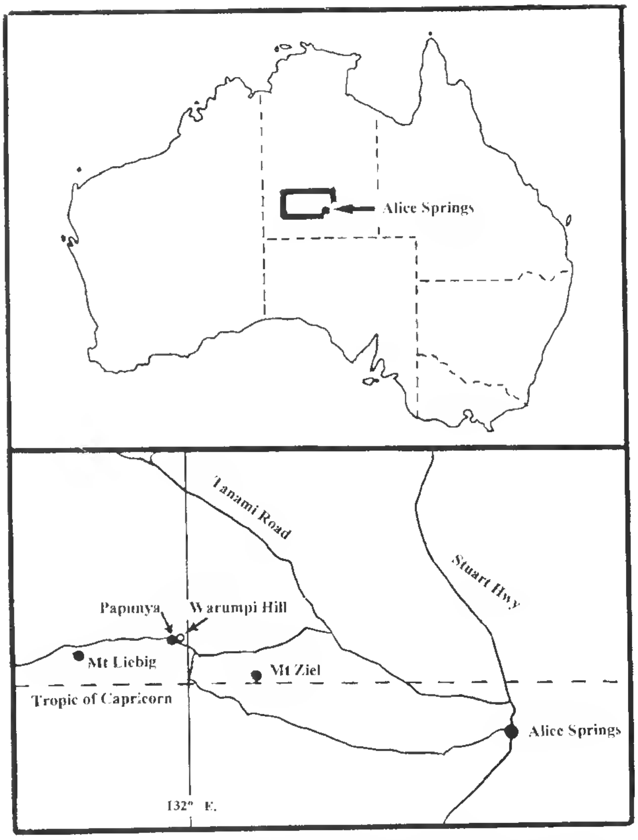

Figure 1. Map showing location of Papunya and Warumpi Hill.

Figure 2. The rock-hole, located in granitic gneiss, appears as a dark lens-shaped object in the central foreground. The hilltop in the distance is a secondary eminence rather than the highest point of Warumpi Hill; the direction of the true summit is to the left and approximately at right angles to the central line of sight (roughly west) of the photograph.

because of its lenticular or half-eye appearance in plan. The Warumpi Hill rock-hole thus differs significantly from the more common gnammas described and figured by Bayly (1999b).

The rock-hole was first observed on 24 March, 1998, when it held a small amount of water (depth *ca* 10 cm) in the bottom. This water was probably the remains of a flooding produced by the 38 mm of rain that fell 45 days earlier on 7 February. Between 24 March and 20 April, only 5 mm of rain was registered at Papunya and the mean daily maximum temperature was 32 °C. It may therefore be assumed that no free water remained in the rock-hole immediately before the deluge that occurred on 20-21 April, 1998. Heavy rain commenced in the evening of 20 April and 53 mm had been registered at Papunya by 07:45h on 21 April. It was this episode that provided the opportunity for this study.

Methods

The Warumpi Hill rock-hole was first sampled on the afternoon of 26 April, 1998, or almost six days after the start of the downpour. During the next seven weeks a further nine samples were taken at intervals ranging from 3-9 days and averaging 6 days (Table 1). Sampling ceased on 16 June when a small amount of water was still present (there was no significant rainfall between 21 April and 16 June.) The rock-hole was re-inspected on 19 July when no free water was left, but damp mud was found on the bottom. A 500 ml sample of this mud was collected and was used by Nicholas & Hodda (2000) for a detailed study of the nematodes during the latter half of 1999. Despite a year's storage, an abundance of live nematodes were still present in this material which had remained moist in a sealed container.

Invertebrates were collected with a rectangular net (opening 20 x 30 cm, mesh size 150 mm), preserved in 95% ethanol, and sorted under a Wild M7 stereo-microscope. Maximum depth of water was determined with a flexible steel measure. The conductivities of water samples collected in polyethylene bottles were determined with a Radiometer CDM2e conductivity meter.

Results

The maximum depth of water in the rock-hole and the conductivity of the water are plotted in Fig 3. The depth decreased from 74 cm on 26 April to 17 cm on 16 June, 1998. The conductivity rose from 114 μS cm^{-1} on 5 May to 993 μS cm^{-1} on 16 June (conductivity for 26 April and 14 May was not determined). Despite the steep rise, the final conductivity was still indicative of fresh water.

The occurrence and periodicity of invertebrate taxa are shown in Table 1. At first sampling, six species were present, three in immature form. Eight larvae of *Aedes (Macleaya)* sp were recorded on this occasion but none were found subsequently. From 5 to 18 May, 1998, there was a stable community consisting of eight species. With the disappearance of large phyllopods, no more than five species occurred during the period 1 to 16 June.

From the mud sample taken on 19 July, 1998, Nicholas & Hodda (2000) obtained not only *Dorylaimus* sp nov (a species present in all net-samples, except for one) but also *Mesodorylaimus rotundolabiatus* and *Heterocephalobus* sp. Both of these last two species are smaller than *Dorylaimus* sp nov and were probably present throughout the life of the pool but not collected because the mesh size

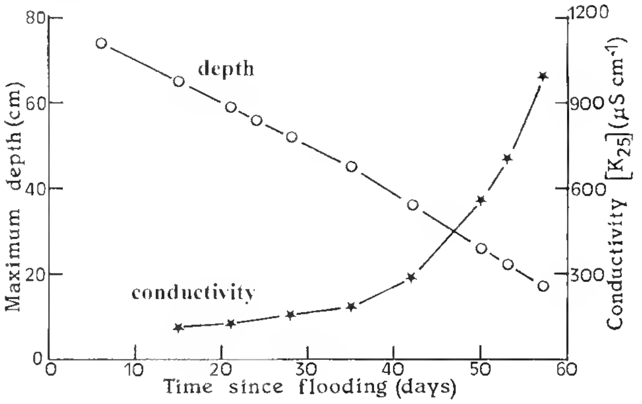

Figure 3. Temporal changes in maximum depth and electrical conductivity of the Warumpi Hill rock-hole.

Table 1. List of taxa collected in 1998 from a rock-hole on Warumpi Hill, Northern Territory, and their period of occurrence (X; or A, adults; I, immature stages) or absence (-).

Sampling date	**26 Apr**	**5 May**	**11 May**	**14 May**	**18 May**	**25 May**	**1 Jun**	**9 Jun**	**12 Jun**	**16 Jun**
Time since flooding (days)	6	15	21	24	28	35	42	50	53	57
CRUSTACEA: ANOSTRACA										
Streptocephalus sp	I	I	A	A	A	A	-	-	-	-
CRUSTACEA: CONCHOSTRACA										
Lynceus sp	I	A	A	A	A	-	-	-	-	-
CRUSTACEA: NOTOSTRACA										
Triops australiensis Spencer & Hall	I	A	A	A	A	A	-	-	-	-
CRUSTACEA: CLADOCERA										
Moina micrura Kurz	-	X	X	X	X	X	X	X	X	X
CRUSTACEA: OSTRACODA										
Heterocypris aff *tatei*	X	X	X	X	X	X	X	X	X	X
Ilyocypris sp nov	-	X	X	X	X	X	X	X	X	X
INSECTA: DIPTERA										
Aedes (Macleaya) sp	X	-	-	-	-	-	-	-	-	-
Dasyhelea sp	X	X	X	X	X	X	X[a]	-	-	X[a]
NEMATODA: DORYLAIMIDAE										
Dorylaimus sp nov	-	X	X	X	X	X	X	X	X	X

[a] one specimen only.

of the net was too coarse. *Heterocephalobus* was the numerically dominant nematode in the mud sample.

Discussion

The fauna of this central Australian rock-hole differs strikingly in a number of features from that of the granite gnammas studied by Bayly (1982, 1997) in south-western Australia. Some unexpected species were present, and some expected species were absent.

The occurrence of the anostracan genus *Streptocephalus* in the central Australian rock-hole is surprising. Sars (1896) described the species *S. archeri* from a solitary female raised from a dried mud sample collected near Rockhampton, Queensland. Linder (1941) noted that a further six females, collected from the same locality at a later date, agreed well with Sars's description, but was dubious about the assignment of these seven Rockhampton specimens to *Streptocephalus* in the absence of males. Geddes (1981), in his revision of Australian freshwater Anostraca, treated *Branchinella* as the only genus present. Likewise, Williams (1980) excluded *Streptocephalus* from his taxonomic key to Australian anostracans. For many years, therefore, the consensus has been that the only genus of freshwater fairy shrimp present in Australia was *Branchinella*. However, Sars (1896) stands vindicated; *Streptocephalus* does indeed occur in Australia, a new species from Walkamin, north Queensland, being described by Herbert & Timms (2000). With the present record, this genus is now known from 12 Australian localities, all but three of which are unpublished (B V Timms, University of Newcastle, personal communication). In contrast, *Branchinella longirostris* was the only anostracan found in the southern Western Australian gnammas studied by Bayly (1982,1997).

Adult conchostracans and notostracans were already present only 15 days after flooding. The rapid rate of development of *Triops* ("not more than two weeks") in central Australia was emphasized by Spencer & Hall (1896). Anostracans took somewhat longer to reach maturity. All large branchiopods had disappeared from the water column before six weeks after flooding.

A notable absence was chydorid cladocerans. No fewer than 19 species of Chydoridae, including several with restricted distributions, were recorded by Bayly (1982,1997) from granite gnammas in southern Western Australia. The only cladoceran found at Warumpi Hill, *Moina micrura* (Table 1), is widely distributed (occurring also outside Australia) and was recorded from three Northern Territory localities by Smirnov & Timms (1983).

The ostracod *Heterocypris* occurred in all samples taken from Warumpi Hill (Table 1), but this genus has been found only once in Western Australian rock-holes (Bayly 1997). A new species of *Ilyocypris* was present in all samples except one, but this genus has not been found in Western Australian gnammas.

Culicid mosquito larvae of the subgenus *Aedes (Macleaya)* made a brief appearance shortly after the flooding of the rock-hole. Most species in this taxon are tree-hole breeders, although one widespread species, *A. (M.) tremulus*, has previously been found in rock pools (P S Cranston, CSIRO Entomology Division, personal communication). Ceratopogonid larvae of the genus *Dasyhelea* were abundant in all samples up to and including 25 May, 1998, but thereafter they were rare or absent (Table 1). This genus is common in granite pools in Western Australia (Jones 1971) and in pools on sandstone at two localities near Sydney (Bishop 1974).

A new species of *Dorylaimus* (Nematoda) occurred in all samples save the first. Nicholas & Hodda (2000) have described this species and commented on the other nematodes recovered from the mud sample. Bishop (1974) recorded *Dorylaimus* from sandstone pools at North Head, Sydney, and Kanangra Walls, Blue Mountains.

A noteworthy feature is the complete absence of copepods crustaceans. In the granite gnammas of southern Western Australia, one of the commonest species is the calanoid copepod, *Boeckella opaqua*. This species is, however, endemic to that State. Cyclopoid copepods were not only absent from the Warumpi Hill rock-hole, but seem generally unimportant in this type of habitat.

Insects were poorly represented in comparison with granite gnammas in Western Australia. Those capable of lengthy flight like dytiscids, corixids and notonectids were all absent. The rock-hole may have been too remote from permanent-water refuges for the presence of these "Group C" animals (see Bayly 1997).

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Note from the Honorary Editor:

This column in the *Journal of the Royal Society of Western Australia* helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA) .

References are abstracted from Current Contents by searching for Western Australia in the title and abstract. The references are separated into Physical Sciences and Biological Sciences.

P C Withers
Honorary Editor
Royal Society of Western Australia
c/o Western Australian Museum
Francis Street
Perth WA 6000

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Vegetation, flora and recommendations for conservation management of Jingaring Nature Reserve: A "botanical gem" in the Western Australian wheat-belt.

F J Obbens, R W Davis & L W Sage

Western Australian Herbarium, Department of Conservation and Land Management,
Locked Bag 104, Bentley Delivery Centre WA 6983

(received February 1999, accepted December 2000)

Abstract

The significance of larger remnants at retaining local bio-diversity in an essentially cleared and fragmented agricultural landscape is generally accepted, but small intact remnants also contribute significantly to overall bio-diversity. This was highlighted by our comprehensive survey of vascular flora of Jingaring Nature Reserve, which included every season over a two-year period. The exceptionally diverse flora of this relatively undisturbed wheatbelt remnant identified six distinct communities encompassing heaths and woodlands. Over 260 vascular species were recorded, including two rare, five priority and a number of species of special interest from 51 families. Weeds accounted for 27 species, but the extent of invasion is relatively low. The known limit of many species' distributions occur near or at the reserve and this may be an evolutionary artefact of significant importance. Higher species diversity per unit area was recorded compared to other unpublished surveys of larger areas around this district.

Several management issues are of concern for Jingaring Nature Reserve including protection of rare and priority flora, weed invasion, fire management and damage caused by unauthorised access. Eradication of rabbits and localised weed control around rabbit warrens in the reserve should result in regeneration of these areas.

Keywords: vegetation, flora, Jingaring Nature Reserve, wheat-belt, remnant vegetation.

Introduction

Jingaring Nature Reserve is a species-rich remnant (see species list in appendix) of high conservation value (*i.e.* "A" class nature reserve). It is located 155 km directly east-south-east of Perth near Pingelly, Western Australia (Fig 1). The district has a dry Mediterranean-type climate with very warm, dry summers and very cool, wet winters. Average annual rainfall for the reserve is about 400 mm, which places the reserve within the wetter western (inner) margins of the wheatbelt (Fig 1). The landscape surrounding Jingaring Nature Reserve is undulating hills with interspersed plains. Overall height relief is low and there are few large granite outcrops or extensive lateritic ridges as found in western parts of this district (Beard 1980a). The reserve is a small triangular remnant (34 ha) situated in the upper reaches of the Avon River, the river being a few kilometres to the north. Drainage of the immediate area is via Sandplain Creek, that runs through the extreme south-western corner of the reserve heading firstly north west, then to the north, before it drains into the Avon River. Jingaring Nature Reserve is actually a remnant portion of creek floodplain and gently sloping valley side. The reserve is surrounded by expanses of cleared agricultural land that forms an integral feature of the Western Australian wheatbelt region. Beard (1980b) classified the dominant vegetation of the district as a mixture of York gum (*Eucalyptus loxophleba*) and wandoo (*E. wandoo*), with scrub-heath on intervening sandplain areas. This describes the situation in the immediate surrounds of the reserve. Further east (~25 km) the wandoo gives way to the more xeric-adapted salmon gum (*E. salmonophloia*), while 20 km south in the Shire of Cuballing, groves of jam (*Acacia acuminata*) and sheoak (*Allocasuarina huegeliana*) surround significant areas of granite outcropping (Beard 1980b).

Currently, there are few published wheatbelt remnant surveys available, but notable are the pioneering surveys of 24 reserves compiled in the Records of the Western Australian Museum (Muir 1977a). There are several other significant, and unpublished, flora surveys of wheatbelt remnants; however, few of these submitted vouchers to the Western Australian Herbarium (PERTH) so that the specimens would be available and taxonomically relevant into the future. Reasons for the lack of published survey information to date are the costs of extensively surveying remnants and the vastness of the region (*i.e.* 18 million hectares). Larger remnants (*i.e.* >2000 ha) are generally considered as important areas for conserving this wealth of bio-diversity and these areas are also particularly necessary for fauna conservation. The aim of this survey was to highlight the contribution that smaller remnants, (particularly intact remnants) can make towards the overall flora diversity within the wheatbelt region. Additionally, it emphasizes that these small intact remnants should not be overlooked nor precluded from future acquisitions of conservation estate.

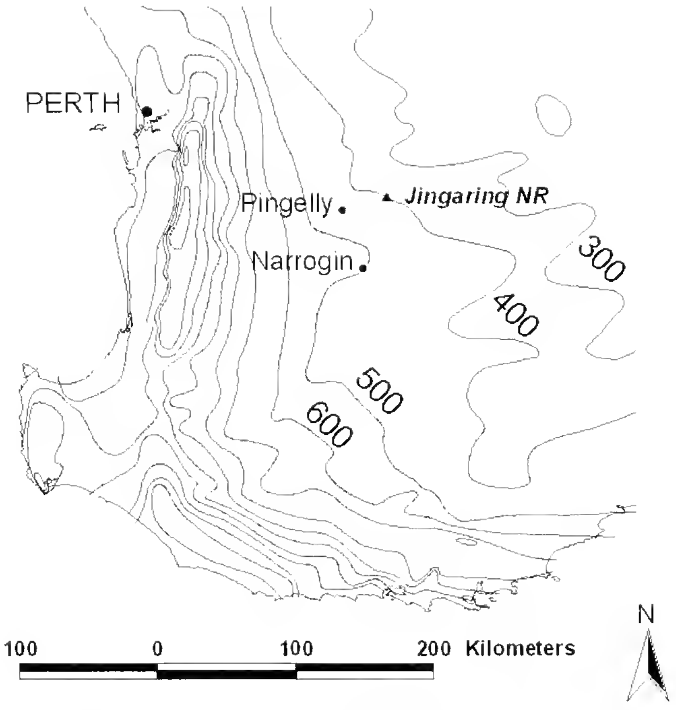

Figure 1. Location of Jingaring Nature Reserve, near Pingelly, in the southwest of Western Australia showing rainfall isohyets.

Methods

The vegetation communities of Jingaring Nature Reserve were interpreted from a 1996 aerial photograph and confirmed in the field during 1999. Classification of these vegetation communities is based on Muir (1977b). This classification assesses vegetation structure by taking measures of lifeform/height class and canopy cover/density class to produce a vegetation type. For example, trees 15-30 m with a 10-30% canopy cover were designated woodlands, while the same trees with a canopy cover of 2-10% would be designated as open woodlands. To a significant extent this classification also reflects species compositional differences. Additionally, brief investigations were made of the soils in each vegetation community. This included taking soil samples (~3 cm depth) to nominally assess soil texture and colour.

The flora survey and collections were accomplished by walking along transects (spaced 150 m apart) which spanned the full width of the reserve in a north-south orientation. The first transect began at approximately 50 m in from the reserve's south-west corner, in the vicinity of Sandplain Creek. Every vegetation type was traversed several times using this technique. This transect survey was undertaken during late spring 1998, but various additional surveys were also carried out during mid autumn, early and late winter, early and mid spring, and early summer over 1998 and 1999. On these occasions a technique known as 'randomized stratified walk' (Hopper *et al.* 1997) was employed. As the name suggests, this method involves specimen collections via random walks in each habitat type. The purpose of this intensive surveying was to obtain a good flowering specimen of each species and to compile a more complete vascular flora list (*i.e.* as a benchmark survey).

The authors identified most specimens with some assistance from specialist staff of the WA Herbarium. All specimens were submitted for incorporation at the WA Herbarium. Species names follow WACENSUS (WA Herbarium census of Western Australian vascular plants), while conservation status of species is according to Department of Conservation and Land Management's

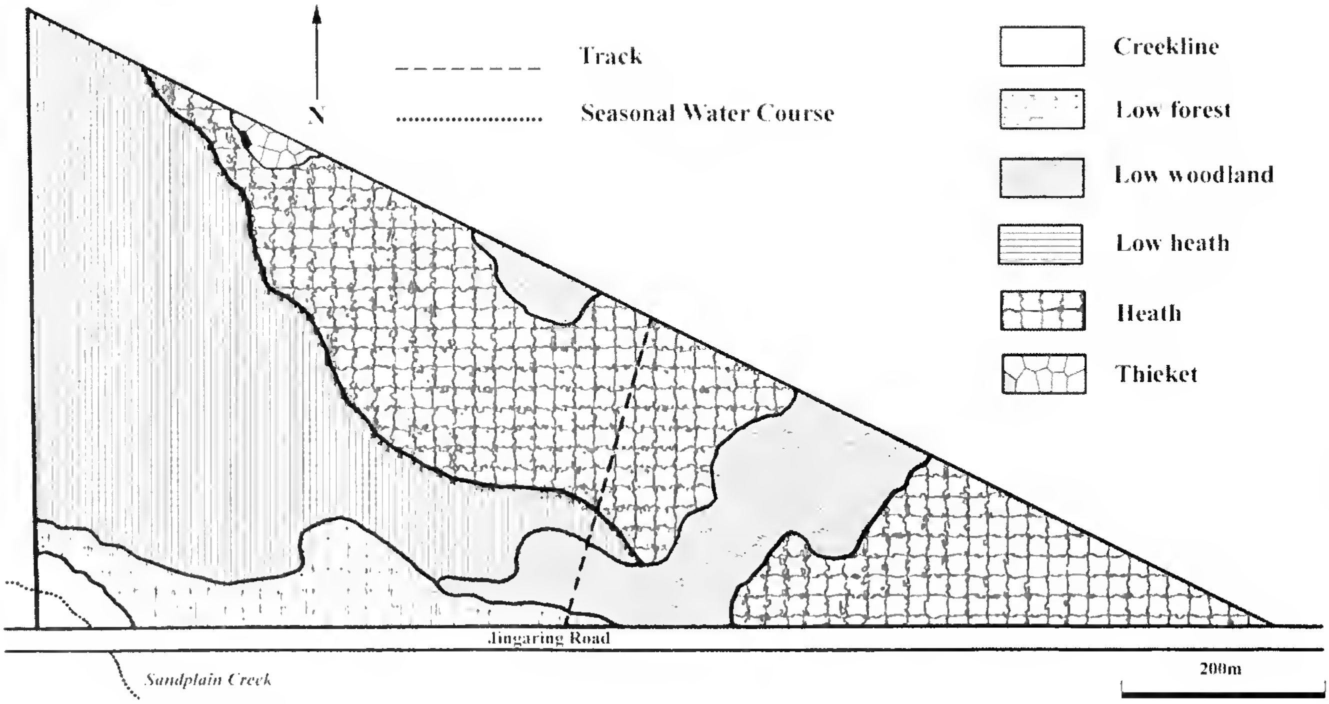

Figure 2. Vegetation communities of Jingaring Nature Reserve.

Table 1. Vegetation communities and their predominant plant species as recognized at Jingaring Nature Reserve.

Community	Plant species
Dense Low Forest	Dense canopy of *Eucalyptus loxophleba*, *E. rudis* and *Allocasuarina huegeliana*. Mid canopy of *Acacia saligna*, *A. acuminata* and *Melaleuca sp*. The understorey is degraded and dominated by weeds.
Low Forest	*Allocasuarina huegeliana*, *Acacia acuminata* and some scattered *Eucalyptus wandoo*, with a mainly herbaceous species understorey occurring on flat plain.
Low Woodland	*Eucalyptus wandoo* with scattered *Acacia acuminata* and sparse, open shrub understorey or sedges.
Low Heath	A very diverse mix of shrubs and sub-shrubs (<1.5 m), abundant sedges, occurring on flat plain.
Heath	A very diverse mix of shrubs and sub-shrubs (most 1-2 m), some sedges, occurring on sloping ground.
Thicket	A mid-dense mix of tall shrubs (most >2 m) occurring on gently sloping ground.

(CALM) Declared Rare Flora and Priority Flora list (Atkins 1999). The authors also received invaluable information from WA Herbarium database records (WAHERB) and (FLORABASE).

Results

Vegetation and habitat

Interpretation of the aerial photograph and site survey indicated six major vegetation types (Table 1 & Fig 2), five quite distinctive, and a sixth being a variant of reasonable species differences and of sufficient area to be considered as separate (*i.e.* 5: Heath from Table 1).

The creekline community covers a small area (~ 3 ha) and has variable soil types, the creek banks being a mixture of gravels bound in fine to coarse sandy clay. *Eucalyptus loxophleba*, *E. rudis*, *Acacia saligna* and *Melaleuca sp* are common, while further out *Allocasuarina huegeliana* becomes more dominant on brown sandy loam. Numerous wind-dispersed agricultural grass weeds, such as *Avena barbata*, *Ehrharta longiflora*, *Bromus diandrus* and *Lolium rigidum*, are well established here preferring the extra moisture and nutrients.

The low forest community occurs on grey/brown sandy loam in a narrow band east of the creek line (plains country) and parallel to the road. *Allocasuarina huegeliana* and *Acacia acuminata* predominate, interspersed with *Eucalyptus wandoo* and resulting in a mid-dense canopy cover (30-70%), the open patches being more woodland like. There are a few scattered shrubs, but most of the understorey is quite open and rich in annuals and other herbaceous species. The wandoo woodland community slightly intergrades at the boundary with the previous low forest community and again occurs on sandy loams. This vegetation type traverses the slope with the understorey on the lower slopes consisting of scattered low shrubs (mainly Fabaceae) and sedges (predominantly *Lepidobolus preissianus* and *Desmocladus asper*), while on the mid to upper slope there are more frequent bare patches containing wandoo leaf litter. Another pocket of open wandoo woodland also occurs up slope on the reserve's mid northern boundary and extends onto adjacent farmland (Fig 2).

The low heath community covers most of the extensive low-lying plain of the reserve and has a light grey/brown sandy loam appearance. The area is reasonably inundated at times during winter. Low shrubs and sub-shrubs predominate, but there are also scattered patches of taller vegetation including *Allocasuarina campestris*, *Santalum spicatum* and some Acacia species. The heath is species rich with a number of common shrubs such as *Calothamnus brevifolius*, *Melaleuca carrii*, *Beaufortia bracteosa*, *Acacia lasiocarpa*, *Daviesia cardiophylla*, *Comesperma scoparium*, *Hakea lissocarpha*, *Dodonea pinifolia*, *Petrophile ericifolia*, *Laxmannia omnifertilis* and *Allocasuarina humilis* to name but a few. *Mesomelaena preissii* is the most commonly occurring sedge.

Farther up the slope the low heath changes subtly to heath. This community covers a considerable area of the reserve in two large parts separated by wandoo woodland. The soil varies from light grey to light grey/brown sandy loams often with a thin layer of bleached white sand on top. Soil depth also increases farther up slope, which might explain the differences in shrub height for this community. Most of the species mentioned in the previous community occur here also, however, others such as *Banksia sphaerocarpa*, *B. violacea*, *Isopogon buxifolius*, *Pimelea imbricata*, *Leptospermum erubescens* and *Grevillea cagiana* appear to be specifically located within this vegetation type.

The last community is a small patch of thicket dominated by tall *Allocasuarina campestris* and *Dryandra purdieana*, with a mid-dense understorey of *Banksia sphaerocarpa*, *Hakea incrassata* and *Calothamnus brevifolia*. The soils are again a light grey/brown loam and appear to have similar depth to the heath community.

Flora

A total of 264 vascular species (237 natives and 27 introduced weeds) from 51 families were listed for Jingaring Nature Reserve (Appendix). The ten largest families were Proteaceae (28), Myrtaceae (27), Asteraceae (22), Poaceae (18), Papilionaceae (16), Cyperaceae (15), Mimosaceae (13), Orchidaceae (12) Goodeniaceae (11) and total 'Liliaceae' (13). Half of the Poaceae species are weeds. The ten genera with the greatest number of species are *Acacia* (13), *Verticordia* (9), *Hakea* (6), *Caladenia* (6), *Schoenus* (6), *Drosera* (6), *Dryandra* (5), *Daviesia* (5), *Goodenia* (5) and *Stylidium* (5).

Two declared rare species, *Verticordia fimbrilepis* ssp *fimbrilepis*, a variant of *Dryandra ionthocarpa* (currently under review) and five priority species, *Acacia anarthos*, *Anigozanthos bicolor* ssp *exstans*, *Calothamnus brevifolius*, *Calytrix* sp (Jingaring) and *Dryandra lindleyana* ssp *agricola* were recorded for the reserve. There were also several species of special interest (see discussion).

Discussion

Vegetation and habitat

Most of the vegetation communities of the reserve were distinctive, but considered as not particularly unique, there being several other remnants in the area having similar habitat types. The low heath community is not as common locally; however, all habitat types were in relatively good condition.

Flora

Jingaring Nature Reserve, with 264 species located within 34 ha, represents an exceptionally species-rich area. As a comparison, a 'random stratified' flora survey of Yilliminning Rock reserve, just east of Narrogin and about 55 km directly south of Jingaring Nature Reserve, found 238 vascular species in 80 ha (Pigott & Sage 1997). A quadrat-based flora survey near Popanyinning (~30 km south-west of Jingaring Nature Reserve) by Gunness (1998) found 249 vascular species in 60 ha of bushland remnant. Additionally, several surveys over a number of years for the nearby Tutanning Nature Reserve (2310 ha) have so far recognized 628 species for that reserve. Some of the differences found in species richness of these areas might be attributed to the different survey techniques used (*i.e.* not comparable), to different habitats surveyed and to the intensity of surveying (*i.e.* one season or more). Regardless of these factors, Jingaring Nature Reserve has an unusually high concentration of flora species and thus plays a big role for its size in conserving wheatbelt biodiversity. Any future intensive surveys using a similar methodology could act as benchmarks. These benchmark surveys of reserves/remnants spaced equally distant and appropriately throughout the wheatbelt would help to increase our knowledge of the flora in this highly fragmented landscape.

Declared Rare Flora. Two declared rare species are listed for the reserve, *Verticordia fimbrilepis* ssp *fimbrilepis* and a variant of *Dryandra ionthocarpa* (currently under review). The latter record extends that species range by approximately 240 km (former distribution just south of the Stirling Range). Both these species have the IUCN ranking of critically endangered.

Priority species. Five priority species have been identified, and along with the other rare flora this reaffirms the high conservation value of the reserve.

Acacia anarthros. Priority 3. This species is known from more than a dozen small remnants and the Jingaring Nature Reserve find represents one of the larger populations with secure conservation tenure. This population, and another slightly north near Lake Mears, are the only outliers from the known major populations centred around Calingiri, approximately 160 km away.

Anigozanthos bicolor ssp *exstans*. Priority 3. Scattered populations of this species are found from Meckering to south of Pingelly, and appear to be associated with open woodland areas. So far, less than 5 plants have been discovered in the reserve, all in the typical woodland habitat.

Calothamnus brevifolius. Priority 3. Its distribution is a relatively wide area from Marchagee (north) to Tammin and Corrigin (east) and to the Brookton area (south). The large Jingaring population is significant compared to the other smaller roadside remnants.

Calytrix sp (Jingaring). Priority 2. Recently, this taxa has been recognised as distinct from *Calytrix asperula* whose populations are all distributed near the south coast. There are only three populations of *Calytrix* sp (Jingaring) now recognized, on the reserve, at Aldersyde, and over 100 km eastwards near Narembeen. It is doubtful whether this last population still exists as the original collection was made in 1929 prior to significant land clearing there.

Dryandra lindleyana ssp *agricola*. Priority 1. A number of scattered populations are known over a relatively small area from east of Brookton to Kondinin. There are thousands of individual plants in the reserve, making this one of the largest populations.

Species of interest. *Persoonia inconspicua* has a distribution centred around Southern Cross and the Jingaring record represents a significant range extension. A presumed hybrid between *Dryandra pteridifolia* ssp *pteridifolia* (southern sandplains) and *Dryandra pteridifolia* ssp *vernalis* (northern sandplains) occurs on the reserve (taxonomic status to be determined). The reserve locality is also the distribution limit for *Lagenophora huegelii*, *Patersonia occidentalis*, *Hibbertia hypericoides*, *Sowerbaea laxiflora* (most eastern margin); *Adenanthos argyreus*, *Conostylis petrophiloides*, *Grevillea cagiana*, *Logania tortuosa* (most western margin); *Kunzea micromera*, *Banksia violacea* (most northern margin) and *Acacia acuaria*, *A. anarthros* and *Grevillea eriostachya* (most southern margin). This suggests that Jingaring Nature Reserve was part of a possible refugium where past climatic fluctuations have caused the maximal species interactions *i.e.* a central meeting point for potential speciation (Hopper 1979). In these terms, the reserve is a significant 'evolutionary showcase'.

Introduced weeds. There were 27 weed species (10% of the flora) recorded for Jingaring Nature Reserve compared to 19 weed species (8% of the flora) for Yilliminning Rock and 37 weed species (15% of the flora) for the Popanyinning remnant survey. These weed ratios range from low to moderate with some wheat-belt remnants containing higher numbers of weed species (unpublished personal observations). The number of weed species does not necessarily correspond to the extent of weed invasion. Jingaring Nature Reserve has serious weed infestation throughout the creekline community. Here, grass weeds such as *Avena barbata*, *Briza maxima*, *Bromus diandrus*, *Ehrharta longiflora*, *Hordeum geniculatum* and *Lolium rigidum* dominate the understorey. Broadleaf weeds such as *Arctotheca calendula*, *Brassica tournefortii* and *Hypochaeris glabra* are also locally common. The reserve boundary abutting farmland also has dense weed invasion, but by far the larger part of the reserve is relatively weed-free. Some very localized weed incursions also occur around disturbed areas (*i.e.* rabbit warrens, service track edges and an old gravel pit/rubbish site). There are low levels of *Parentucellia latifolia* and *Romulea rosea* scattered in the woodland areas, while *Ursinia anthemoides* is scattered throughout the reserve. These latter weeds appear innocuous, but *Romulea rosea* is a serious woodland weed in the wetter wheat-belt regions (Hussey *et al.* 1997).

Conservation management

Conservation reserves are generally smaller in the inner (*i.e.* western) wheat-belt areas compared to more eastern areas (CALM records). Management of small reserves with large perimeter to area ratios in a fragmented landscape is difficult (Panetta & Hopkins 1991) and has been exacerbated by a long history of disturbance and degradation. This includes more frequent fires, weed invasions due to human intervention and habitat modification, and also rising water-tables leading to increased salinity (Hobbs 1993). In outward appearances, Jingaring Nature Reserve seems relatively undisturbed in comparison to other small remnants in the area. Variable levels of weed incursion were found, but most native vegetation appears relatively healthy. There were no obvious signs of tree or shrub deaths that might indicate increasing salinity, but the reserve may still be at risk due to its low position in the landscape and its proximity to the Avon River. Important management issues include the protection of rare and priority flora, weed abatement, fire management and the protection of vegetation from inappropriate and unauthorised access (*i.e.* trail bikes, horses *etc*).

With two critically endangered and five priority species, the reserve needs a high level of protection from potential threats. The reserve has distinct vegetation communities and its geographical position makes the flora special (as discussed previously). Weeds are a threat to the reserve's integrity because weeds have been shown to displace native species, alter fire regimes, change local hydrology and reduce faunal resources (Hobbs 1991; Humphries *et al.* 1993; Pigott 1994; Adair 1995). Areas of weeds targeted specifically should provide the best management results. For instance, any attempt to eradicate weeds from the degraded creek line or boundary zones is unlikely to produce adequate regeneration of native species. This is because understorey seed-banks are often depleted in long-degraded areas such as these, and/or these areas may require specialised techniques to effect a reasonable germination event (Arnold *et al.*1998; unpublished personal observations). Additionally, these areas easily become weedy again due to wind-transported propagules and this will hinder the growth of any regenerated native seedlings. Ongoing weed control followed by planting out/seeding of local understorey species may be the only option left to rehabilitate these areas. This requires considerable management resources and may not produce equivalent results to the inputs needed. Most rabbit warrens are located in the central portion of the reserve where regular baiting for rabbits and localized weed control should prove more successful at regenerating these areas in the medium term (*i.e.* native seed rain still occurring in the immediate vicinity and weed reinvasion limited). A regular monitoring program must be implemented to determine the effectiveness of management measures and whether or not more control work is required to achieve a better outcome.

Fire is an essential part of most Australian ecosystems, but too-frequent burning of fragmented landscapes can be disastrous leading to weed invasion within small remnants which in turn perpetuates more fire events (Bridgewater & Kaesehagen 1979; Wycherley 1984; Hussey & Wallace 1993; B Muir, Muir Environmental Consultants, personal communication). CALM district records show that the reserve has not had a fire since 1980 and likely many years prior to that date. It appears that the localized weed invasions in the reserve are the results of localized soil disturbance rather than too-frequent fires. Any future fire plans should consider mosaic burns supplemented with post-fire weed control if required. Grading fire-breaks prior to mosaic burns is not recommended due to the increased potential for weed invasion along these breaks (*i.e.* increased soil disturbance) and increased fragmentation of these small reserves. Brush-cutting narrow bands of vegetation may provide the necessary fire-breaks. The potential for fire to adversely impact upon the reserve's rare flora must be considered. These areas should be kept fire-free until recovery plans have been successfully implemented which would include research into the fire response of these species.

There has been some evidence of trail bikes and horses using the area. The open nature of the reserve allows easy access. A management track cuts through the centre of the reserve and another overgrown track leads to the reserve's north-west corner (not shown on Fig 2). At this stage, the damage to vegetation from vehicles and horses has been minor. It would be advisable to erect signs that these activities are not appropriate or authorised, and to more clearly distinguish the area as a nature reserve.

In conclusion, the survey has highlighted aspects that need management attention despite the reserve's relatively pristine appearance. It demonstrates that 'in depth' surveys are especially useful at detecting potential issues prior to these situations becoming real management problems.

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Appendix

The vascular plant species recorded for Jingaring Nature Reserve listed by family. The family sequence is based on Engler's phylogenetic classification of plant families. The collector's number for each specimen is included in parentheses after the species authority name. * symbol represents species which are naturalized weeds.

Poaceae

* *Alopecurus pratensis* L (LWS1308)
Amphipogon strictus R Br (LWS1315)
Amphipogon turbinatus R Br (RD6376)
Austrodanthonia acerosa (Vickery) HP Linder (LWS1346)
Austrodanthonia caespitosa (Gaudich) HP Linder (LWS1300)
Austrostipa elegantissima (Labill) SWL Jacobs & J Everett (LWS1282)
Austrostipa hemipogon (Benth) SWL Jacobs & J Everett (FO236/99)
Austrostipa semibarbata (R Br) SWL Jacobs & J Everett (LWS1352)
Austrostipa sp (LWS1351)
* *Avena barbata* Link (LWS1345)
* *Briza maxima* L (RD6557)
* *Bromus diandrus* Roth (LWS1356)
* *Ehrharta longiflora* Sm (LWS1357)
* *Hordeum geniculatum* All (LWS1314)
* *Lolium rigidum* Gaudin (LWS1306)
Neurachne alopecuroidea R Br (RD6553)
* *Pentaschistis airoides* (Nees) Stapf (LWS1334)
* *Vulpia muralis* (Kunth) Nees (RD6550)

Cyperaceae

Baumea sp (RD6397)
Caustis dioica R Br (LWS1259)
Chorizandra enodis Nees (LWS1321)
* *Cyperus tenellus* L f (LWS1287)
Lepidosperma brunonianum Nees (FO34199)
Lepidosperma costale Nees (LWS1367)
Lepidosperma sp (LWS1382)
Lepidosperma sp A2 Island Flat (GJ Keighery 7000) (LWS1384)
Mesomelaena preissii Nees (RD6543)
Schoenus discifer Tate (LWS1320)
Schoenus sp (LWS1289)
Schoenus sp A2 Kulin (BG Briggs 7939)(LWS1271)
Schoenus sp smooth culms (KR Newbey 7823)(FO41/99)
Schoenus subflavus Kuek subsp long leaves (KL Wilson 2865)(LWS1358)
Schoenus subflavus Kuek subsp *subflavus*(RD6535)

Restionaceae

Anarthria polyphylla Nees (LWS1272)
Desmocladus asper (Nees) LAS Johnson & BG Briggs (RD6384)
Harperia lateriflora W Fitzg. (FO232/99)
Lepidobolus chaetocephalus Benth (RD6379)
Lepidobolus preissianus Nees subsp *preissianus* (LWS1260)

Dasypogonaceae

Calectasia grandiflora Endl (RD6334)
Chamaexeros serra (Endl) Benth (RD6375)
Lomandra effusa (Lindl) Ewart (LWS1251a)
Lomandra sp (LWS1251b)

Xanthorrhoeaceae

Xanthorrhoea drummondii Harv (LWS1307)

Phormiaceae

Dianella revoluta R Br (LWS1309)
Stypandra glauca R Br (RD6532)

Anthericaceae

Chamaescilla corymbosa (R Br) Benth (FO238/99)
Chamaescilla spiralis (Endl) Benth (RD6525)
Dichopogon preissii (Endl) Brittan (LWS1359)
Laxmannia omnifertilis Keighery (RD6451)
Laxmannia squarrosa Lindl (LWS1278)
Sowerbaea laxiflora Lindl (RD6455)
Thysanotus patersonii R Br (FO242/99)
Tricoryne tenella R Br (LWS1303)

Colchicaceae

Wurmbea tenella (Endl) Benth (RD6341)

Boryaceae

Borya laciniata Churchill (RD6448)
Borya sphaerocephala R Br (RD6539)

Haemodoraceae

Anigozanthos bicolor subsp *exstans* Hopper (FO311/99)
Conostylis petrophiloides Benth (LWS1274)
Conostylis villosa Benth (LWS1374)
Haemodorum discolor T Macfarlane (LWS1375)
Tribonanthes longipetala Lindl (RD6527)

Iridaceae

Orthrosanthus laxus var *gramineus* (Endl) Geerinck (RD6456)
Patersonia juncea Lindl (LWS1376)
Patersonia occidentalis R Br (LWS1355)
* *Romulea rosea* var *australis* (Ewart) MP de Vos (RD6447)

Orchidaceae

Caladenia hiemalis Hopper & AP Brown ms (RD6450b)
Caladenia pendens Hopper & AP Brown subsp *pendens* ms (FO245/99)
Caladenia radialis RS Rogers (FO246/99)
Caladenia reptans Lindl (FO243/99)
Caladenia vulgata Hopper & AP Brown ms (FO244/99)
Cyanicula deformis (R Br) Hopper & AP Brown ms (RD6441)
Diuris corymbosa Lindl (RD6416)
Diuris laxiflora Lindl (LWS1311)
Diuris setacea R Br (LWS1310)
Eriochilus helonomos Hopper & AP Brown ms (FO33/99)
Pterostylis recurva Benth (FO235/99)

Casuarinaceae

Allocasuarina campestris (Diels) LAS Johnson (FO6A&B/99)
Allocasuarina huegeliana (Miq) LAS Johnson (RD6328)
Allocasuarina humilis (Otto & F Dietr) LAS Johnson (RD6327)
Allocasuarina microstachya (Miq) LAS Johnson (RD6339)

Proteaceae

Adenanthos argyreus Diels (RD6318)
Banksia sphaerocarpa R Br (RD6316)
Banksia violacea CA Gardner (RD6332)
Dryandra ionthocarpa AS George (LWS1350)
Dryandra lindleyana subsp *agricola* AS George (LWS1383)
Dryandra pteridifolia R Br (RD6337)
Dryandra purdieana Diels (RD6329)
Dryandra vestita Meisn (RD6336)

Grevillea cagiana McGill (LWS1339)
Grevillea eriostachya Lindl (LWS1347)
Grevillea uncinulata Diels subsp *uncinulata* (RD6438)
Hakea brownii Meisn (RD6325)
Hakea cygna Lamont subsp *cygna* (RD6322)
Hakea lissocarpha R Br (RD6439)
Hakea prostrata R Br (LWS1329)
Hakea scoparia Meisn (LWS1349)
Hakea trifurcata (Sm) R Br (RD6369)
Isopogon buxifolius R Br (RD6370)
Isopogon teretifolius R Br subsp *teretifolius* ms (LWS1338)
Persoonia inconspicua PH Weston (FO239/99)
Persoonia sp (LWS1381)
Persoonia striata R Br (FO330/98)
Petrophile brevifolia Lindl (RD6372)
Petrophile ericifolia R Br subsp *ericifolia* (RD6388)
Petrophile seminuda Lindl (RD6380)
Petrophile squamata R Br (RD6377)
Synaphea aff *interioris* (RD6321)
Synaphea spinulosa subsp *major* AS George (RD6340)

Santalaceae

Santalum spicatum (R Br) A DC (RD6454)

Loranthaceae

Nuytsia floribunda (Labill) Fenzl (FO31/99)

Polygonaceae

Muehlenbeckia adpressa (Labill) Meisn (LWS1325)

Amaranthaceae

Ptilotus drummondii (LWS1296)
Ptilotus declinatus Nees (LWS1333)
Ptilotus manglesii (Lindl) F Muell (LWS1254)
Ptilotus polystachyus (Gaudich) F Muell (FO/99)

Caryophyllaceae

* *Spergularia rubra* (L) J Presl & C Presl (FO312/99)
* *Spergularia salina* J Presl & C Presl (LWS1288)

Lauraceae

Cassytha glabella R Br (FO2/99)
Cassytha pomiformis Nees (LWS1316)

Fumariaceae

* *Fumaria muralis* WDJ Koch (RD6446)

Brassicaceae

* *Brassica tournefortii* Gouan (FO240/99)
* *Raphanus raphanistrum* L (LWS1370)

Droseraceae

Drosera bulbosa Hook subsp *bulbosa* (FO30/99)
Drosera erythrorhiza subsp *squamosa* (Benth) Marchant & Lowrie (FO4/99)
Drosera glanduligera Lehm (RD6538)
Drosera macrantha Endl subsp *macrantha* (RD6457)
Drosera menziesii DC subsp *menziesii* (FO310/99)
Drosera sulphurella Planch (RD6554)

Crassulaceae

Crassula colorata (Nees) Ostenf (FO231/99)

Pittosporaceae

Sollya heterophylla Lindl (RD6383)

Mimosaceae

Acacia acuaria W Fitzg (FO159/99)
Acacia acuminata Benth (LWS1283)
Acacia anarthros Maslin (FO15/99)
Acacia lasiocalyx CRP Andrews (RD6324)
Acacia lasiocarpa var *sedifolia* (Meisn) Maslin (RD6381)
Acacia leptospermoides Benth (FO233/99)
Acacia microbotrya Benth (LWS1262)
Acacia multispicata Benth (FO234/99)
Acacia saligna (Labill) HL Wendl (LWS1292)
Acacia sessilispica Maiden & Blakely (RD6533)
Acacia stenoptera Benth (RD6330)
Acacia subflexuosa Maiden subsp *subflexuosa* (RD6338)
Acacia tratmaniana W Fitzg (RD6391)

Papilionaceae

Bossiaea spinescens Meisn (RD6385)
Chorizema aciculare (DC) CA Gardner subsp *aciculare* (RD6536)
Daviesia aff *cardiophylla* (FO40/99)
Daviesia brachyphylla Meisn (FO156/99)
Daviesia cardiophylla F Muell (RD6315)
Daviesia hamata Crisp (RD6333)
Daviesia incrassata subsp *teres* Crisp (LWS1373)
Gastrolobium spinosum var *triangulare* Benth (LWS1275)
Gompholobium marginatum R Br (LWS1270)
Isotropis cuneifolia (Sm) BD Jacks (RD6556)
Isotropis drummondii Meisn (LWS1302)
Jacksonia condensata Crisp & JR Wheeler (LWS1327)
Jacksonia racemosa Meisn (LWS1378)
Mirbelia trichocalyx Domin (LWS1281)
Nemcia sp A Avon (MD Crisp 6183)(RD6530)
* *Trifolium arvense* L (LWS1318)

Geraniaceae

* *Erodium botrys* (Cav) Bertol (LWS1336)
Erodium cygnorum Nees (FO230/99)

Oxalidaceae

* *Oxalis corniculata* L (FO313/99)

Rutaceae

Boronia coerulescens F Muell subsp *coerulescens* (RD6440)
Boronia ramosa subsp *anethifolia* (Bartl) PG Wilson (FO315/99)

Tremandraceae

Tetratheca confertifolia Steetz (LWS1340)

Polygalaceae

Comesperma scoparium Steetz (RD6389)

Euphorbiaceae

Poranthera microphylla Brongn (LWS1313)

Stackhousiaceae

Stackhousia monogyna Labill (LWS1279)

Sapindaceae

Dodonaea pinifolia Miq (RD6367)

Rhamnaceae

Cryptandra leucopogon Reissek (RD6540)
Cryptandra myriantha Diels (RD6319)

Cryptandra pungens Steud (RD6320)
Stenanthemum intricatum Rye (FO36/99)

Dilleniaceae

Hibbertia exasperata (Steud) Briq (RD6531)
Hibbertia hypericoides (DC) Benth (RD6526)

Violaceae

Hybanthus floribundus (Lindl) F Muell subsp *floribundus* (FO42/99)

Thymelaeaceae

Pimelea argentea R Br (RD6445)
Pimelea imbricata var *piligera* (Benth) Diels (LWS1284)

Myrtaceae

Baeckea crispiflora F Muell (LWS1361)
Baeckea preissiana (Schauer) Domin (LWS1360)
Beaufortia bracteosa Diels (RD6335)
Calothamnus brevifolius Hawkeswood (RD6386)
Calothamnus quadrifidus R Br (RD6373)
Calytrix acutifolia (Lindl) Craven (RD6390)
Calytrix leschenaultii (Schauer) Benth (RD6323)
Calytrix sp. Jingaring (F Obbens, R Davis & LW Sage) (LWS1332)
Eremaea pauciflora (Endl) Druce var *pauciflora* (RD6387)
Eucalyptus loxophleba Benth subsp *loxophleba* (LWS1348)
Eucalyptus rudis Endl (FO14/99)
Eucalyptus wandoo Blakely subsp *wandoo* (RD6326)
Kunzea micromera Schauer (RD6442)
Leptospermum aff *nitens* (LWS1319)
Leptospermum erubescens Schauer (RD6534)
Melaleuca carrii Craven ms (LWS1362)
Melaleuca subtrigona Schauer (LWS1331)
Scholtzia sp (FO241/99)
Verticordia acerosa var *preissii* (Schauer) AS George (RD6374)
Verticordia brachypoda Turcz (LWS1263)
Verticordia chrysantha Endl (LWS1341)
Verticordia densiflora Lindl (FO332/98)
Verticordia eriocephala AS George (LWS1343)
Verticordia fimbrilepis Turcz subsp *fimbrilepis* (GD113)
Verticordia grandiflora Endl (LWS1268)
Verticordia picta Endl (RD6437)
Verticordia sp (LWS1342)

Haloragaceae

Glischrocaryon aureum var *angustifolium* (Nees) Orchard (LWS1258)

Apiaceae

Hydrocotyle callicarpa Bunge (RD6549)
Trachymene pilosa Sm (LWS1256)

Epacridaceae

Andersonia lehmanniana subsp *pubescens* (Sond) L Watson (RD6331)
Astroloma compactum R Br (FO38/99)
Astroloma serratifolium (DC) Druce (FO37/99)
Leucopogon conostephioides DC (FO43/99)
Leucopogon dielsianus E Pritz (FO8/99)
Leucopogon fimbriatus Stschegl (RD6372)
Lysinema ciliatum R Br (RD6529)

Primulaceae

* *Anagallis arvensis* L (LWS1330)

Loganiaceae

Logania flaviflora F Muell (LWS1261)
Logania tortuosa DA Herb (LWS1301)

Lamiaceae

Hemiandra incana Bartl (RD6317)
Microcorys sp stellate (A Strid 21885) (LWS1267)

Scrophulariaceae

* *Parentucellia latifolia* (L) Caruel (RD6555)

Rubiaceae

Opercularia spermacocea Juss (RD6371)
Opercularia vaginata Juss (LWS1255)

Goodeniaceae

Anthotium odontophyllum Sage (LWS1335)
Dampiera juncea Benth (RD6444)
Dampiera lavandulacea Lindl (RD6453)
Dampiera lindleyi de Vriese (LWS1299)
Dampiera sacculata Benth (RD6443)
Goodenia berardiana (Gaudich) Carolin (FO316/99)
Goodenia caerulea R Br (LWS1337)
Goodenia glareicola Carolin (FO333/99)
Goodenia helmsii (F Pritz) Carolin (LWS1369)
Goodenia pulchella Benth (LWS1372)
Verreauxia reinwardtii (de Vriese) Benth (LWS1368)

Stylidiaceae

Levenhookia pusilla R Br (RD6547)
Levenhookia stipitata (Sond) F Muell (LWS1312)
Stylidium dichotomum DC (LWS1323)
Stylidium leptophyllum DC (LWS1265)
Stylidium luteum subsp *clavatum* Carlquist (LWS1264)
Stylidium piliferum R Br subsp *piliferum* (LWS1380)
Stylidium repens R Br (LWS1324)

Asteraceae

* *Arctotheca calendula* (L) Levyns (RD6542)
Argentipallium niveum (Steetz) Paul G Wilson (LWS1294)
Blennospora drummondii A Gray (RD6541)
Brachyscome pusilla Steetz (RD6551)
Ceratogyne obionoides Turcz (RD6548)
Cotula coronopifolia L (LWS1298)
Gnephosis tenuissima Cass (LWS1257)
Helichrysum leucopsideum DC (LWS1252)
* *Hypochaeris glabra* L (LWS1377)
Lagenophora huegelii Benth (FO158/99)
Lawrencella rosea Lindl (RD6449)
Millotia tenuifolia Cass var *tenuifolia* (RD6545)
Olearia rudis (Benth) Benth (RD6552)
* *Osteospermum clandestinum* (Less) Norl (FO237/99)
Podolepis capillaris (Steetz) Diels (LWS1297)
Podolepis lessonii (Cass) Benth (RD6558)
Podotheca angustifolia (Labill) Less (RD6544)
Pterochaeta paniculata Steetz (LWS1305)
Rhodanthe manglesii Lindl (RD6559)
* *Sonchus oleraceus* L (LWS1290)
* *Ursinia anthemoides* (L) Poir (RD6546)
Waitzia acuminata Steetz var *acuminata* (LWS1353)

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Long-term changes in vigour and distribution of *Banksia* and *Melaleuca* overstorey species on the Swan Coastal Plain

P K Groom[1], R H Froend[1], E M Mattiske[2] & R P Gurner[1]

[1]Centre for Ecosystem Management, School of Natural Sciences,
Edith Cowan University, 100 Joondalup Drive, Joondalup WA 6027

email: p.groom@ecu.edu.au   r.froend@ecu.edu.au

[2]Mattiske Consulting Pty Ltd, PO Box 437, Kalamunda WA 6076

email: admin@mattiske.com.au

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Abstract

Long-term changes in vigour and distribution of the dominant *Banksia* (5 species) and *Melaleuca* (1 species) overstorey species were examined within four vegetation transects overlying the Gnangara Groundwater Mound, a superficial unconfined shallow aquifer on the northern Swan Coastal Plain, Western Australia. All transects were positioned along topographical gradients and monitored over a 20-30 year period. The two co-dominant overstorey species (*Banksia attenuata* and *B. menziesii*) inhabited a range of topographical positions within the landscape, from dune crest to low lying areas, with only *B. attenuata* increasing its distribution (moving further downslope) within the transects over time. Both species displayed a reduction in vigour, as indicated by foliage condition, during the monitored period. Species commonly inhabiting low-lying winter-wet areas (*e.g. Banksia littoralis, Melaleuca preissiana*) showed the greatest loss of tree vigour in response to declining groundwater levels, with *B. littoralis* replaced by the more drought tolerant *B. prionotes. M. preissiana* populations were overall more resilient to altered groundwater regimes, responding over a much greater time period (many decades) than *B. littoralis* (<10 years). Overall, changes in species distribution and vigour were primarily caused by long-term declines in groundwater levels resulting from the cumulative effects of abstraction and below average annual rainfall (low groundwater recharge). Long-term distribution trends and overall observed reductions in population vigour within the transects may be a function of the species' dependency on groundwater to fulfil its water requirements. This may explain declining vigour and tree numbers of *B. ilicifolia* on the Gnangara Groundwater Mound, as this species is considered an important indicator of significant long- and short-term reductions in groundwater levels.

Keywords: *Banksia* woodland, *Melaleuca*, groundwater, Gnangara Groundwater Mound, rainfall

Introduction

A large proportion of the total water usage (~70%) by metropolitan Perth is obtained from groundwater resources, which is used to supply domestic, industrial and agricultural water requirements (Davidson 1995). The Gnangara Groundwater Mound is the larger of the two superficial unconfined shallow aquifers from which water is abstracted. Groundwater abstraction lowers the water table, and may have a detrimental impact on ecosystems dependent on shallow groundwater (Kite & Webster 1989). To facilitate adaptive management of groundwater resources and conservation of native groundwater-dependent vegetation, we require greater knowledge of vegetation response to changes in groundwater levels than is currently available.

In the context of future long-term reductions in groundwater levels caused by abstraction and decreasing rainfall recharge, several authors have commented on potential changes in the overstorey composition of the *Banksia* woodlands overlying the Mound. In particular a shift in composition towards species capable of tolerating extended periods of drought has been predicted and/or observed (Havel 1975; Aplin 1976; Heddle 1980; Dodd & Heddle 1989), especially in low-lying areas where groundwater levels are typically at their shallowest. This could mean a decrease in abundance and distribution of drought sensitive tree species that fringe the many wetlands (*e.g. Banksia littoralis* R Br, *Melaleuca preissiana* Schauer) or inhabit low lying areas (*e.g. B. ilicifolia* R Br), and their replacement by the more drought tolerant *B. attenuata* R Br or *B. menziesii* R Br (Havel 1975; Muir 1983). Muir (1983) also suggested that *B. menziesii* could be expected to replace *B. attenuata* on the dune slopes, where local groundwater levels are at their deepest.

To examine changes in vegetation structure and composition, a triennial monitoring regime was established in 1976 by the Western Australian Forestry Department, and later the Water Authority of Western Australia, to coincide with the development of abstraction bore fields on the Mound. This monitoring program utilized existing and new transects that were positioned along topographical gradients (see Heddle 1980), starting at a localized depression and ending at a high point in the landscape, usually a dune crest. Existing transects were established in 1966 as part of an assessment of site suitability for pine plantations (Havel 1968).

This paper utilizes parts of the resulting datasets to investigate changes occurring between 1966 and 1996 in distribution and potential vigour of the dominant *Banksia* and *Melaleuca* overstorey species present within four transects, and complements a similar study involving myrtaceous shrub species (Groom *et al.* 2000a). In particular, this paper examines the changes in overstorey distribution and vigour as a function of the transect's hydrological and fire history and presence of plant disease, particularly the dieback fungus *Phytophthora cinnamomi*.

Methods

Study area

The Gnangara Groundwater Mound (Fig 1) underlies seasonal and permanent wetlands, pine plantations and extensive areas of native *Banksia* woodlands of the Swan Coastal Plain, north of Perth, Western Australia. The Mound is one of two large, shallow unconfined aquifers on the Plain that are recharged directly by rainfall. The distribution of vegetation on the northern Swan Coastal Plain is predominately determined by the underlying landforms, soils, depth to water table and climatic conditions (Heddle *et al.* 1980; Cresswell & Bridgewater 1985). The vegetation of the three main dune systems (Bassendean, Spearwood and Quindalup) is dominated by an evergreen *Banksia* overstorey with occasional *Eucalyptus* and *Allocasuarina* stands, and an understorey consisting mainly of low shrubs from the Myrtaceae, Fabaceae and Proteaceae. The many seasonal damplands, swamps and permanent wetlands are often fringed by *Banksia littoralis* and *Melaleuca* tree species with a variable understorey consisting of species mainly from the Cyperaceae, Juncaceae and Myrtaceae (Semeniuk *et al.* 1990). The northern Swan Coastal Plain experiences a dry mediterranean-type climate (Beard 1984), with hot dry summers (December-March) and cool wet winters (June-August) with a long-term average of 870 mm annual rainfall recorded at the Perth meteorological station.

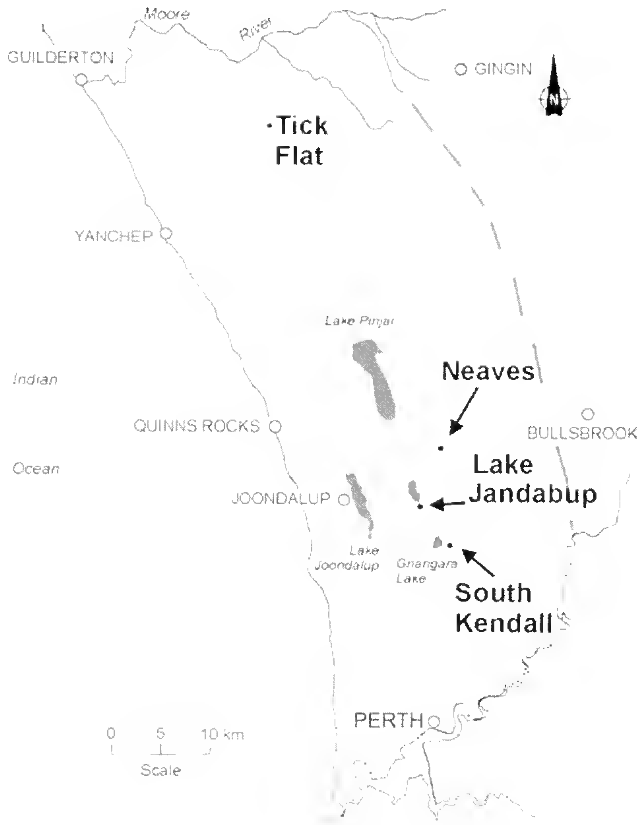

Figure 1. Location of four long-term vegetation monitoring transects (Lake Jandabup, Neaves, South Kendall, Tick Flat) on the northern Swan Coastal Plain, in relation to town sites and local lakes. Eastern boundary of coastal plain is represented by a dashed line. Underlying this section of the Plain is the Gnangara Groundwater Mound, a superficial unconfined shallow aquifer.

Vegetation transects

Long-term vegetation monitoring of the *Banksia* woodlands overlying the Gnangara Groundwater Mound initially started in 1966 when four transects (named Neaves, South Kendall, Tick Flat and West Gironde) were established to provide an ecological assessment of suitable sites for establishing pine plantations (Havel 1968). These four transects were re-monitored in 1976 (Heddle 1980), when it was decided that these four transects would provide useful data on the floristic composition on the Mound prior to the commencement of public groundwater abstraction. In 1976, transects adjacent to Lake Jandabup were established, in response to concerns about the effects of decreasing lake levels on the fringing native vegetation. All transects occur within conservation reserves or on crown land and are positioned along a topographical gradient, commencing at a localized depression (dampland or wetland) and ending at a high point in the landscape, usually a dune crest.

From 1976, the plant species occurring within these transects were surveyed every 2-3 years during September and October of the designated year, and the transects are continually monitored as part of the current groundwater management program. The only exception is the West Gironde transect which was partially cleared for urban development in 1987. Neaves (31° 42′ S, 115° 53′ E), Lake Jandabup (31° 45′ S, 115° 51′ E) and South Kendall (31° 47′ S, 115° 52′ E) transects are located on the southern part of the Mound (Fig 1) within 10 km of each other and within close proximity (<2 km) to groundwater production bores. The Tick Flat transect (31° 24′ S, 115° 42′ E) is >25 km from the nearest production bore. Transects varied from 200 to 520 m in length, and were subdivided into two parallel bands (each 20 m wide) down the length of the transect. Each band was further subdivided into 20 x 20 m plots for overstorey assessment. For this paper, data from the two longitudinal parallel bands that formed each transect were pooled because of their topographical and groundwater depth similarity. Thus, instead of using data from two adjacent 20 x 20 m plots along the same topographic position as separate entities, overstorey data was combined to form one 20 x 40 m plot.

For each assessment, the number of stems at breast height (~1.5 m) and total number of adult plants per overstorey species within a plot were recorded. Adult plants were defined as those plants ≥ 1.5 m in height and showing signs of being reproductively active. For individual trees, a subjective assessment of potential vigour was recorded for each major branch at breast height based on foliage condition. Three categories of potential vigour were used; healthy (majority of foliage was green), stressed (majority of foliage was orange/brown), or dead (entire foliage was orange/brown or no leaves present). Because any one plant can have multiple branches at breast height, each individual tree was categorised as healthy, stressed or dead based on the condition of the majority of branches. Trees recorded as dead were still classified as dead in subsequent years unless they had fallen over.

To examine the relatively long-term changes in overstorey vigour and distribution occurring within the transects, only data collected at approximately 10 year intervals (1966, 1976, 1987 and 1996) were assessed. In contrast to the other transects, the initial monitoring of overstorey species at Lake Jandabup transect commenced in 1976. The transect was re-monitored in 1987, but unlike the other transects was not remonitored in 1996. In the absence of 1996 data, data obtained from monitoring in 1993 was used for comparing long-term changes in species distribution and vigour.

Hydrological data, fire history and dieback

Relating species distribution and changes in adult abundance to past groundwater levels experienced by the transects was difficult because past groundwater levels within the transects have not been monitored. Instead, species response to past groundwater regimes were analysed using hydrographical data (1975 onwards) from the closest groundwater monitoring bore to the transects (usually up to 1 km away from a transect) from data provided by the Water and Rivers Commission. Current groundwater levels within the transects were measured in June 1998 with a hand auger, every 30 m along the transects up to a depth of 10 m, the limit of the soil auger used.

Soil samples collected from each transect were analysed by the Western Australian Department of Conservation and Land Management for the presence of the dieback fungus *Phytophthora cinnamomi* (see Shearer & Dillon 1995 for details), a common cause of death in *Banksia* woodlands on the Swan Coastal Plain (Shearer & Hill 1989; Shearer & Dillon 1996). The fire history of each transect between 1966-1996 was obtained from maps and microfiche records of the Department of Conservation and Land Management, Western Australia. Annual rainfall data (1960 onwards) were obtained from the Western Australian Bureau of Meteorology, for the Perth meteorological station.

Results

Neaves transect

Between 1976 and 1996, there was an overall reduction in percentage healthy trees of the five *Banksia* and one *Melaleuca* species occurring within all transects (Fig 2). Within the Neaves transect, the lowest proportion of healthy trees for all species was recorded in 1987, coinciding with a decrease in the number of healthy trees for all species except *B. attenuata*. The proportion of healthy trees increased by 1996, although not to the same level as in 1976. Between 1976 and 1996, the greatest reduction in percentage healthy trees was for *B. menziesii* (40%), which was the only species to have a substantial reduction in number of healthy plants over this period.

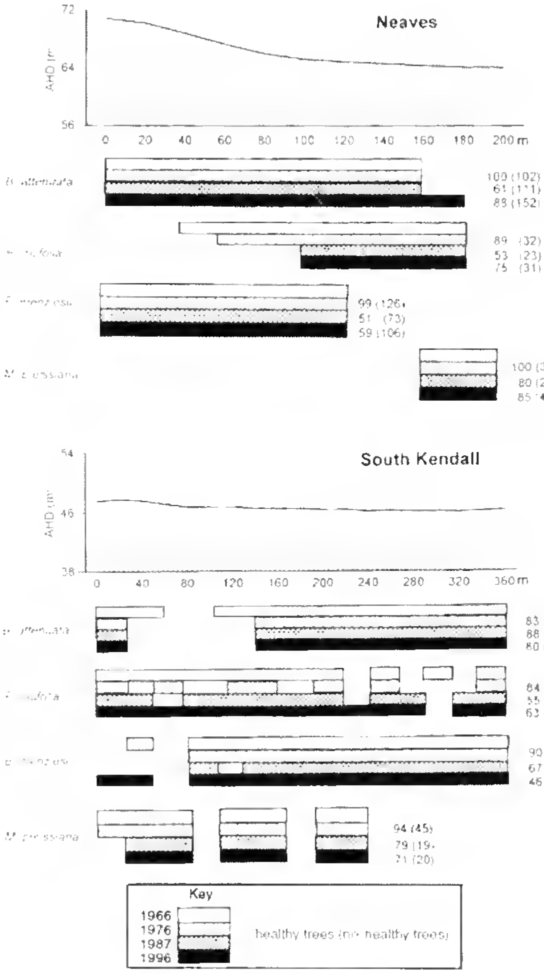

Figure 2. Distribution and vigour of overstorey species within the Neaves and South Kendall transects. Data shown for 1966 (open bar), 1976 (light hatching), 1987 (cross-hatching) and 1996 (solid bar) (see insert). Numbers represent the percentage of trees for a given species that were 'healthy' (majority of the foliage was green) when monitored with the total number of healthy trees in parenthesis. Transect topography (Australian Height Datum, AHD) and groundwater depth profiles (single hatching) are provided for comparative purposes. Groundwater data were collected in August 1998.

By 1996, *B. attenuata* increased in distribution within the Neaves transect, occurring further downslope. *B. ilicifolia* decreased in distribution, losing trees that had previously occurred in the upper and midslope regions of the transect. Despite the restricted distribution of *B. ilicifolia*, the number of healthy trees present did not significantly change, although there was considerable population re-structuring. The distribution of *B. menziesii* and *M. preissiana* did not change throughout the 30 year monitoring history. In 1998, depth to groundwater within the transect varied from 4 m (lower slope) to >10 m (dune crest).

South Kendall transect

The South Kendall transect is different from the other transects described in this paper, with most of the transect represented by a flat low lying sandplain, rising to a relatively small dune crest (Fig 2). In 1998, depth to groundwater within the transect varied from 3.7 m (lower slope) to 5.0 m (dune crest). The distribution of *B. ilicifolia* and *B. menziesii* varied from year to year, with their distribution in 1996 similar to that recorded in 1966. *M. preissiana* occurred on the South Kendall dune crest in 1966 and 1976, but was not recorded thereafter. In 1966 *B. attenuata* occurred on the dune crest and associated slopes, as well as most of the lower lying areas of the transect. By 1976, this had contracted to its current distribution.

The number of healthy *B. attenuata* trees doubled from 1976 to 1996, and the overall percentage of healthy trees remained relatively high (80-88%). In contrast, the number of healthy *M. preissiana* trees and percentage of healthy trees decreased over the same time period. Both *B. ilicifolia* and *B. menziesii* had a decrease in percentage healthy trees between 1979 and1996, although the number of healthy *B. ilicifolia* trees increased.

Tick Flat transect

Tick Flat had the greatest change in population vigour over time, with only 8-35% of the main overstorey species trees in 1996 categorised as healthy, compared with 67-100% in 1976 (Fig 3). The exception was *B. prionotes*, with 72% of trees categorised as healthy. *B. prionotes* was the only species at Tick Flat to significantly increase in distribution within the transect since 1976. *M. preissiana* and *B. littoralis* had the greatest reduction in population size and vigour. Within the lower slope section of the Tick Flat transect, the number of healthy *B. littoralis* trees fell from 67 to 2 between 1976 and 1996. Further upslope (within the middle slope section of the transect) the number of healthy *M. preissiana* trees fell from 20 to 2 over the same 20-year period. In 1996, the two remaining healthy trees of *M. preissiana* and *B. littoralis* represented 8-10% respectively of the existing populations. *Banksia ilicifolia* and *B. menziesii* also had a significant reduction in number of healthy trees present within the transect. *B. menziesii* was the only species to show a relatively substantial increased in distribution within the transect since 1966; *B. littoralis* was the only species to have had a substantial reduction in distribution over the same time period. In 1998, depth to groundwater within the transect varied from 6.9 m (lower slope) to >10 m (dune crest).

Lake Jandabup transect

At Lake Jandabup, all overstorey species occurred on the mid- and upper slopes of the transect, where groundwater depth varied from 1.5 m (midslope) to 6 m (upper slope) as measured in June 1998 (Fig 3). All species, except *B. ilicifolia*, displayed a decrease in percentage and number of healthy trees within the transect between 1976-1993. For *B. ilicifolia*, the number of healthy trees increased 3-fold, accounting for 71% of the population by 1996. Distribution of the four most common species at Lake Jandabup did not change significantly over the monitoring period.

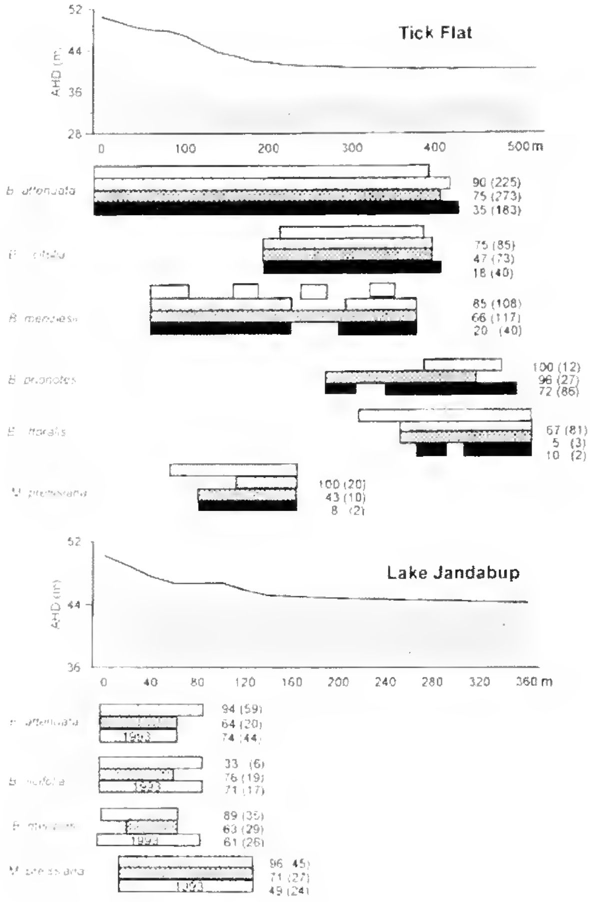

Figure 3. Distribution and vigour of overstorey species within the Tick Flat and Lake Jandabup transects. Data shown for 1966 (open bar), 1976 (light hatching), 1987 (cross-hatching) and 1996 (solid bar). For Lake Jandabup 1993 data was used in the absence of 1996 data. See Fig 2 for further details.

Hydrology

Similar annual hydrological cycles were observed at the closest monitoring bores to the four transects. Maximum groundwater depth occurred in March-April resulting from a 3-4 month period of summer drought (Fig 4). Annual groundwater recharge is dependent entirely on rainfall, occurring during the winter and spring months (April-October).

Since 1976, groundwater monitoring bores near the four vegetation transects have shown a gradual decrease in groundwater levels (Fig 4A), coinciding with periods of below average rainfall (Fig 4B). This decrease was greatest near Neaves and Tick Flat, where the maximum groundwater drawdown during the 20-year period was approximately 2 m, compared with less than 1 m for South Kendall and Lake Jandabup. Between 1979-1985, Perth experienced several years of below average (<870 mm) rainfall (Fig 4B) associated with an overall decrease in groundwater levels ranging from 0.2 m (Neaves) to 0.8 m (Tick Flat).

Comparing 1976-1986 with 1987-1996 groundwater data, mean annual minimum groundwater depths decreased by 1.2 m for Neaves but only 0.1 m at Tick Flat. In

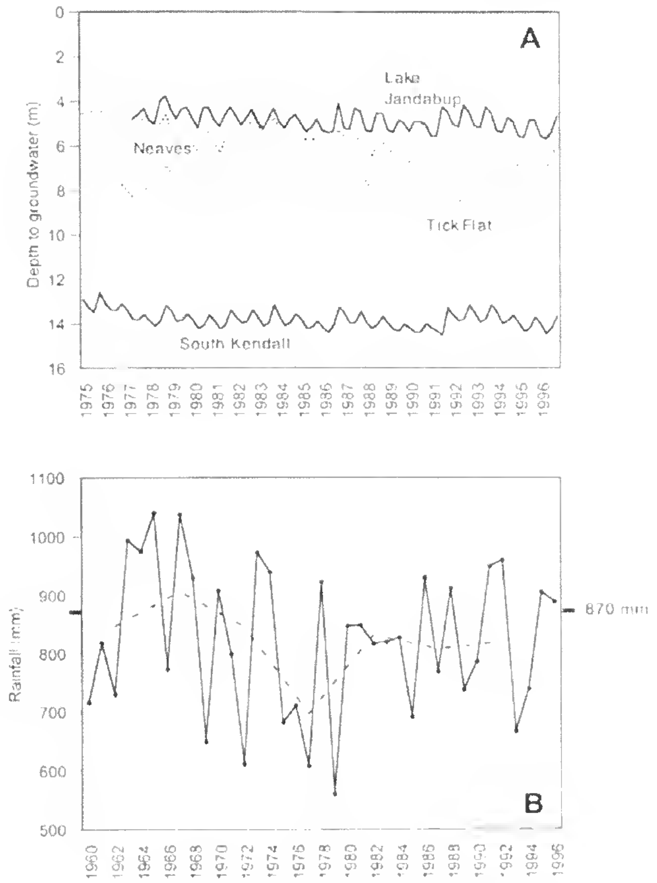

Figure 4. A: Hydrographs from the closest groundwater monitoring bores to the four vegetation transects. **B**: Total (solid line) and 5 yearly mean (dashed line) rainfall for Perth for 1960-1996. Perth's long term average annual rainfall is 870 mm.

comparison, groundwater depths decreased by 0.2 and 0.4 m at South Kendall and Lake Jandabup respectively. Below average rainfall in 1989 and 1990 (750 and 790 mm respectively), may have caused a decrease in water levels in 1991 at all four monitoring bores as a direct result of poor groundwater recharge.

Fire history and dieback

Fires have been relatively uncommon, with only two or three fires occurring within each transect between 1966-1996. The most recent fire event within the four transects occurred during 1980-83 (Neaves, South Kendall, Lake Jandabup) and 1985-86 (Tick Flat). The Lake Jandabup transect experienced two fires within 5 years of establishment and has not been burnt since. South Kendall was the only transect to record the presence of *Phytophthora cinnamomi* throughout its monitoring history, with the fungus occurring predominantly within the low-lying areas (Heddle 1980).

Discussion

Long-term monitoring of the native vegetation overlying the Gnangara Groundwater Mound have shown that the floristic composition has been changing continuously as a result of periods of below average annual rainfall, spread of pathogens, impacts of fire, prolonged summer drought and groundwater abstraction (Heddle 1980; Dodd & Heddle 1989; Groom *et al.* 2000b). Of these, neither fire nor *P. cinnamomi* infection can be viewed as having had any significant influence on the distribution and overall vigour/health of *Banksia* and *Melaleuca* overstorey populations within the four study transects, with *P. cinnamomi* detected only within South Kendall. Fire has had a relatively limited impact on vigour, as it has been relatively infrequent (2 or 3 fires during the 30 years) within the transects, although the ability of a particular species to survive a fire depends on the fire's intensity and frequency, and season of burn (Hopkins & Griffin 1989; Bell *et al.* 1992). All overstorey species investigated in this paper recover post-fire via epicormic shoots, except *B. prionotes* which is killed by fire.

Current distribution trends of overstorey species on the Mound may be a function of their groundwater dependency and water-use requirements. The distribution of a species within the landscape is closely associated with groundwater depth, and hence topography, whereby species which rely almost exclusively on groundwater throughout the year (e.g. *Banksia littoralis*, S Zencich, Edith Cowan University, personal communication) typically occur in areas where groundwater is relatively shallow and easily accessible. Current work (S Zencich & R Froend, Edith Cowan University, personal communication) shows that during periods of summer drought, species restricted in distribution by groundwater depth (*e.g. B. ilicifolia*, 2-10 m) are more reliant on groundwater sources than species inhabiting a wider range of groundwater depths (*e.g. B. attenuata*, 2->30 m). If reductions in groundwater levels observed over the past 20 years continue, as a result of below average rainfall and increased groundwater abstraction, groundwater requirements may ultimately determine the topographical distribution of the Mound's overstorey species.

Of all the transects examined in this paper, Tick Flat showed the greatest overall reduction in tree vigour (based on foliage/canopy coloration) over the 30 year monitoring period. Prior to the 1960s, the lower section of Tick Flat was a swamp, which has only recently been filled in naturally with sand from the surrounding dunes (Heddle 1980). Filling in of swamps and damplands is a common scenario impacting other areas of the Swan Coastal Plain, and is primarily a result of decreasing groundwater levels (Muir 1983). It is within such low-lying areas that the greatest loss of tree vigour occurred at Tick Flat, particularly of *B. littoralis* and *M. preissiana*, two species favouring winter-wet locations (Havel 1968).

The combination of reduced recharge and regional drawdown are the most likely cause for the observed decline in health and population numbers of *B. littoralis* at Tick Flat. This population has been gradually replaced by the more drought-tolerant *B. prionotes* (Heddle 1980). The ability of *B. prionotes* to tolerate falling groundwater levels may be due to its fast-growing nature and a deep, dimorphic root system (Pate *et al.* 1998). *B. prionotes* has been shown to access groundwater during the dry summer period via its main tap root, switching to rainfall and soil moisture acquired from lateral and other shallow roots during the wet seasons (Dawson & Pate 1996). This doesn't occur in *B. littoralis*, as both lateral and tap roots access groundwater throughout the year (S Zencich & R Froend, Edith Cowan University, personal communication).

Groundwater levels measured at the closest long-term monitoring bore to Tick Flat have decreased steadily since the 1970s, which is most likely a direct result of poor recharge caused by extended periods of below average rainfall (Davidson 1995). However, despite Tick Flat not being directly influenced by nearby/local groundwater abstraction, we cannot discount the regional effect of abstraction on Tick Flat's groundwater levels. All transects displayed an overall reduction in overstorey vigour regardless of their proximity to abstraction borefields, with the greatest changes in vigour occurring in transects that on average have a current groundwater depth greater than 6 m (*i.e.* Neaves and Tick Flat). Within these two transects groundwater levels have decreased by up to 2 m over a 30-year period, resulting in reduced groundwater availability to overstorey and understorey species.

Summer groundwater dependency may also explain the decline in proportion of healthy *B. ilicifolia* trees at Tick Flat and the loss of individuals on the midslope of Neaves, as both transects have been subjected to relatively high levels of groundwater drawdown. Within the short-term (<10 years) declining *B. ilicifolia* populations can be attributed to poor groundwater recharge, caused by excessive localised groundwater abstraction and/or below average annual rainfall (Groom *et al.* 2000b). In particular up to 80% reduction in *B. ilicifolia* tree numbers has been observed when groundwater levels fell by 2 m between two consecutive summers, in conjunction with extremes in summer temperature (Groom *et al.* 2000b). Reductions in the vigour and population structure of *B. ilicifolia* is considered (*e.g.* Havel 1968; Heddle 1980; Muir 1983) an important indicator of significant long- and short-term reductions in groundwater levels on the Mound and other shallow aquifers on Western Australia's Swan Coastal Plain, although further studies are required to explain the significance and potential impacts of declining groundwater levels on this drought sensitive species.

Unlike the *Banksia* species, *Melaleuca preissiana* showed no change in distribution within the transects over the 30 year period and was typically confined to the low-lying areas. It has previously been concluded that the response of *M. preissiana* populations to altered water regimes occurs over a much greater period of time than for co-occurring species, and is measured in order of decades (Froend *et al.* 1993). Successful seedling recruitment and establishment is essentially episodic in nature, reliant on the combination of seed release, high soil moisture levels and/or flooding events (Froend *et al.* 1993). In contrast, adult plants are more tolerant of water regime extremes (from seasonal flooding to moderately deep groundwater levels), and are often are the only remaining signs of the location of former swamps/damplands. Because *M. preissiana* populations are relatively restricted in their topographical distribution on the Mound, it is assumed that they are groundwater-dependent although their groundwater requirements have yet to be quantified. As for *Banksia* species, the decreased vigour of *M. preissiana* populations over time is most likely a result of decreasing groundwater levels, particularly in areas that once had shallower groundwater levels (*i.e.* Tick Flat).

Muir (1983) suggested that as groundwater levels continue to decline on the Gnangara Groundwater Mound, "*B. menziesii* can be expected to replace *B. attenuata* on dune slopes, being better adapted to drier conditions. *Banksia attenuata* will probably persist in damper areas but *B. ilicifolia*, being very dependent on moisture availability, may succumb completely." However, Muir's concept of overstorey succession in response to groundwater drawdown has not been observed within the study transects, although the loss of *B. ilicifolia* and the potential 'replacement' by *B. attenuata/B. menziesii* has been observed elsewhere on the Mound (Groom *et al.* 2000b). Between 1966 and 1996, *B. attenuata* increased its distribution (at Neaves, Tick Flat and Lake Jandabup), moving further down-slope to lower groundwater depths. These areas may have previously experienced shallow groundwater depths. Soil moisture levels in these lower slope regions have become progressively drier as groundwater levels decreased over time (Heddle 1980) providing a more suitable environment for *B. attenuata* recruitment and long-term survival. As previously mentioned, decreasing groundwater levels may also account for the loss of *B. ilicifolia* from the midslope of Neaves transect, although it is unlikely that *B. ilicifolia* has been 'replaced' by *B. attenuata* or any other overstorey species. The 'replacement' of *B. attenuata* by *B. menziesii* on the dune slopes has not occurred within the study transects, although there is some evidence to suggest that *B. menziesii* is more drought tolerant than *B. attenuata* (Groom *et al.* 2000b), despite exhibiting similar seasonal water relations (Dodd & Bell 1993). Both species co-dominate the *Banksia* woodlands of the Swan Coastal Plain, inhabiting a range of topographical positions within the landscape, and are know to be groundwater-dependent at groundwater depths of 6-7 m (Dodd & Bell 1993), but do not have access to groundwater at deeper depths of >10 m (Farrington *et al.* 1989).

Sustainable management of Perth's shallow groundwater resource must be a major objective to ensure adequate supply to the urban and industrial environments as well as maintaining the intricate link with groundwater-dependent vegetation and wetlands. Management of water extraction is based on a water resources allocation process, which includes the determination of environmental water requirements (Anon 1992). These are determined by identification of values and/or beneficial uses of water-dependent components of the environment, and the establishment of water requirements for ecosystem protection. For the overstorey component of *Banksia* woodlands on the Gnangara Groundwater Mound, identifying environmental water requirements on a plant-community basis needs to take into account the underlying topography and watertable levels, the impact of local or regional groundwater drawdown caused by abstraction, and the impacts of reduced groundwater recharge resulting from below average rainfall. The decreasing trend in average rainfall currently being experienced may be a part of a longer cycle that should show an increasing trend in the future (Davidson 1995). However, it has been predicted that by

2030, Perth may experience up to 10% less winter rainfall, and 5% more, or less, summer rainfall. By 2070, winter rainfall may decrease by 20% with summer rainfall increasing/decreasing by 10% (Anon 1996). Future changes in the groundwater recharge rate may ultimately result in a decline in population vigour and restricted distributions of those overstorey species that are dependent on relatively shallow groundwater sources.

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Flora and vegetation of the Eastern Goldfields Ranges: Part 4. Highclere Hills

N Gibson & M N Lyons

Science Division, Department of Conservation and Land Management, Wildlife Research Center,
PO Box 51 Wanneroo, WA 6065

email: neilg@calm.wa.gov.au mikel@calm.wa.gov.au

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Abstract

A study of the flora and plant communities of the Highclere Hills (which lie some 25 km NNW of Bullfinch) recorded 242 taxa in the spring of 1996. Of these, 217 taxa were native and 25 were weeds. The flora list includes *Acacia xerophila* var *brevior*, *Stenanthemum newbeyi* and *Tricoryne tuberosa* ms, which represent significant range extensions for these taxa. No endemic taxa were found on the Highclere Hills. Five community types were defined from 45 quadrats spread across the Hills. The distribution of these community types appears to be primarily related to edaphic factors that were largely independent of topographic position. None of the five community types is known from conservation reserves. The vegetation patterning of the Highclere Hills is not as complex as that found on nearby ranges due to a more subdued topography. There has been widespread impact on the vegetation of the Highclere Hills by mineral exploration and mining and there is an urgent need to improve environmental management of mineral exploration activities.

Keywords: vegetation, flora, Highclere Hills, survey

Introduction

The Highclere Hills are composed primarily of Archaean (2500 - 3700 MY old) mafic and ultramafic rocks (commonly termed greenstones) and small outcrops of Archaean banded ironstones. Greenstone and banded ironstone ranges are one of the common landforms of the Eastern Goldfields and extend from the Highclere Hills in the west to the Roe Hills some 300 km further east and stretch north-south over 800 km. The Highclere Hills lie some 25 km NNW of Bullfinch, forming part of the western-most greenstone belt in this region. Despite the greenstone ranges being heavily exploited for minerals over the past hundred years, a detailed knowledge of the vegetation and flora of the region is still lacking. The aim of this series is to report on detailed floristic studies on individual ranges to address this deficiency (Gibson *et al.* 1997; Gibson & Lyons 1998ab), and this paper reports recent survey work undertaken in the Highclere Hills.

Study Locality

The geology of the study area (Fig 1) has been mapped and described in detail in Jackson 1: 250000 sheet (Chin & Smith 1983) and the geology and landforms have been summarised by Newbey (1985). The major landscape features are controlled by the Archaean granites, which underlie most of the study area and have weathered into gently undulating plains and broad valleys covered by Tertiary soils (< 65 MY old). Trending NNW to SSE are linear bands of Archaean greenstone (mafic and ultramafic lithologies) and banded ironstone formations that were formed from lacustrine deposits of iron oxides and quartz sand. The Highclere Hills are part of the Bullfinch greenstone belt (Chin & Smith 1983). Widespread laterization of the granites and greenstones is believed to have occurred during the Cainozoic (the last 65 MY). The net result is a very subdued landscape given the long period of erosion this area has undergone. The banded ironstone formation in the Bullfinch belt is relatively thin (< 10 m) unlike that of the Koolyanobbing belt (25 km to the east), which can be 100 m thick (Chin & Smith 1983).

The climate of the region is semi-arid mediterranean with warm winters and hot summers. Mean annual rainfall at Bullfinch (25 km SSE) is 296 mm, but seasonal variation is high. The driest year on record was 1940 with 122 mm, and the wettest was 1963 with 618 mm. Most rain falls in winter and is generally associated with frontal activity from May through August. Summer falls (to 100 mm) are highly erratic and result from thunderstorms. Heaviest falls are associated with rain bearing depressions forming from tropical depressions (Newbey 1985; Anon 1988). The closest meteorological station for which temperature data are available is Southern Cross (60 km SE) where mean maximum temperature is highest in January (34.5 °C) with December through March recording mean annual temperatures above 30 °C with the record highest daily temperature of 45.6 °C. Lowest mean minimum temperatures of below 5 °C are recorded in July and August. Lowest daily minimum temperature on record was -3.8 °C.

The Highclere Hills lie in the South Western Interzone close to the border with the Avon botanical region (Wheatbelt; Beard 1990). The interzone is generally dominated by eucalypt woodlands and shrublands on yellow sandplains and marks the transition in vegetation from the species-rich south-west to the more arid communities of the desert regions. Beard (1972) first described the major structural formations of this area that he grouped into vegetation systems. He defined the vegetation of the greenstones and banded ironstones of the Highclere Hills as forming part of the Highclere System. This System

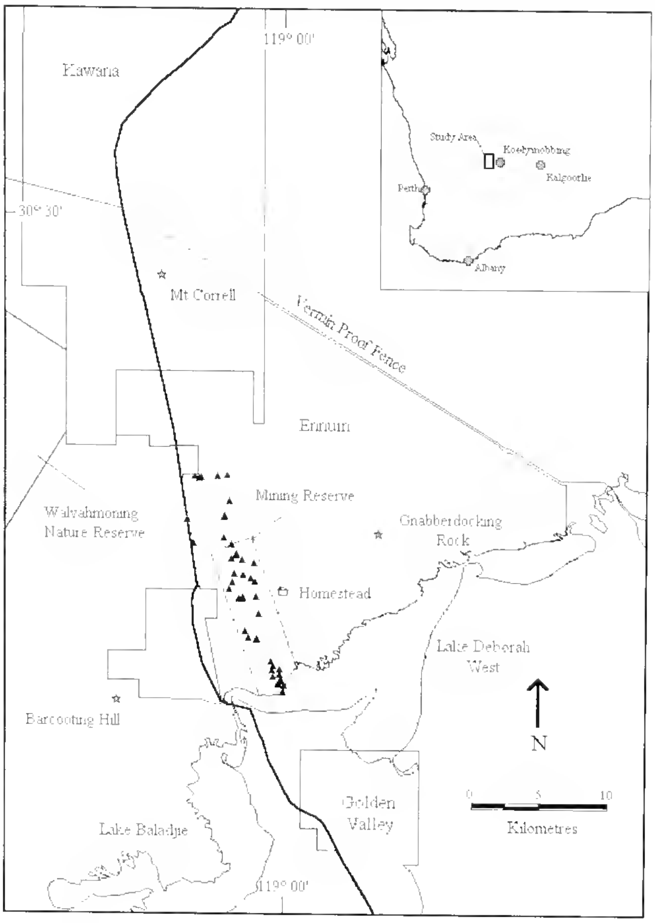

Figure 1. Location of the Highclere Hills study area. Individual quadrats are shown by solid triangles.

also encompasses the greenstone and ironstone areas from near Mt Correll south to Bullfinch. In this system he described the small ironstone outcrops as being covered by thickets of *Acacia quadrimarginea* with a few scattered trees of *Casuarina pauper*, *Brachychiton gregorii* and *Pittosporum phylliraeoides* with *Dryandra arborea* (which is common on the banded ironstone of the Bungalbin System to the east) being entirely lacking. The hilly country of the greenstone areas were described as being covered by woodlands of *Eucalyptus longicornis* and *E. corrugata* with an understorey of saltbush *Atriplex hymenotheca* and *A. nummularia*, while on the flanks of the hills *Eucalyptus salmonophloia*, *E. salubris* and *E. loxophleba* woodlands are found.

In the Jackson-Kalgoorlie report of the eastern goldfields regional survey, Newbey & Hnatiuk (1985) described the vegetation of the Highclere Hills under the heading 'Undulating Plain (greenstone)'. They stated that "the Highclere Hills support mainly *Eucalyptus corrugata* Low Woodland on low stony ridges, and *Eucalyptus salmonophloia* Woodland and *E. salubris* Low Woodland on the colluvial flats. Occurring rarely were shrublands of both *Acacia acuminata* and *A.* aff *aneura* on stony rises, and *Eucalyptus longicornis* Low Woodland on the colluvial flats where the soil pH exceed 8.2."

Both Beard's (1972) survey and the later biological survey of the eastern goldfields were undertaken to provide regional overviews. Consequently, the individual ranges were not sampled extensively.

The work reported here covers the section of the Highclere Hill covered by Ennuin Station and the associated mining reserve (Fig 1). Ennuin Station was the first area taken up for grazing in the region with G Lukin and DB Clarkson overlanding sheep from Toodyay in 1871 (Dell 1985) with the station being occupied more or less continuously ever since. Considerable mining and mineral exploration has occurred along the range since the discovery of gold in the Highclere Hills in 1887 (Dell 1985). The grazing rights to the mining reserve that covers part of the Highclere Hills can only be taken up by Ennuin Station (J Gaunlett, Ennuin Station, personal communication).

Methods

Forty-five 20 m x 20 m quadrats were established on the Highclere Hills, its foot slopes and the outwash plain (Fig 1). These quadrats attempted to cover the major geographical, geomorphological and floristic variation found in the study area. Care was taken to locate quadrats in the least disturbed vegetation available in the area being sampled. No attempt was made to undertake detailed sampling of the Tertiary sandplain on the northern boundary of the station nor the adjacent granitic areas (Chin & Smith 1983) although flora lists were compiled from granitic areas abutting the western side of the Hills. Additional records from the Hills were compiled from collections held in the Western Australian Herbarium.

All vascular plants within each quadrat were recorded in October 1996. Data on topographical position, slope, aspect, percentage litter, percentage bare ground, percentage exposed rock, vegetation structure and condition were collected from each quadrat. Topographical position was scored on a subjective five-point scale from ridge tops (1) and upper slopes (2), to midslopes (3), and to lower slopes (4) and valley flats (5). Slope was scored on a one to three scale from flat to steep. Aspect was recorded as one of 16 cardinal directions. Vegetation structure was recorded using Muir's (1977) classification.

All quadrats were permanently marked with four steel fence droppers and their positions determined using a GPS (Trimble, Transpak II). Twenty four soil samples from the upper 10 cm were collected from each quadrat. These were bulked and analyzed for electrical conductivity, pH, total N, total P, percentage sand, silt and clay, exchangeable Ca, exchangeable Mg, exchangeable Na, and exchangeable K (McArthur 1991).

Quadrats were classified according to similarities in species composition of perennial taxa to facilitate comparisons with classifications from other ranges in the area (Gibson *et al.* 1997; Gibson & Lyons 1998ab). The quadrat and species classifications were undertaken used the Czekanowski coefficient and followed by "unweighted pair-group mean average" fusion method (UPGMA; Sneath & Sokal 1973). Semi-strong hybrid (SSH) ordination of the quadrat data was undertaken to show spatial relationships between groups and to elucidate possible environmental correlates with the classification (Belbin

1991). Statistical relationships between quadrat groups for factors such as species richness, soil parameters, slope, and aspect, were tested using Kruskal-Wallis non-parametric analysis of variance (Siegel 1956).

Nomenclature generally follows Green (1985) and current usage at the Western Australian Herbarium. Manuscript names are indicated by "ms". Selected voucher specimens have been lodged in the WA Herbarium.

Results

Flora

A total of 242 taxa (species, subspecies and varieties), representing 217 native and 25 introduced taxa, were recorded from the Highclere Hills. The best-represented families were Asteraceae (48 taxa including 4 weeds), Poaceae (20 taxa including 8 weeds), Myrtaceae (19 taxa), Chenopodiaceae (13 taxa), Mimosaceae (9 taxa), Myoporaceae (8 taxa), and Brassicaceae (8 taxa including 5 weeds). This pattern is typical of the flora of the South Western Interzone (Newbey & Hnatiuk 1985). Good rains were experienced in the winter and early spring of 1996, reflected by the large numbers of annuals and geophytes on the flora list (Appendix 1). The most common genera were *Eucalyptus* (12 taxa), *Acacia* (9 taxa), and *Eremophila* (8 taxa). Grassy weed species were encountered in almost all quadrats, reflecting a long history of grazing.

During the survey new populations of *Stenanthemum newbeyi* were located on small outcrops of banded ironstone and represent a significant range extension. Previously, *S. newbeyi* was believed to be an endemic of the Helena and Aurora Range some 80 km to the north east (Rye 1995).

An unusual species of *Tricoryne* was collected from two populations, one on a banded ironstone ridge and the second on a greenstone ridge. This is the only species in the genus to have a dense many-flowered globular umbel. This taxon will be described as *Tricoryne tuberosa* ms (GJ Keighery, CALM, pers comm).

A significant range extension was also recorded for *Acacia xerophila* var *brevior*. The main area of this taxon's distribution is between Kalgoorlie and Widgiemooltha (Maslin 1999), an outlying population has previously been collected from near South Mt Rankin (MH Simmons 1225), some 60 km SE of the Highclere Hills.

Several areas of granites on the western side to the range were visited during the survey, and six taxa that were not seen on the range were recorded (*Daviesia nematophylla, Eucalyptus capillosa* subsp *capillosa, Eucalyptus celastroides* subsp *celastroides, Frankenia desertorum, Melaleuca haplantha, Wilsonia humilis*).

Vegetation

Only material that could be identified to species level was included in the analysis (*ca* 99% of records). In the 45 quadrats established on the Highclere Hills, 218 taxa were recorded of which 96 were perennial. Twenty nine perennials occurred at only one quadrat. Preliminary analyses showed these singletons had little effect on the community classification and were therefore excluded. As a result the final data set consisted of 67 perennial taxa in 45 quadrats. Species richness ranged from four to 19 taxa per quadrat, with individual taxa recorded from between two and 38 quadrats.

The classification divided the forty five quadrats into two primary groups (Fig 2), the first group which has *Atriplex* spp and *Sclerolaena* spp as common components in the understorey, and the second which generally lacks these taxa (Table 1). Both of these groups can be further subdivided, with a total of five communities being recognized. Within community types 1 and 4, two subgroups could be recognized.

Table 1. Sorted two-way table of the Highclere Hills quadrats showing species occurrence by community type. Quadrats appear as columns, species as rows.

	Community types						
	1a	1b	2	3	4a	4b	5
SPECIES GROUP A							
Abutilon oxycarpum		*		*		*	
Sida atrovirens ms				* *	*	* * *	
Cheilanthes lasiophylla						* * *	
Maireana planifolia		*				*	
Senna artemisioides subsp *filifolia*		* *	*	* *		* *	
SPECIES GROUP B							
Eucalyptus loxophleba				* *			
Eucalyptus oleosa				*	*		
Hakea recurva				*		*	
Sida spodochroma					* *		
SPECIES GROUP C							
Acacia acuminata				* * * * * * * * * * * * * *	* * *		
Cheilanthes austrotenuifolia				* * * * * * * * * * * * * *	* *	* * * * * *	
Casuarina pauper	*			* * * * * * * * *	* *	*	
Eremophila clarkei				* * * * * * * * * * *		* * * * * *	
Eriostemon brucei				* * * * * * * *		* * * * * *	
Sida calyxhymenia	*			* * * * * * * * * * *	*	* * *	
Brachychiton gregorii				* * * * *		* * * *	
Dodonaea inaequifolia				* * * * * *	* * * *	* * * * *	

Prostanthera althoferi subsp *althoferi*				** * *** **		*	
Acacia quadrimarginea				****		*** *	*
Acacia tetragonophylla	*	*		*	*****	* ****	
Scaevola spinescens	* *	**	*	*	****	** ***	
Ptilotus obovatus	* ***	* *		**** * ***	*****	** ***	
Solanum lasiophyllum	*			****** ** **	**	* **	
Rhagodia drummondii	**	* *		***	**	* ***	
Acacia ramulosa				* * *			
Eremophila serrulata				* *******			
Dianella revoluta				*** *		***	
Austrostipa aff *trichophylla*				***		*	
Mirbelia microphylla				* *			
SPECIES GROUP D							
Comesperma integerrimum				*	*	* **	
Olearia pimeleoides					*	*	
Stenanthemum newbeyi						* *	
Eremophila alternifolia					* **	*	
Santalum spicatum					***	*	
SPECIES GROUP E							
Allocasuarina campestris				*			*
Amphipogon strictus				*			*
Melaleuca uncinata				** *			
SPECIES GROUP F							
Alyxia buxifolia				*		*	
Centaurea melitensis	*			*			
Pimelea microcephala				*			*
SPECIES GROUP G							
Acacia erinacea	* **	* *			*		
Eremophila oppositifolia	* *	* * *			*	*	
Atriplex nummularia	******	* * **			**		
Atriplex vesicaria	*** **	******* **			*		
Sclerolaena densiflora	** ***	****** ****			**		
Sclerolaena diacantha	******	***********			** *	*	
Maireana trichoptera	*****	******* **	*		*		
Maireana georgei	****	***** *				*	
Eucalyptus longicornis		****** ** *					
Eucalyptus salubris		**** ****					
Enchylaena tomentosa	** *	****** * *			**	*****	
Austrostipa elegantissima	*** *	*** **** *		** *	** **	**** *	
Austrostipa trichophylla	******	*********	*	******* * ** *	*****	******	
Eucalyptus corrugata	** ***	* **	*		**		
Olearia muelleri	****	****	*		**		
Exocarpos aphyllus	* *	* * **			**		
SPECIES GROUP H							
Amyema miquelii		* *					
Eremophila interstans	**	* * *					
Austrostipa nitida		**					
Eucalyptus salmonophloia		** *					
Sclerolaena fusiformis	*	*					
Chenopodium curvispicatum		* * *			*		
Eremophila scoparia	**	* ***				*	
Santalum acuminatum		* *			*		
Dodonaea stenozyga		* *					
Eucalyptus yilgarnensis		* **					
Eucalyptus sheathiana		** *	*				

Community type 1 is typically eucalypt woodland variously dominated by *Eucalyptus longicornis*, *E. salubris*, *E. salmonophloia* and /or *E. corrugata* with understoreys dominated by chenopods such as *Atriplex* spp, *Maireana* spp, *Sclerolaena* spp as well as other species in species group G (Table 1). This species group is largely lacking from community types 3, 4 and 5 except for the perennial *Austrostipa* spp and *Enchylaena tomentosa*. Within community type 1, quadrats solely dominated by *Eucalyptus corrugata* can be separated (type 1a) from quadrats dominated by *Eucalyptus longicornis*, *E. salubris*, and/or *E. salmonophloia* (type 1b), although *E. corrugata* can co-occur with these species. This division is not correlated with any significant change in the understorey except that *Ptilotus obovatus* appears to be more faithful to type 1a (Table 1).

Community type 2 appears to be a very species poor variant of community type 1. The single quadrat that makes up community type 2 was very species poor (7 taxa) compared to community type 1 (mean 13 taxa/quadrat). It was noted that occasional large open areas occurred in the woodlands of community type 1, which were almost totally devoid of vegetation.

Community type 3 is typically dominated by *Acacia acuminata* with *Casuarina pauper* being a common component. Species group C is generally both faithful and constant to types 3 and 4; however there are clearly different patterns in species occurrences between these types within this species group. There are also obvious differences in species dominance between these types, with almost all quadrats in community type 3 being dominated by an *Acacia acuminata* shrubland. Mean species richness is 11 taxa/quadrat. Both community types show low representation of species group F (except for the *Austrostipa* spp and *Enchylaena tomentosa* as previously mentioned).

Community type 4 is characterized by species such as *Acacia tetragonophylla* and *Scaevola spinescens*. Species group D is almost totally restricted to community type 4. Mean species richness is 15.7 taxa/quadrat. This community type can be subdivided into two subgroups. Type 4b is entirely restricted to ridges of massive banded ironstone and can easily be separated from type 4a by the occurrence of such species as *Eremophila clarkei, Eriostemon brucei, Acacia quadrimarginea* and *Stenanthemum newbeyi*, while community type 4a generally occurs on somewhat deeper soils lower in the landscape.

Community type 5 is represented by a single quadrat located on an eroding lateritic breakaway. This landform was rare in the study area. This quadrat contained few shared perennial taxa (4 only) while a further 10 perennial taxa were recorded only at this quadrat. The quadrat was dominated by *Allocasuarina campestris, Baeckea elderiana* and *Grevillea paradoxa*. A similar community type has previously been encountered on lateritic areas in the Hunt and Mt Manning Ranges some 70–100 km to the north east (Gibson, unpublished data).

Environmental Correlates

Soil and geomorphological parameters

Soil parameters were highly inter-correlated, however altitude, slope and topographic position were not significantly correlated with any soil parameter (Table 2). Percentage sand, silt and clay showed the least inter-correlation with other soil parameters; percentage sand was not correlated with any nutrient while percentage clay was significantly correlated with pH and percentage silt with exchangeable K. This is at variance with results from the Bremer and Parker Ranges where high correlations were found between percentage soils fractions and soil nutrients (Gibson & Lyons 1998a,b).

Community types 2 and 5,which were represented by single quadrats, were excluded from statistical analysis of the environmental differences. There were no significant differences between mean altitude, slope or topographic position occupied by the community types 1, 3 and 4 (Table 3). Within community type 4, one subgroup (4b) generally occupied ridge tops or upper slopes. The major division in the dendrogram between community types 1 and 2 and community types 3, 4 and 5 are also apparent in the soil nutrient data (Table 4). Community type 1 occurred on calcium-rich sites with significantly higher pH, and exchangeable ion than community types 3 and 4. These soils generally show high levels of soil P, similar to community type 4.

Soils from community types 3 and 4 could most easily be differentiated by pH, total P, total N, and exchangeable ions, with community type 3 having lower values, with almost a 50% reduction in terms of total N and P.

Soil from the single quadrat of community type 2 was essentially similar to the means reported for community type 1, consistent with the interpretation that it is a depauperate example of that community type. Community type 5 was represented by a single quadrat from the top of a lateritic breakaway. The soils from this quadrat recorded the lowest pH (6.2) and had very low levels of all soil nutrient compared with all other quadrats. Soils at this quadrat contained a high percentage of sand (90%) compared with values of 66.3 to 74.5% for the other community types.

Ordination results

Ordination of the quadrat data was undertaken to show spatial relationships between groups and to better elucidate possible environmental correlates with the classification. The results of a three-dimensional ordination (stress level 0.16) shows good separation of most of the classificatory groups. The first and second axes separated

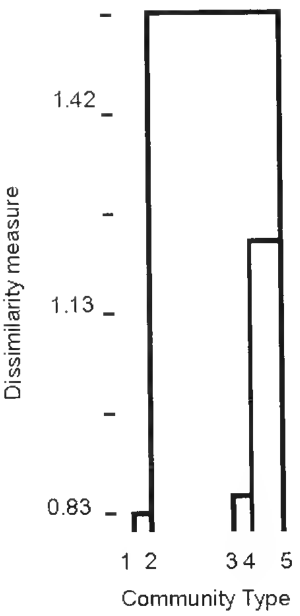

Figure 2. Dendrogram of the floristic quadrats from the Highclere Hills showing the five group level classification.

Table 2. Matrix of Spearman rank correlation coefficients between environmental parameters. Only correlations significant at $P < 0.01$ shown ($r^2 \geq 0.3721$). See methods for soil parameter codes.

	Altitude	Aspect	Ca	Clay	EC	K	Mg	Na	Total N	pH	Total P	Sand	Silt	Slope
Aspect	-	1.000	-	-	-	-	-	-	-	-	-	-	-	-
Ca	-	-	1.000	-	-	-	-	-	-	-	-	-	-	-
Clay	-	-	-	1.000	-	-	-	-	-	-	-	-	-	-
EC	-	-	0.798	-	1.000	-	-	-	-	-	-	-	-	-
K	-	-	0.701	-	0.681	1.000	-	-	-	-	-	-	-	-
Mg	-	-	0.569	-	0.510	0.567	1.000	-	-	-	-	-	-	-
Na	-	-	-	-	0.501	0.505	0.754	1.000	-	-	-	-	-	-
Total N	-	-	0.768	-	0.643	0.469	-	-	1.000	-	-	-	-	-
pH	-	-	0.659	-0.379	0.763	0.694	0.621	-	0.375	1.000	-	-	-	-
Total P	-	-	0.412	-	-	-	-	-	0.719	-	1.000	-	-	-
Sand	-	-	-	-0.754	-	-	-	-	-	-	-	1.000	-	-
Silt	-	-	-	-	-	0.393	-	-	-	-	-	-0.855	1.000	-
Slope	-	-	-	-	-	-	-	-	-	-	-	-	-	1.000
Topography	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3. Plant community mean values for altitude, topographic position (1-ridge top to 5-valley floor), slope class (1-flat to 3-steep), aspect (16 cardinal directions) and species richness. Differences between means for community types 1, 3 and 4 (in bold) tested using Kruskal-Wallis non-parametric analysis of variance. (ns indicates not significant, ** indicates $P < 0.01$).

Community type	1	2	3	4	5
Altitude ^{ns}	**381**	370	**403**	**386**	420
Topography ^{ns}	**2.9**	4.0	**2.8**	**2.2**	1.0
Slope ^{ns}	**2.0**	2.0	**2.1**	**2.2**	1.0
Aspect ^{ns}	**4.4**	3.0	**5.1**	**4.0**	0.0
Species richness **	**13.1**	7.0	**11.0**	**15.8**	4.0

Table 4. Plant community mean values for soil parameters. Differences between means for community types 1, 3 and 4 (in bold) tested using Kruskal-Wallis non-parametric analysis of variance. (ns indicates not significant, * indicates $P < 0.05$, ** indicates $P < 0.01$, *** indicates $P < 0.001$, **** indicates $P < 0.0001$).

Community type	1	2	3	4	5
EC****	**18.1**	11.0	**3.7**	**10.3**	1.0
pH****	**8.18**	8.50	**6.63**	**7.11**	6.20
Total N****	**0.198**	0.128	**0.085**	**0.192**	0.032
Total P***	**213.3**	107.0	**150.5**	**286.5**	79.0
% Sand ^{ns}	**68.2**	74.5	**66.3**	**69.0**	90.0
% Silt*	**19.1**	17.0	**18.6**	**15.3**	4.5
% Clay*	**12.7**	8.5	**15.1**	**15.8**	5.5
Exchangeable Ca****	**18.5**	10.5	**6.3**	**11.8**	0.9
Exchangeable Mg****	**6.04**	2.91	**2.35**	**3.20**	0.26
Exchangeable Na****	**0.34**	0.06	**0.10**	**0.11**	0.02
Exchangeable K***	**1.30**	0.64	**0.69**	**0.77**	0.10

community type 5 from all other quadrats, further indicating its very different nature. The first and the third axes show the gradation from community type 1 (bottom left) through community type 4 (center) to community type 3 (top right; Fig 3). The outlying nature of community type 5 is still apparent as is the relationship between the species poor community type 2 to community type 1.

Superimposed on the figure are the best fit linear correlations ($r > 0.70$) of the environmental parameters measured using principal axis correlation (Belbin 1993). The four most highly correlated soil parameters were pH, exchangeable Ca, conductivity and exchangeable K. All four parameters show gradients in virtually the same direction, consistent with a major nutrient gradient decreasing from the lower left of the figure toward the upper right. Quadrats on banded ironstones (type 4a) form the tight cluster in the center of the figure.

Discussion

The section of the Highclere Hills on Ennuin Station has a rich flora of some 242 taxa and the flora list for the station would be considerably extended if detailed surveys were

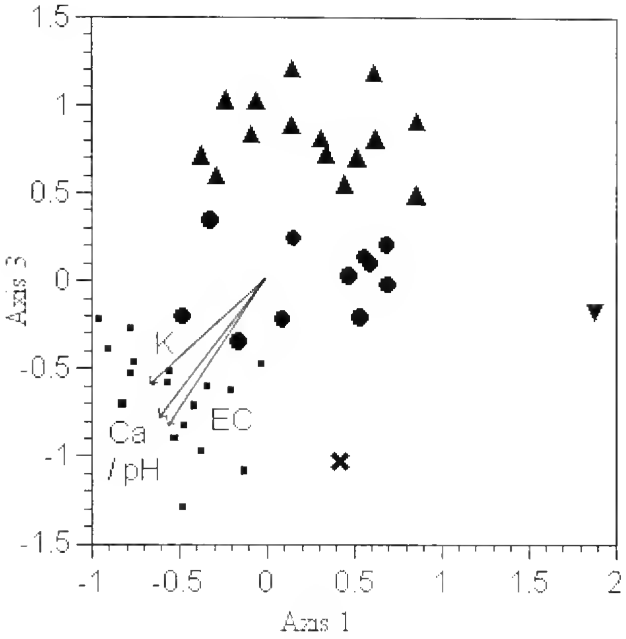

Figure 3. Ordination of Highclere Hill floristic quadrats coded by community type (1 square, 2 cross, 3 triangle, 4 circle, 5 inverted triangle). Arrows show the direction of the best fit linear correlation for the four most significant environmental parameters, exchangable K, exchangable Ca, pH and electrical conductivity (EC).

undertaken of the granitic and sandplain areas. The discovery of two populations of *Stenanthemum newbeyi* represents a significant range extension for the taxon from the Helena and Aurora Range some 80 km to the north east, where it was believed to be endemic to the massive banded ironstones of that range. *Stenanthemum newbeyi* occurred in the same habitat on the Highclere Hills but, as was noted above, this habitat is very much more restricted in the Highclere Hills.

Two populations of *Tricoryne tuberosa* ms were recorded from the range. This species was previously known from two collections from Karroun Hill area (100 km NW of Ennuin). A recent collection of a *Tricoryne* in bud (R Soullier 628) from the Mingenew area may be attributable to this taxon but further survey is required to determine its precise distribution and conservation status.

The collection *Acacia xerophila* var *brevior* from the Highclere Hills and the earlier collection from South Mt Rankin (some 60 km SE) suggests that this taxon may be more widespread along the western most greenstone belt than earlier supposed.

Two species, *Hakea rigida* (= *Hakea* sp (KRN 9589)) and *Leptosema aculeatum* (= *L. chambersii* subsp nov (KRN 9597)), that Newbey & Hnatiuk (1985) highlighted as notable range extensions to the Highclere Hills, were not located during the present survey. *Hakea rigida* is now known to occur in the central wheatbelt and South Western Interzone from Lake Campion north to Wialki and east to area north of Southern Cross (Barker *et al.* 1999). The Highclere Hills population of *L. aculeatum* represents the western extent of this species.

The flora list for the Highclere Hill is somewhat poorer than that recorded for Helena and Aurora Range and similar to that of the Bremer Range and the Parker Range (Table 5). However, the latter two ranges were sampled in a very dry year and numbers of annuals and geophytes would be significantly underestimated (Gibson *et al.* 1997; Gibson & Lyons 1998ab). The smaller flora list for the Highclere Hills (given the abundance of annuals recorded) probably reflects the much more subdued topography of the Hills compared to the other ranges and hence lower level of habitat heterogeneity.

There is some consistency in the biogeographic patterns seen in the diversity of species-rich genera with those reported for the Helena and Aurora Range, located some 80 km to the north-east (Gibson *et al.* 1997). The Hills showed a similar decrease in number of eucalypt and *Melaleuca* spp compared with the more southerly the Bremer and Parker Ranges. However, fewer *Acacia* and *Eremophila* spp were recorded on the Hills than were found on the Helena and Aurora Range. No endemic taxa have been recorded from this section of the Highclere Hills.

The effects of this subdued habitat are also seen in the vegetation classification. Both Beard (1972) and Newbey & Hnatiuk (1985) considered that the low stony rises of the Highclere Hills were covered with *Eucalyptus corrugata* and/or *E. longicornis* woodlands with chenopod understoreys, with the associated colluvial flats being dominated by *Eucalyptus salmonophloia* and *E. salubris* woodlands. There is little evidence in our data of this topographic segregation on the Hills, with distribution being highly correlated with edaphic factors (Table 4). For example, localized areas of deeper calcareous soils allow *E. salubris* and *E. salmonophloia* to develop over most

Table 5. Comparison of the floras of the Highclere Hills, the Helena and Aurora Range, the Bremer Range and the Parker Range. Note that data from Bremer and Parker Ranges were collect in a dry year and underestimate the annual floras.

	Highclere Hills	Helena & Aurora Range	Bremer Range	Parker Range
Flora	242	324	267	254
Weeds	25	21	8	10
Endemic taxa	-	4	3	5
Taxa - first collections	-	1	2	2
Eucalyptus spp	12	19	30	29
Acacia spp	9	17	17	20
Eremophila spp	8	14	11	7
Melaleuca spp	2	5	19	14

of the landscape. While it is possible to split the woodlands into those dominated by *E. corrugata* (type 1a) and those dominated by *E. salubris*/*E. salmonophloia* (type 1b) there is little evidence of any significant change in the understorey species between these subtypes (Table 1). The Highclere Hills has fewer eucalypt-dominated communities than the other three ranges for which comparable survey work is available (Gibson *et al.* 1997; Gibson & Lyons 1998ab).

Anand *et al.* (1997) showed high correlation between calcretes and erosional regimes of greenstone lithologies. Within the Highclere Hills both calcareous and acid soils were found developed on the erosional regimes of greenstone lithologies. The highly calcareous soils (mean pH 8.2-8.5) were dominated by community types 1 and 2, while the more acid soils (mean pH 6.6) developed on the same lithology were dominated by community type 3 and to a lesser degree by community type 4a.

Newbey & Hnatiuk (1985) describe shrublands of both *Acacia acuminata* and *A.* aff *aneura* rarely occurring on stony rises. In fact these *Acacia* shrublands (type 3) are one of the more widespread community types on the Ennuin section of the Highclere Hills. Indeed much of the eastern slopes are dominated by this community type. Other *Acacia* shrublands (community type 4a) are also widely distributed on the Hills.

The community of the massive ironstones (type 4b) is fundamentally different from those recorded from the Helena and Aurora Range. The most obvious components of that community (*Dryandra arborea* and *Calycopeplus paucifolius*) appear to be absent from the Highclere Hills. The areas of massive banded ironstone habitat on Ennuin Station are very small and fragmented. The soils of community type 4, although generally thin (<10 cm depth), were near neutral and had similar total P levels to community type 1.

The lateritic community (type 5) was very restricted on Ennuin but is similar in species composition to similar landforms in the Hunt Range and Mt Manning Range (Gibson, unpublished data). Laterization was widespread during the Tertiary and similar laterite communities are widespread in the goldfields ranges.

Beard (1972) classified all of the greenstone and banded ironstone areas of the Highclere Hills into the Highclere vegetation System, extending from north of Mt Correll to just south of Bullfinch. Ennuin Station occupies the middle third of this band. None of this area is covered by any existing conservation reserve and most of the Hills are in a mining reserve.

The Highclere Hills have had a long history of grazing. This is reflected in the vegetation by a high frequency of annual grasses in the 45 quadrats established. While the number of annual grasses is similar to that found on the Helena and Aurora Range they are much more widespread. As quadrats were established in the vegetation in the best condition no detailed analysis of grazing impacts is possible from our dataset. It was noted however, that significant invasion of the introduced *Centaurea melitensis* (Malta thistle or Maltese cockspur) had occurred along some tracks, around old sheep camps and in areas disturbed by mining. This thistle is a native of the Mediterranean region, Asia and Africa, and is a widespread weed in south-west Western Australia. There is also a significant population of *Carrichtera annua* (Ward's weed) around the homestead and yards.

Mineral exploration and mining have had significant local impacts along the Highclere Hills. As with most exploration and mining in the goldfields ranges, there has been little effort to minimize impacts or rehabilitate areas once exploration or mining have ceased. Uncapped drill holes, open costines, abandoned drilling infrastructure, bagged drill hole material and piles of rock cores were common, especially on the northern section of Ennuin. There is an urgent need for stricter environmental conditions to be placed on exploration and mining leases and for more detailed monitoring of these activities.

Acknowledgements: We would like to thank J & G Gauntlett for the invitation to work on Ennuin Station and their hospitality during our stay. The following people are thanked for assistance with identifications in their particular field of expertise: G Keighery, B Lepschi, B Maslin, B Rye, M Trudgen, and P Wilson. Soil chemical analyses were undertaken by the Chemistry Center (WA).

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Appendix

Flora list for the Highclere Hills (ms denotes a manuscript name, * indicates a weed).

Adiantaceae

Cheilanthes austrotenuifolia
Cheilanthes lasiophylla

Aizoaceae

Gunniopsis rubra
* *Mesembryanthemum nodiflorum*
Tetragonia moorei

Amaranthaceae

Ptilotus carlsonii
Ptilotus divaricatus
Ptilotus exaltatus
Ptilotus gaudichaudii
Ptilotus holosericeus
Ptilotus obovatus
Ptilotus spathulatus

Anthericaceae

Arthropodium dyeri
Caesia occidentalis
Thysanotus patersonii
Thysanotus speckii
Tricoryne tuberosa ms

Apiaceae

Daucus glochidiatus
Hydrocotyle rugulosa
Trachymene cyanopetala
Trachymene ornata
Trachymene pilosa
Uldinia ceratocarpa

Apocynaceae

Alyxia buxifolia

Asclepiadaceae

Rhyncharrhena linearis

Asteraceae

Actinobole uliginosum
Angianthus milnei
Asteridea athrixioides
Blennospora drummondii
Brachyscome ciliaris
Brachyscome ciliocarpa
Calotis hispidula
* *Centaurea melitensis*
Cephalipterum drummondii
Chrysocephalum semicalvum
Erymophyllum ramosum subsp *ramosum*
Gilberta tenuifolia
Gilruthia osbornei
Gnephosis tenuissima
Hyalosperma cotula
Hyalosperma demissum
Hyalosperma glutinosum subsp *glutinosum*
Hyalosperma zacchaeus
* *Hypochaeris glabra*
Isoetopsis graminifolia
Lawrencella rosea
Leucochrysum fitzgibbonii
Millotia myosotidifolia
Millotia tenuifolia
Olearia muelleri
Olearia pimeleoides
Podolepis canescens
Podolepis capillaris
Podolepis lessonii
Podotheca angustifolia
Podotheca gnaphalioides
Pogonolepis stricta
Rhodanthe chlorocephala subsp *rosea*
Rhodanthe haigii
Rhodanthe laevis
Rhodanthe manglesii
Rhodanthe oppositifolia
Rhodanthe polycephala
Rhodanthe rubella
Schoenia cassiniana
Senecio glossanthus
* *Sonchus oleraceus*
Streptoglossa liatroides
Trichanthodium skirrophorum
* *Urospermum picroides*
Vittadinia humerata
Waitzia acuminata
Waitzia citrina

Boraginaceae

Plagiobothrys plurisepalus

Brassicaceae

* *Brassica tournefortii*
* *Carrichtera annua*
* *Heliophila pusilla*
Lepidium rotundum
* *Sisymbrium irio*
* *Sisymbrium runcinatum*
Stenopetalum filifolium
Stenopetalum lineare

Caesalpiniaceae

Senna artemisioides subsp *filifolia*
Senna cardiosperma subsp *cardiosperma*

Campanulaceae

Wahlenbergia preissii
Wahlenbergia tumidifructa

Caryophyllaceae

* *Cerastium glomeratum*
* *Silene gallica*
Stellaria filiformis

Casuarinaceae

Allocasuarina acutivalvis
Allocasuarina campestris
Casuarina pauper

Chenopodiaceae

Atriplex nummularia
Atriplex vesicaria
Chenopodium curvispicatum
Enchylaena tomentosa
Maireana carnosa
Maireana georgei
Maireana planifolia
Maireana trichoptera
Maireana triptera
Rhagodia drummondii
Sclerolaena densiflora
Sclerolaena diacantha
Sclerolaena fusiformis

Colchicaceae

Wurmbea murchisoniana

Convolvulaceae

Wilsonia humilis

Crassulaceae

Crassula colorata

Cuscutaceae

* *Cuscuta epithymum*

Cyperaceae

Schoenus nanus

Dilleniaceae

Hibbertia glomerosa

Droseraceae

Drosera menziesii

Epacridaceae

Leucopogon breviflorus

Euphorbiaceae

Euphorbia drummondii
Poranthera microphylla

Frankeniaceae

Frankenia desertorum

Geraniaceae

* *Erodium cicutarium*
Erodium cygnorum

Goodeniaceae

Brunonia australis
Goodenia berardiana
Goodenia krauseana
Goodenia mimuloides
Goodenia occidentalis
Scaevola spinescens
Velleia rosea

Haloragaceae

Gonocarpus nodulosus
Haloragis gossei

Lamiaceae

Hemigenia brachyphylla
Prostanthera althoferi subsp *althoferi*
Prostanthera incurvata

Lobeliaceae

Lobelia heterophylla
Lobelia winfridae

Loganiaceae

Phyllangium paradoxum

Loranthaceae

Amyema benthamii
Amyema gibberula var *tatei*
Amyema miquelii

Malvaceae

Abutilon oxycarpum
Alyogyne hakeifolia
Lawrencia repens
Sida atrovirens ms
Sida calyxhymenia
Sida spodochroma

Mimosaceae

Acacia acuminata
Acacia assimilis subsp *assimilis*
Acacia coolgardiensis subsp *effusa*
Acacia erinacea
Acacia nyssophylla
Acacia quadrimarginea
Acacia ramulosa
Acacia tetragonophylla
Acacia xerophila var *brevior*

Myoporaceae

Eremophila alternifolia
Eremophila clarkei
Eremophila gibbosa
Eremophila interstans
Eremophila oppositifolia
Eremophila oppositifolia var *angustifolia* ms
Eremophila scoparia
Eremophila serrulata

Myrtaceae

Baeckea elderiana
Calothamnus gilesii
Chamelaucium pauciflorum subsp *thryptomenioides* ms
Eucalyptus capillosa subsp *capillosa*
Eucalyptus celastroides subsp *celastroides*
Eucalyptus corrugata
Eucalyptus ewartiana
Eucalyptus longicornis
Eucalyptus loxophleba
Eucalyptus oleosa
Eucalyptus salmonophloia
Eucalyptus salubris
Eucalyptus sheathiana
Eucalyptus transcontinentalis
Eucalyptus yilgarnensis
Euryomyrtus maidenii ms
Malleostemon tuberculatus
Melaleuca haplantha
Melaleuca uncinata

Ophioglossaceae

Ophioglossum sp (Cranfield & Spencer 7734)

Orchidaceae

Caladenia roei
Cyanicula amplexans
Microtis media
Pterostylis picta
Pterostylis spathulata
Thelymitra aff *macrophyllum*

Papilionaceae

Daviesia nematophylla
* *Medicago laciniata*
* *Medicago minima*
Mirbelia microphylla
Swainsona kingii

Phormiaceae

Dianella revoluta

Plantaginaceae

Plantago aff *hispidula* (NG & ML 1732)

Poaceae

* *Aira caryophyllea*
Amphibromus nervosus
Amphipogon strictus
Aristida holathera
Austrodanthonia caespitosa
Austrostipa elegantissima
Austrostipa nitida
Austrostipa scabra
Austrostipa trichophylla
Austrostipa aff *trichophylla*
Bromus arenarius
* *Bromus diandrus*
* *Bromus rubens*
Cymbopogon sp (Newbey 9550)
Elymus scaber
* *Hordeum leporinum*
Monachather paradoxus
* *Pentaschistis airoides*
* *Rostraria pumila*
* *Schismus barbatus*
* *Vulpia myuros*

Polygalaceae

Comesperma integerrimum

Portulacaceae

Calandrinia corrigioloides
Calandrinia eremaea

Primulaceae

* *Anagallis arvensis*

Proteaceae

Grevillea obliquistigma
Grevillea paradoxa
Grevillea sarissa subsp *sarissa*
Hakea preissii
Hakea recurva

Rhamnaceae

Stenanthemum newbeyi
Stenanthemum stipulosum
Trymalium myrtillus

Rutaceae

Eriostemon brucei

Santalaceae

Exocarpos aphyllus
Santalum acuminatum
Santalum spicatum

Sapindaceae

Dodonaea divaricata
Dodonaea inaequifolia
Dodonaea stenozyga

Solanaceae

Nicotiana occidentalis
Solanum cleistogamum
Solanum lasiophyllum
Solanum simile

Sterculiaceae

Brachychiton gregorii
Rulingia sp (Newbey 9588)

Surianaceae

Stylobasium spathulatum

Thymelaeaceae

Pimelea microcephala

Urticaceae

Parietaria debilis

Violaceae

Hybanthus floribundus subsp *floribundus*

Zygophyllaceae

Zygophyllum eremaeum
Zygophyllum ovatum

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Floral biology of the Western Australian endemic 'yellow bells', *Geleznowia verrucosa* Turcz (Rutaceae)

L M Broadhurst & B H Tan

School of Environmental Biology, Curtin University of Technology, GPO Box U1987 Perth WA 6845

email: lindabr@calm.wa.gov.au

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Abstract

Aspects of the floral biology of the two subspecies of *Geleznowia verrucosa* and one intermediate population were examined for possible differences in their reproductive strategy(ies). Movement of reproductive organs, stigma receptivity prior to anther dehiscence, and an apparent lack of pollinators indicate that *G. verrucosa* is a protogynous facultative selfer. Hand-pollination treatments confirm that although self-pollination does produce seed, higher levels of seed are set when flowers are pollinated with pollen outcrossed from within the population. Differing responses by the taxa to the various pollination treatments suggests that contrasting reproductive strategies are employed. The ssp *verrucosa* ms is more oriented towards self-pollination while ssp *formosa* ms has characteristics of a mixed mating system. Responses of the intermediate population suggest that it may be a hybrid.

Keywords: flower, reproductive organs, pollination, *Geleznowia verrucosa*

Introduction

Plant reproductive strategies play an important role in gene transmission, population genetic structure, selection response, and speciation (Brown & Allard 1970; Grant 1981; Lyons & Antonovics 1991; Ellis & Sedgley 1992; Barrett *et al.* 1996). Evolutionary shifts in the breeding strategies of plants are usually associated with a move from obligate outbreeding to predominantly self-fertilisation, although reverse shifts are known (Stebbins 1970; Gottlieb 1973; Jain 1976). These shifts are often correlated with changes in floral morphology and resource allocation. Selfing populations frequently exhibit smaller petals, stamens and styles, reduced nectar and pollen production, and lower pollen:ovule ratios, essentially investing fewer resources in floral attractants while setting more seed (Jain 1976; Ritland & Ritland 1989). In contrast, predominantly outcrossing species possess larger and more abundant flowers, but set a lower proportion of fruit and seeds (Lyons & Antonovics 1991).

The 'yellow bells', *Geleznowia verrucosa* Turcz (Rutaceae), is a small woody endemic Western Australian species characterised by terminal clusters of bright yellow flowers. The genus is widely distributed across Western Australia, extending from Cape Range (21° 50′ S 116° 12′ E) in the north of Western Australia, to Dowerin (31° 12′ S 117° 02′ E) in the eastern wheatbelt (Hnatiuk 1990; Keighery & Gibson 1993). Although once considered monospecific, recent allozyme and morphometric studies have confirmed the existence of two subspecies and a series of intermediate populations (Fig 1), which are thought to be of ancient hybrid origin (Broadhurst *et al.* 1999; Broadhurst 2000). Genetically, the smaller ssp *verrucosa* (manuscript) is allied with the intermediate populations but morphologically the intermediate populations are more similar to the larger ssp *formosa* (ms, Broadhurst *et al.* 1999; Broadhurst 2000). Formal revision of the genus is being undertaken.

Like many Western Australian plant genera, little is known about the reproductive biology of *G. verrucosa*. An understanding of the reproductive mechanisms employed was considered essential for interpreting patterns of genetic and morphological variation. The presence of reproductive isolating mechanisms would also provide further evidence of divergence between the taxa. Aspects of the floral biology and the results of pollination experiments designed to determine the reproductive strategy(ies) employed by *G. verrucosa* are reported here.

Materials and methods

Sampling strategy

Experimental populations were selected from across the species distribution to include two populations of the subspecies *verrucosa* ms and *formosa* ms and one population of the intermediate form (Table 1). Although a population of ssp *verrucosa* occurred in the north of this subspecies' range at Indarra Nature Reserve, flowering was poor, limiting experimental populations to Arinya and Coorow located in the south. All sampling and pollination experiments were undertaken during 1995 and 1996.

Flowering events, phenology and pollinators

Flowering events were observed in the field and the laboratory. In the field, flowers were tagged on 3 to 4 plants in each population, and events from flower opening to closing were recorded and photographed. Stems of inflorescences were also transported to the laboratory, maintained in vases of water and floral events observed, recorded and photographed.

The commencement and completion of flowering at the five populations was recorded during monthly visits to the sites. Opportunistic day-time and nocturnal obser-

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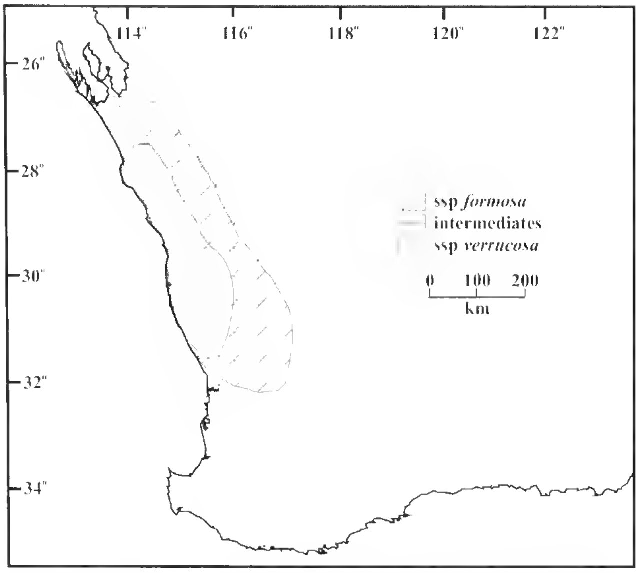

Figure 1. Distribution of *Geleznowia verrucosa* specimens recorded at the WA Herbarium and mapped using WABIOTA. Data correct at 14 July 2000.

vations were also undertaken during these visits with the type and activity of invertebrates on the plants noted.

Stigma receptivity

Stigmas from buds and flowers of various ages were examined both in the field and the laboratory. To determine timing and length of receptivity, pistils from buds and flowers of varying ages were detached from the ovary and placed in 3% hydrogen peroxide (Galen & Kevan 1980; Dafni 1992). Stigmas which are receptive should produce bubbles (Dafni 1992). The size, abundance and distribution of bubbles from the stigmatic surface were qualitatively assessed.

Pollen viability and pollen tube growth

Stems with inflorescences were collected from each population, placed in sealed plastic bags, stored at 4 °C and transported to the laboratory. Flowers were allowed to open naturally and dehiscing anthers were collected, bulked and pollen viability immediately determined. Attempts to indirectly measure pollen viability by germinating pollen grains in a suitable sucrose solution (Dafni 1992) were unsuccessful. Instead, viability was assessed by staining pollen grains with either Alexander's stain (Alexander 1980) or fluorescein diacetate (Heslop-Harrison & Heslop-Harrison 1970). Two hundred pollen grains were scored as either red (viable) or green (non-viable) following Alexander's stain while 500 pollen grains were scored as either bright (viable) or non-stained (non-viable) following staining with fluorescein diacetate and viewed with a violet exciter filter (λ = 395-415 nm).

Table 2. Pollen source for experiments observing pollen tube growth.

	Arinya	Geraldton	Meanarra Hill 1
Maternal	ssp verrucosa	ssp formosa	ssp formosa
	x	x	x
Paternal	ssp formosa	ssp verrucosa	intermediate
Pollen Source	Meanarra Hill 1	Indarra Reserve	Nearby population

To determine whether pollen tube growth was influenced by pollen source, 4 to 5 flowers on five plants were hand-pollinated using pollen from within the population. A further 4 to 5 flowers on these plants were hand-pollinated with pollen sourced from a different taxon (Table 2). Hand-pollinations were conducted by wiping mature dehiscing anthers across the stigmatic surface of emasculated receptive flowers until pollen was clearly visible. The flowers were collected after 24 h, fixed in formalin:proprionic acid:ethanol (40:50:10 v/v) and stored at 4 °C in 70% ethanol. The pistils were later autoclaved in sodium sulphate (50 g L^{-1}) for 30 min at 121 °C, stained with decolourised aniline blue for 24 h, and viewed under fluorescent light using a violet exciter filter (λ = 395-415 nm; Martin 1958; Dafni 1992). Stigmas and styles were examined for pollen germination, pollen tube growth and abnormalities. Due to the limited number of receptive flowers available for both this and the pollination experiment, pollen tube growth could not be assessed at either Coorow 1 and Hutt River.

Pollination experiments

Field pollination experiments were conducted during 1996. Newly opened flowers with undehisced anthers were manipulated as outlined in Table 3. Hand pollinations were undertaken by wiping dehiscing anthers over receptive stigmas until pollen was clearly visible. Differences in flowering times necessitated pollen for the cross pollination treatment between populations (X_{OTHER}) at the two ssp *verrucosa* ms sites being stored until experiments could be conducted. The pollen was stored in dark, cool conditions and viability was assessed using fluorescein diacetate prior to use. Transfer of pollen to stigmas was facilitated using a fine hair brush. Potential pollinators were excluded from flowers by tying a nylon stocking bag over the inflorescences and applying a clear sticky substance (Bird-Off, Rentokil) around the stem below the tie. To prevent seed from treated and untreated flowers mixing, the fruit of treated flowers were collected before maturity and seed

Table 1. Location of sampled *G. verrucosa* populations; n_{est} is the estimated population size.

Population	Taxon	n_{est}	Latitude (°S)	Longitude (° E)
Arinya	ssp *verrucosa*	50	31° 19′ 52″	116° 58′ 36″
Coorow 1	ssp *verrucosa*	20	29° 54′ 08″	116° 00′ 05″
Hutt River 2	intermediate	200	28° 05′ 28″	114° 28′ 02″
Geraldton	ssp *formosa*	24	28° 35′ 25″	114° 37′ 57″
Meanarra Hill 1	ssp *formosa*	25	27° 41′ 40″	114° 13′ 00″

Table 3. Pollination treatments undertaken for *G. verrucosa* populations (after Dafni 1992).

	Test	Treatment
Open	Open-pollination	Untreated, unbagged
Selfed	Self-pollination	Untreated, bagged
X_{SAME}	Cross-pollination within populations	Emasculated, pollen from within site
X_{OTHER}	Cross-pollination between populations	Emasculated, pollen from outside site
No pollen	Non-sexual	Emasculated, bagged

set assessed. Although the fruits were green, the seeds were well formed and empty carpels were clearly distinguishable.

One-way Analyses of Variance (ANOVA) were conducted using SuperANOVA (Abacus Concepts 1989) to determine whether treatments varied within and between populations. Means were compared using Tukey's Compromise (Tukey's b; Winer 1962) *post hoc* test. To test for possible bias due to the large differences in values between open-pollinated and the remaining treatments, the former values were removed, the ANOVA conducted again and contrasts between means re-assessed.

To assess the effects of the cross-pollination treatments, an index of self-incompatibility (ISI = fruit set from self-pollination/fruit set from cross-pollination; Zapata & Arroyo 1978; Kenrick 1986) was calculated for both pollination treatments (X_{SAME} and X_{OTHER}). This calculation indicates the compatibility of pollen to set seed. Values of <0.2 indicate self-incompatibility, 0.2-0.9 partial self-compatibility, 1.0 self compatibility and >1.0 preferential self-pollination (Zapata & Arroyo 1978; Kenrick 1986).

Results

Flowering events, phenology and pollinators

The inflorescences of *G. verrucosa* are comprised of a complex suite of developmental stages from bud to fruit. Mature flowers consist of several large yellow bracts surrounding five sepals of similar shape and colour, with five smaller, thinner and darker yellow petals inside (Fig 2). Mature buds generally open within a short space of time during early morning, although this may be delayed on overcast days. The flowers remain open for a single day. The sequence of flowering events begins as the bud bursts open, splaying petals outwards; the sepals are already extended outwards at this time (Fig 2, parts 1-3). Upon opening, the long style, bent over in the closed bud, is released, and straightens. The style and stamens move away from each other and by mid-morning are at their furthermost (Fig 2, part 4). The anthers now dehisce, limiting the possibility of self pollen falling on its own stigma. After midday, the style and stamens begin to move towards each other and by mid-afternoon, are close together (Fig 2, part 5). The petals begin to close in the late afternoon, enclosing both pistil and stamens (Fig 2, part 6).

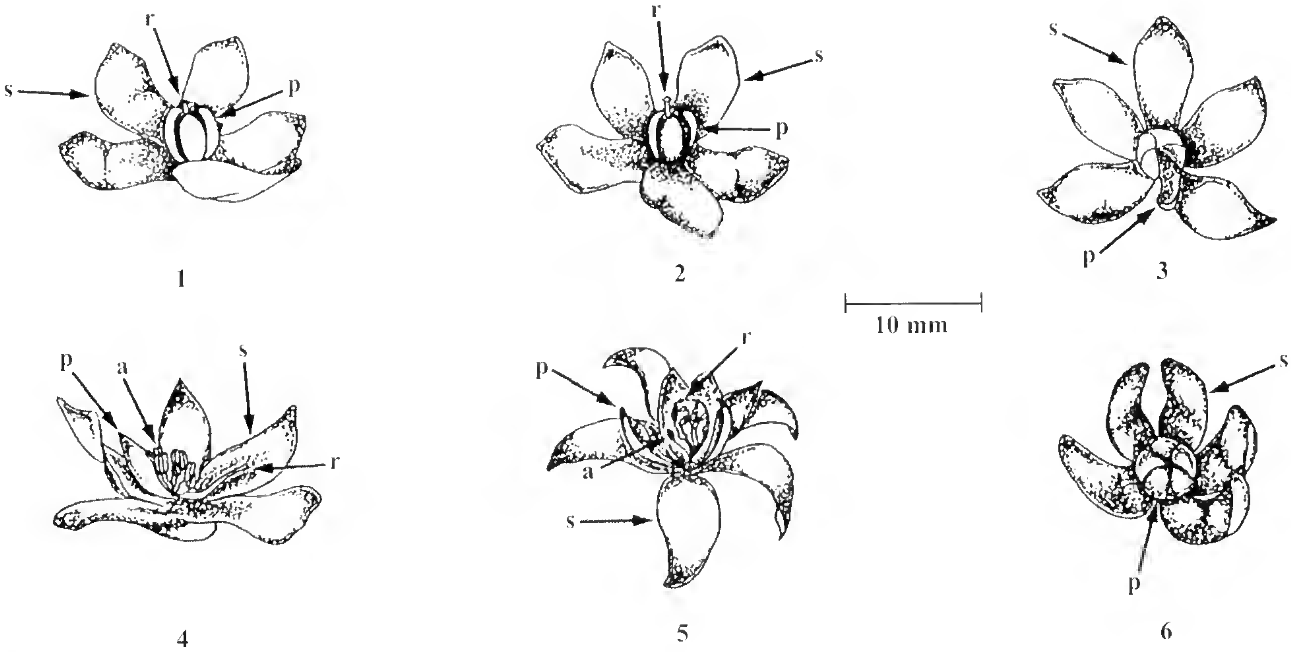

Figure 1. Flowering stages for *G. verrucosa* (drawings by E Ladhams). a, anthers; p, petals; r, style; s, sepals.

Table 4. Flowering seasons for all *G. verrucosa* populations over two years.

Population	Taxon	Flowering season 1995	Flowering season 1996
Arinya	ssp *verrucosa*	Sept - Oct	Aug - Nov
Coorow 1	ssp *verrucosa*	Aug - Oct	Sept - Nov
Hutt River 2	intermediate	May - Aug	May - July
Geraldton	ssp *formosa*	July - Oct	Aug - Oct
Meanarra Hill 1	ssp *formosa*	June - Sept	July - Aug

While all taxa exhibited a similar pattern of flowering phenology, separation between the pistils and anthers of ssp *verrucosa* ms did not appear to be as pronounced as that observed in ssp *formosa* ms.

Commencement and length of flowering differed between populations and years (Table 4). Flowering in the ssp *verrucosa* ms populations commenced later (August/September) than in the ssp *formosa* ms populations (June/July). In contrast, flowering in the intermediate population at Hutt River 2 was earliest in both years (May). The 1995 flowering period was longer than that experienced during 1996.

Despite obvious floral attractants such as large yellow bracts and prominent oil glands, no significant diurnal or nocturnal pollinators were observed visiting *G. verrucosa* plants during flowering. A small moth (Lepidoptera) was occasionally observed during the day and larvae found in some buds suggests that flowers act as a nursery. Ants (Hymenoptera) were noted apparently removing pollen on two plants at the Geraldton site. Although the ants did not appear to contact the style, it is possible that some accidental pollination does occur. Small beetles (Coleoptera) were also observed during flowering. The low number of insects observed suggests that none are significant pollinators of *G. verrucosa*.

Stigma receptivity

In the tests for stigma receptivity, several small bubbles were observed on the stigmatic surface when buds were green, or yellow-green and unopened, indicating that receptivity to pollen was weak. The stigmatic surface of buds which were yellow and just opened produced larger bubbles, suggesting increased receptivity. The stigmas of open flowers in which 0-50% of the anthers were dehisced produced many large bubbles, which increased in number when all anthers were dehisced and as the flower was closing, indicating greater pollen receptivity.

Pollen viability and pollen tube growth

All populations exhibited similarly high pollen viability (>90%) for both the Alexander's and fluorescein diacetate stains. Little misshapen or abnormal pollen was observed for any population.

All pollen tubes grew in the stylar tissue towards the ovary regardless of pollen source and no abnormal pollen tube growth was observed. While pollen tube growth in pollinated flowers from Geraldton and Meanarra Hill 1 extended the length of the style, at Arinya pollen tube growth was not as pronounced. Too few flowers were available at Coorow 1 and Hutt River for this experiment.

Pollination experiments

Within populations no significant variation was noted between plants for any of the treatments, allowing the data to be pooled. The experimental populations responded differently to the treatments (Table 5). All populations, except Geraldton, set significantly more open-pollinated seed than for any other treatment. At Geraldton, open-pollinated seed set was comparable to that of both cross-pollination treatments. While no variation occurred between the remaining treatments at Arinya and Meanarra Hill 1, the selfed and X_{SAME} treatments at Coorow produced more seed than the X_{OTHER} and pollen exclusion treatments. Self-pollination in the Hutt River 2 population produced more seed than both cross-pollination treatments; insufficient flowers were available for the pollen exclusion treatment at this population. Removing the open-pollinated values from the analysis did not significantly change these patterns.

Comparisons of treatments between populations highlighted several important differences (Table 5). Open-pollination seed set at Geraldton and Meanarra Hill 1 was considerably lower than in the other populations ($F_{4,163}$ = 19.56; P = 0.0001), while significantly more self-pollinated seed was set at Hutt River 2 ($F_{4,150}$ = 12.10; P = 0.0001). The X_{SAME} treatment produced similarly high levels of seed set at Coorow 1 and Geraldton and low levels at Arinya and Meanarra Hill 1, with intermediate levels set at Hutt River 2 ($F_{4,143}$ = 9.17; P = 0.0001). Low seed set occurred following the X_{OTHER} treatment at Arinya, Coorow 1 and Meanarra Hill 1 ($F_{4,128}$ = 11.39; P = 0.0001).

There was substantial variation in ISI values between populations (Table 6). The Arinya and Coorow 1 populations were partially self-compatible when pollinated with X_{SAME} pollen, but preferentially self-pollinating when pollinated with X_{OTHER} pollen sourced from the ssp *formosa* ms. The intermediate population at Hutt River 2 was preferentially self-pollinating regardless of pollen source, while the ssp *formosa* ms populations were partially self-compatible irrespective of pollen source.

Although populations responded to the various pollination treatments differently, some trends were apparent. To investigate this further, data for the different subspecies were pooled and compared (Fig 3). The ssp *formosa* ms set considerably less open-pollinated seed than either ssp *verrucosa* ms or the intermediate population. Seed set from selfing was highest in the intermediate population and lowest in ssp *formosa* ms, while all populations set similar levels of seed following X_{SAME} pollination. The X_{OTHER} treatment elicited similar levels of seed set in ssp *formosa* ms and the intermediate population but significantly lower

Table 5. Tukey's Compromise comparison of mean seed set per flower for pollination treatments within and between populations. Same letter within columns indicates no significant difference. -, insufficient flowers; number in parentheses. *P=0.001, **P=0.0001.

Within populations Treatment	Arinya	Coorow 1	Population Hutt River 2	Geraldton	Meanarra Hill 1
Open	3.42^{a} ± 0.21 (33)	4.03^{a} ± 0.15 (31)	4.33^{a} ± 0.18 (27)	2.00^{a} ± 0.27 (47)	2.30^{a} ± 0.26 (30)
Selfed	0.88^{b} ± 0.29 (25)	1.68^{b} ± 0.36 (25)	3.05^{b} ± 0.46 (19)	0.98^{b} ± 0.22 (53)	0.12^{b} ± 0.12 (33)
X_{SAME}	0.80^{b} ± 0.26 (30)	2.19^{b} ± 0.29 (27)	1.33^{b} ± 0.56 (15)	2.37^{a} ± 0.25 (46)	0.53^{b} ± 0.21 (30)
X_{OTHER}	0.16^{b} ± 0.16 (25)	0.09^{c} ± 0.09 (23)	1.58^{b} ± 0.50 (19)	1.96^{a} ± 0.26 (44)	0.50^{b} ± 0.18 (22)
No pollen	0.80^{b} ± 0.53 (10)	0.07^{c} ± 0.05 (28)	-	0^{c} (33)	0^{b} (20)
F_{df} P	$28.67_{4,118}$ **	$59.98_{4,129}$ **	$12.96_{3,76}$ **	$14.22_{4,218}$ **	$25.42_{4,130}$ **

Between Populations Population	Open	Selfed	Treatment X_{SAME}	X_{OTHER}	No pollen
Arinya	3.42^{b} ± 0.21 (33)	0.88^{bc} ± 0.29 (25)	0.80^{b} ± 0.26 (30)	0.16^{b} ± 0.16 (25)	0.80^{a} ± 0.53 (10)
Coorow 1	4.03^{ab} ± 0.15 (31)	1.68^{b} ± 0.36 (25)	2.19^{a} ± 0.29 (27)	0.09^{b} ± 0.09 (23)	0.07^{b} ± 0.05 (28)
Hutt River 1	4.33^{a} ± 0.18 (27)	3.05^{a} ± 0.46 (19)	1.33^{ab} ± 0.56 (15)	1.58^{a} ± 0.50 (19)	-
Geraldton	2.00^{c} ± 0.27 (47)	0.98^{bc} ± 0.22 (53)	2.37^{a} ± 0.25 (46)	1.96^{a} ± 0.26 (44)	0^{b} (33)
Meanarra Hill 1	2.30^{c} ± 0.26 (30)	0.12^{c} ± 0.12 (33)	0.53^{b} ± 0.21 (30)	0.50^{b} ± 0.18 (22)	0^{b} (20)
F_{df} P	$19.56_{4,163}$ **	$12.10_{4,150}$ **	$9.17_{4,143}$ **	$11.39_{4,128}$ **	$5.75_{3,87}$ *

Table 6. Index of self-incompatibility (ISI) for the cross pollination treatments in *G. verrucosa* populations. ISI values: <0.2 self-incompatibility, 0.2-0.9 partial self-compatibility, 1.0 self compatibility and >1.0 preferential self-pollination. l, partially self-compatible; u, preferential self-pollination.

Pollen source	Population	maternal	x	paternal	ISI	
X_{SAME}	Arinya	ssp *verrucosa*	x	ssp *verrucosa*	0.92	l
	Coorow 1	ssp *verrucosa*	x	ssp *verrucosa*	0.78	l
	Hutt River 2	intermediate	x	intermediate	2.65	u
	Geraldton	ssp *formosa*	x	ssp *formosa*	0.52	l
	Meanarra Hill 1	ssp *formosa*	x	ssp *formosa*	0.25	l
X_{OTHER}	Arinya	ssp *verrucosa*	x	ssp *formosa*	5.50	u
	Coorow 1	ssp *verrucosa*	x	ssp *formosa*	21.00	u
	Hutt River 2	intermediate	x	ssp *formosa*	1.77	u
	Geraldton	ssp *formosa*	x	ssp *verrucosa*	0.66	l
	Meanarra Hill 1	ssp *formosa*	x	intermediate	0.36	l

seed was produced by ssp *verrucosa* ms. This subspecies also set a small amount of seed despite pollen exclusion.

Discussion

The movement of reproductive organs during flower opening and closing, stigma receptivity prior to anther dehiscence, and the apparent absence of pollinators suggest that *G. verrucosa* is a protogynous facultative selfer. Seed production following hand pollination supports this premise. In all populations except the intermediate population at Hutt River 2, the levels of seed set were similar to, or higher, in flowers that were outcrossed within the population, compared with flowers that were allowed to naturally self-pollinate. The ISI values further reflect that these populations are partially, rather than completely, self-compatible. It would appear that although *G. verrucosa* plants were more receptive to outcrossed pollen, seed set can still occur when this pollen is unavailable. Seed set following pollination between the various taxa elicited various responses.

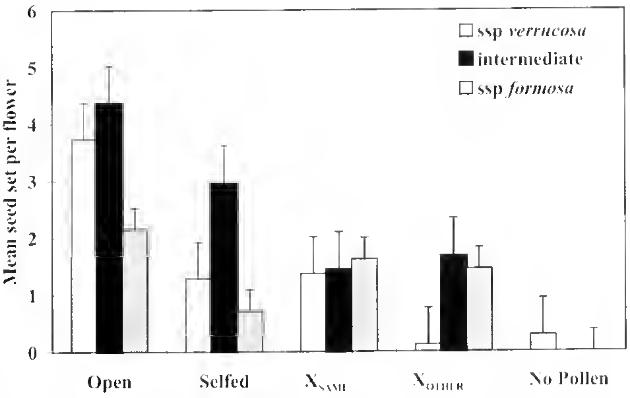

Figure 3. Mean seed set per flower for *G. verrucosa* taxa. Bars indicate one standard error

Both the ssp *verrucosa* ms populations set considerably fewer seed when pollinated with pollen from ssp *formosa* ms, and had ISI values consistent with preferential self-pollination. This result may reflect a decline in pollen viability due to storage. However, since storage did not affect pollen viability, it is more plausible that some other mechanism is responsible for this result. In contrast, the two ssp *formosa* ms populations had partial self-compatible ISI values when crossed with either a ssp *verrucosa* ms or the intermediate population. Interestingly, although pollen sourced from outside the population elicited the same response in ssp *formosa* ms, more seed was set following pollination with ssp *verrucosa* ms pollen than with pollen from the intermediate population. A lack of abnormalities in pollen tube growth suggest that these responses probably result from post- rather than pre-zygotic barriers to fertilisation. The responses elicited by the two subspecies suggest that different reproductive the strategies are employed.

While both populations of the two subspecies exhibited partial self-compatibility ISI values when outcrossed within the population, the values for ssp *verrucosa* ms were considerably higher. Given that these populations were preferentially self-pollinating when crossed from outside populations, it would appear that this taxon is more oriented towards selfing than ssp *formosa* ms. The production of some seed in crosses with a non-preferred pollen source however, indicates that reproductive isolation is not complete and some ability to outcross with related taxa has been preserved. The similar levels of seed set by ssp *formosa* ms regardless of pollen source, are suggestive of a mixed mating system. Although an allozyme study undertaken to confirm these differences failed to find sufficient polymorphism for a complete analysis, observations did confirm that ssp *formosa* ms had a mixed mating system (Broadhurst 1998).

The differences in timing and length of flowering between the *G. verrucosa* taxa may also be indicative of reproductive differences. The later flowering of the two ssp *verrucosa* ms populations may reflect an ecological gradient as flowering moves across the south-west botanical district from the north-west to the south-east. Indeed, in a population approx 50 km south of Kalbarri where both subspecies co-occur, some overlap in flowering has been noted (Broadhurst 1998). However, this population appears to be a hybrid zone where the introgression of genetic material from ssp *formosa* ms to ssp *verrucosa* ms has occurred, possibly explaining the flowering overlap (Broadhurst *et al.* 2001). At another site located to the east of Kalbarri, several ssp *verrucosa* ms plants co-occur with an intermediate population. Flowering patterns here are quite distinct with the intermediate plants finishing prior to ssp *verrucosa* ms commencing flowering (Broadhurst 1998) suggesting that some underlying genetic, rather than ecological component, influences flowering patterns.

Seed set in the intermediate population at Hutt River 2 was not consistent with trends observed in either of the two subspecies. Since evolutionary shifts in breeding strategy can be mediated through a series of mixed mating systems (Stebbins 1957), this population could represent a transitional form between ssp *formosa* ms and ssp *verrucosa* ms. The high levels of natural seed set, significantly higher selfing rates, and strong preference for self-pollination in the intermediate population suggest that this is not a transitional form. The Hutt River 2 population belongs to a group of populations thought to be of ancient hybrid origin (Broadhurst *et al.* 1999) and as such a selfing mechanism would ensure reproductive success in the event of reproductive isolation from parental types.

Differences in breeding strategies are themselves not necessarily indicative of systematic separation. However, speciation often follows events which prevent gene flow and promote strong natural selection (Grant 1981). The ssp *verrucosa* ms is widely distributed with many populations occurring in the transitional-rainfall zone, a region characterised by the evolution of small, disjunct populations (Hopper 1992). When pollen movement is limited, morphological and physiological traits which promote selfing may be favoured, particularly where plant density is low or pollinators scarce (Jain 1976; Lloyd 1980; Schemske & Lande 1985). Self-fertilisation is commonly associated with ecological radiation into temporary, pioneer habitats (Stebbins 1957; Jain 1976; Lloyd 1980). The ssp *verrucosa* ms occurs in drier, more marginal habitats, and a shift towards selfing would ensure reproductive success in a difficult and unpredictable environment, particularly given the periodic drought experienced in the transitional rainfall zone. Retaining some ability to outcross may be significant during range expansions and contractions facilitated by environmental fluctuation, and lead to gene exchange between populations and taxa.

Reproductive strategy(ies) vary within the *G. verrucosa* taxa. The ssp *formosa* ms employs a mixed-mating system while ssp *verrucosa* ms is more oriented towards a selfing strategy. The intermediate population exhibited a strong self-compatible mechanism, suggesting that it may be the product of hybridisation between the two subspecies.

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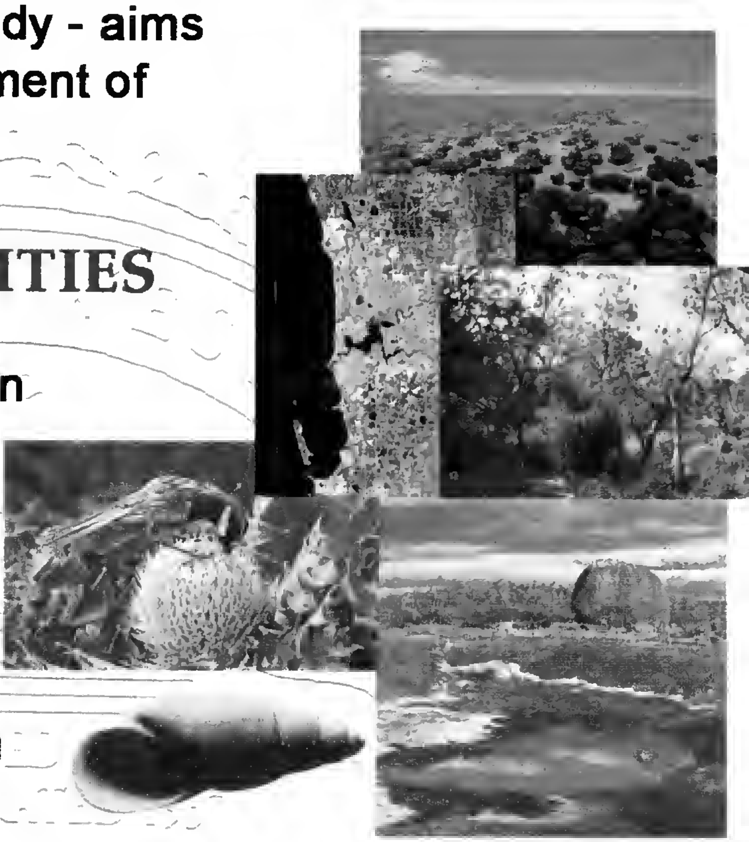

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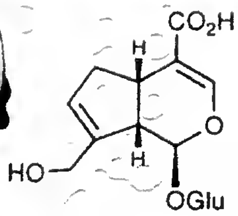

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Corolla venation in Stylidiaceae

J A Wege

Department of Botany, The University of Western Australia, Crawley WA 6009
email: triggerplants@hotmail.com

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Abstract

Corolla venation in 112 species of Stylidiaceae was studied using light microscopy. *Levenhookia*, *Phyllachne* and two annual species of *Stylidium* exhibit the simplest pattern of venation in which the midvein remains unbranched or, as observed in *P. colensoi*, branches once. In *Forstera*, *Oreostylidium* and the remaining species of *Stylidium*, the midvein branches at the base producing an almost palmate pattern that varies in complexity according to the species in question. In *Stylidium*, the labellum always has a simpler pattern of venation than its four larger counterparts; the midvein often remaining unbranched. A feature unique to the *S. scandens* complex is a vascular trace in the long basal labellum appendages. The throat appendages of 10 species were found to have a vascular supply.

Keywords: corolla, venation, Stylidiaceae, taxonomy, systematics

Introduction

The family Stylidiaceae comprises five genera and over 240 species that are characterized by the presence of a central floral column that bears the anthers and stigma at the apex. In the most prolific genus, *Stylidium*, the column is typically touch-sensitive, hence the common name of "trigger plants". The flowers in all family members are usually pentamerous, although some species of *Phyllachne* and *Forstera* are variable for this trait and have between five and nine corolla segments (Mildbraed 1908; Allan 1961; Curtis 1963). *Phyllachne*, *Forstera* and *Oreostylidium* all have corolla lobes that are regularly arranged and of similar size. The two remaining genera have a highly modified anterior petal, termed the labellum, which is hooded over the column in *Levenhookia*, and greatly reduced (yet morphologically diverse) in *Stylidium*. The corolla lobes in all genera are united at the base to form a corolla tube.

Gustafsson (1995) examined corolla venation patterns in five species of Stylidiaceae as part of a broader study on the petal venation trends within the Asterales and, in a systematic study on Stylidiaceae, Laurent *et al.* (1999) further investigated this character in an additional 20 species. Corolla venation patterns are shown in the illustrations from a recent taxonomic revision of *Stylidium* subgenus *Andersonia* (Bean 2000), although they are not specifically mentioned in the text. The present study examined corolla venation patterns in a broad range of species, with the aim of investigating differences in venation between the four larger corolla lobes and the labellum. The throat appendages (or paracorolla) located at the base of the corolla lobes in many species of *Stylidium* and *Levenhookia* were also examined for the presence of a vascular supply. This research forms part of a wider study on the systematics of Stylidiaceae.

Methods

One hundred and twelve species were investigated, including representatives from all genera and each of the main morphological groupings within *Stylidium* (Table 1). Whole corollas were cleared in 70% ethanol and, where necessary, the labellum (which typically has a thickened area of tissue termed the boss) was cleared in 25% sodium hydroxide. Corolla venation patterns were then studied using light microscopy. Several flowers of each taxon were studied from one or more populations. Herbarium voucher specimens will be lodged at PERTH on completion of related research.

Results and Discussion

In all of the taxa examined, a solitary vascular trace feeds each of the corolla segments. The trace remains solitary in both *Phyllachne uliginosa* (Gustafsson 1995) and *P. clavigera* (Laurent *et al.* 1999); however, in *P. colensoi* the vein may branch once (Fig 1A). In contrast, the corolla veins in *Forstera tenella* are sparsely branched; the midvein diverges near the base of the corolla lobes and the lateral branches, which often branch again, extend towards the margins of the lobes (Fig 1B). This general pattern was first observed by Gustafsson (1995) and has also been recorded for *F. bidwillii* and *F. bellidifolia* (Laurent *et al.* 1999).

In accordance with previous observations, species of *Levenhookia* have a single unbranched vascular trace in both the corolla lobes and the hooded labellum (Fig 1C). An unbranched trace also occurs in both *Stylidium despectum* and *S. utricularioides* (Fig 1D) and is evident in the illustrations of *S. cordifolium* and *S. divergens* provided by Bean (2000).

In the majority of trigger plants, the vascular trace diverges at the base of each corolla lobe producing an

Table 1

Specimens of Stylidiaceae examined for the description of corolla venation patterns. Species are organized alphabetically under the groupings of Mildbraed (1908). Species in which a solitary vein was observed in the labellum are indicated with an asterix. JAW = J A Wege.

Phyllachne: _P. colensoi_ (Hook f) Bergg JAW 189.

Forstera: _F. tenella_ Hook f JAW 559.

Oreostylidium: _O. subulatum_ (Hook f) Berggr JAW 558.

Levenhookia: *_L. leptantha_ Benth JAW 194a, JAW 251; *_L. pauciflora_ Benth JAW 209, JAW 363, JAW 380; *_L. preissii_ (Sond) F Muell JAW 151, JAW 154; *_L. pusilla_ R Br JAW 100, JAW 179, JAW 360; *_L. stipatata_ F Muell JAW 96, JAW 120, JAW 512.

Stylidium subgenus _Centridium_ (Lindl) Mildbr: *_S. calcaratum_ R Br JAW 7, JAW 196, JAW 500; *_S. edentatum_ Lowrie & Carlquist JAW 370, JAW 371; *_S. perpusillum_ Hook f JAW 248, JAW 364.

Stylidium subgenus _Forsteropis_ (Sond) Mildbr: *_S. imbricatum_ Benth JAW 563; *_S. leeuwinense_ Lowrie & Kenneally JAW 522; *_S. preissii_ (Sond) F Muell JAW 66; *_S. semaphorum_ Lowrie & Kenneally JAW 523.

Stylidium subgenus _Andersonia_ (R Br) Mildbr: *_S. candellabrum_ Lowrie & Kenneally JAW 483; *_S. lobuliflorum_ F Muell JAW 478, JAW 481; *_S. ensatum_ A R Bean JAW 470; *_S. schizanthum_ F Muell JAW 473, JAW 480.

Stylidium subgenus _Tolypangium_ (Endl) Mildbr:

Section _Despectae_ Mildbr: *_S. despectum_ R Br JAW 304, JAW 440; *_S. inundatum_ R Br JAW 138, JAW 274, JAW 416; *_S. longitubum_ Benth JAW 314; *_S. obtusatum_ Sond JAW 508; *_S. periscelianthum_ Erickson & Willis JAW 218, JAW 235; *_S. pulchellum_ Sond JAW 116, JAW 273; *_S. roseo-alatum_ Erickson & Willis JAW 118, JAW 281; *_S. udusicola_ Lowrie & Kenneally JAW 329; *_S. utricularioides_ Benth JAW 125, JAW 452.

Section _Debilia_ Mildbr: *_S. semipartitum_ F Muell JAW 471, JAW 476.

Section _Floodia_ Mildbr: *_S. turbinatum_ Lowrie & Kenneally JAW 477, JAW 484.

Section _Sparsifoliae_ (Benth) Mildbr: _S. glandulosum_ Salisb JAW 65.

Section _Repentes_ Mildbr: _S. repens_ R Br JAW 286; *_S. sacculatum_ (Erickson & Willis) Lowrie, A H Burb & Kenneally JAW 19.

Section _Guttatae_ Mildbr: _S. guttatum_ R Br JAW 119, JAW 175, JAW 461.

Section _Junceae_ Mildbr: _S. junceum_ R Br JAW 30, JAW 279; _S. laciniatum_ C A Gardner JAW 185; _S. squamosotuberosum_ Carlquist JAW 180.

Section _Verticillatae_ (Benth) Mildbr: _S. galioides_ C A Gardner JAW 375; _S. nonscandens_ Carlquist JAW 21, JAW 219, JAW 224; _S. scandens_ R Br JAW 297, JAW 377, JAW 423, JAW 443, JAW 462; _S. verticillatum_ F Muell JAW 159.

Section _Echinospermum_ Mildbr: _S. limbatum_ F Muell JAW 256.

Section _Saxifragoideae_ Mildbr: _S. aeonioides_ Carlquist JAW 397; _S. albolilacinum_ (Erickson & Willis) Lowrie & Carlquist JAW 222; _S. amoenum_ R Br JAW 103, JAW 421; _S. articulatum_ R Br JAW 162; _S. assimile_ R Br JAW 178; _S. barleei_ F Muell JAW 98, JAW 444; _S. brunonianum_ Benth JAW 284, JAW 400; _S. carlquistii_ Lowrie JAW 28, JAW 417; _S. carnosum_ Benth JAW 490; _S. diuroides_ Lindl JAW 31, JAW 287, JAW 418; _S. glabrifolium_ Lowrie & Kenneally JAW 392; _S. lineatum_ Sond JAW 110, JAW 122; _S. lowrieanum_ Carlquist JAW 147, JAW 438; _S. luteum_ R Br JAW 169, JAW 305; _S. maitlandianum_ E Pritzel JAW 211; *_S. pritzelianum_ Mildbr JAW 524; _S. rupestre_ Sond JAW 61, JAW 366; _S. spathulatum_ R Br JAW 437; _S. squamellosum_ DC JAW 355, JAW 390; _S. striatum_ Lindl JAW 289; _S. violaceum_ R Br JAW 163, JAW 428.

Section _Lineares_ (Benth) Mildbr: *_S. arenicola_ Carlquist JAW 255b, JAW 257; _S. caespitosum_ R Br JAW 181; *_S. ciliatum_ Lindl JAW 102, JAW 420; _S. drummondianum_ Lowrie & Carlquist JAW 192, JAW 326; _S. hispidum_ Lindl JAW 158, JAW 278; _S. piliferum_ R Br JAW 14, JAW 208; _S. spinulosum_ R Br JAW 164, JAW 177.

Section _Squamosae_ (Benth) Mildbr: _S. affine_ Sond JAW 499; _S. albomontis_ Carlquist JAW 56, JAW 79; _S. caricifolium_ Lindl JAW 238; _S. crossocephalum_ F Muell JAW 22, JAW 207; _S. hirsutum_ R Br JAW 165, JAW 298; _S. leptocalyx_ Sond JAW 29, JAW 513; _S. macranthum_ Carlquist JAW 64, JAW 365; _S. maritimum_ Lowrie, Coates and Kenneally JAW 491; _S. nungarinense_ S Moore JAW 264, JAW 356; _S. pilosum_ Labill JAW 373; _S. plantagineum_ Sond JAW 301; _S. pseudohirsutum_ Mildbr JAW 302; *_S. scabridum_ Lindl JAW 509; _S. schoenoides_ DC JAW 84, JAW 348.

Stylidium subgenus _Nitrangium_ (Endl) Mildbr:

Section _Sonderella_ Mildbr: _S. divaricatum_ Sond JAW 115, JAW 453; _S. kalbarriense_ Lowrie & Kenneally JAW 198, JAW 317; *_S. macrocarpum_ (Benth) Erickson & Willis JAW 285; _S. ricae_ Carlquist JAW 345; _S. tenuicarpum_ Carlquist JAW 45, JAW 395; _S. torticarpum_ Lowrie & Kenneally JAW 404, JAW 406.

Section _Appressae_ Mildbr: *_S. adpressum_ Benth JAW 205, JAW 514; *_S. choreanthum_ Erickson & Willis JAW 255a, JAW 258.

Section _Thyrsiformes_ (Benth) Mildbr: _S. bulbiferum_ Benth JAW 516; _S. burbidgeanum_ Lowrie & Kenneally JAW 405, JAW 409; _S. confluens_ Banyard & James JAW 341, JAW 342; _S. crassifolium_ R Br JAW 92, JAW 433; _S. dichotomum_ DC JAW 40, JAW 454; _S. elongatum_ Benth JAW 197, JAW 318; *_S. eriopodum_ DC JAW 294; _S. induratum_ M Scott JAW 335; _S. lateriticola_ Kenneally JAW 457; *_S. leptophyllum_ DC JAW 20, JAW 133; _S. merrallii_ (F Muell) T Durand & B D Jackson James sn (Yannamooning Rock); _S. neglectum_ Mildbr JAW 130, JAW 131; _S. pycnostachyum_ Lindl JAW 132, JAW 408; _S. uniflorum_ Sond JAW 48, JAW 139.

Section _Rhynchangium_ Benth: *_S. adnatum_ R Br JAW 97, JAW 435, JAW 520; *_S. falcatum_ R Br JAW 87; *_S. fasciculatum_ R Br JAW 143, JAW 434; *_S. rhynchocarpum_ Sond JAW 141, JAW 313.

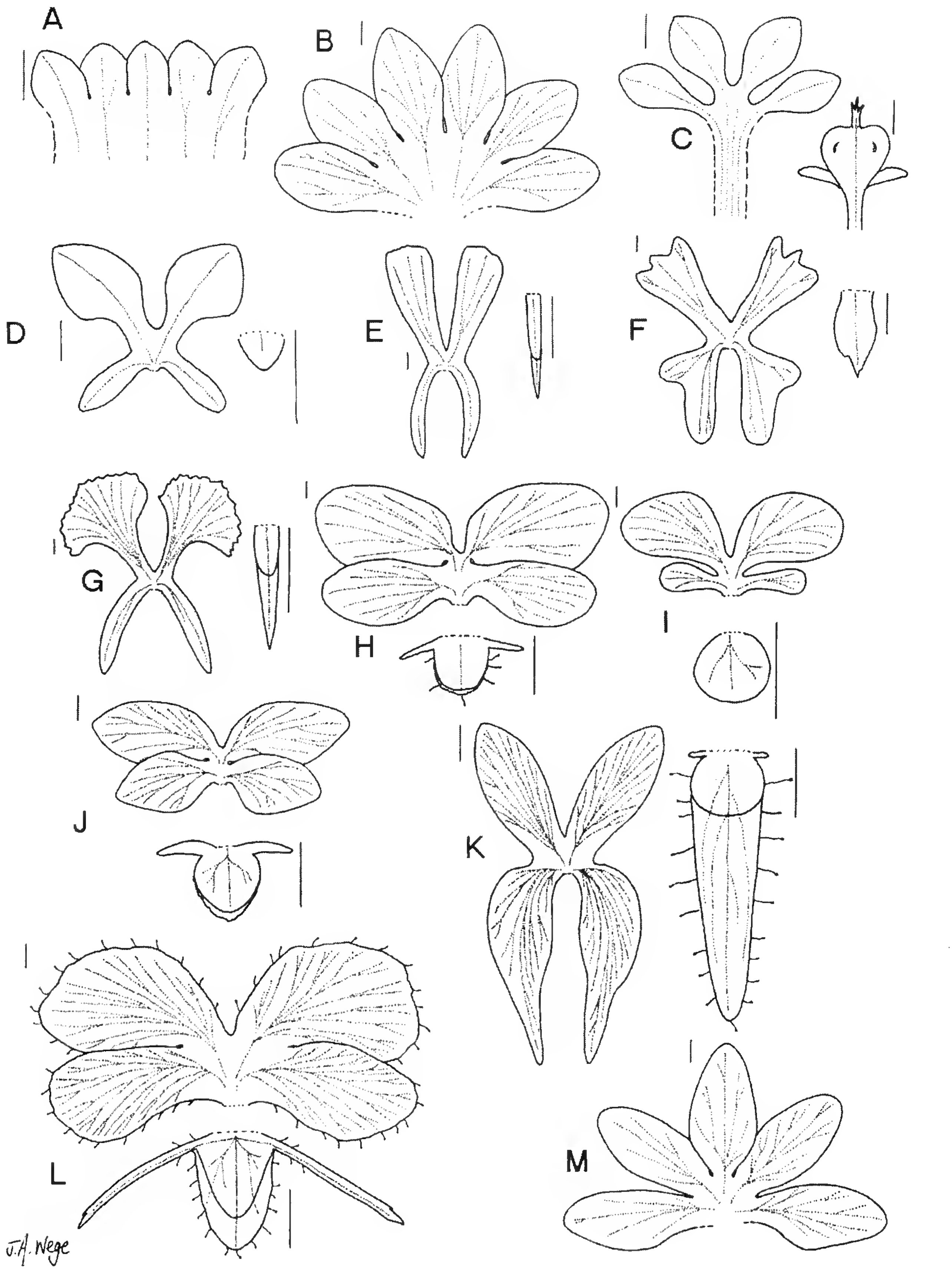

Figure 1. Corolla venation patterns in Stylidiaceae. Where present, the labellum has been detached and drawn separately at a different scale: in vertically-paired flowers it is positioned to the right of the four main corolla lobes, whereas in laterally-paired flowers it is situated underneath. Scale bars at 1 mm. **A**: *Phyllachne colensoi*; **B**: *Forstera tenella*; **C**: *Levenhookia preissii*; **D**: *Stylidium utricularioides*; **E**: *S. obtusatum*; **F**: *S. calcaratum*; **G**: *S. choreanthum*; **H**: *S. fasciculatum*; **I**: *S. burbidgeanum*; **J**: *S. glandulosum*; **K**: *S. crossocephalum*; **L**: *S. scandens*; **M**: *Oreostylidium subulatum*.

almost palmate pattern that varies in complexity across the genus (Figs 1E-L). In those species that bear corolla lobes of unequal size, the smaller lobes often have a solitary vein whilst their larger counterparts have a branched pattern (*e.g.* Fig 1E; *cf* Figs 3G, 5C & 7F of Bean 2000). The largest flowers, such as those belonging to subgenus *Tolypangium* sections *Squamosae* and *Verticillatae*, have the most complex pattern of venation with a number of branches occurring along the midvein and at the tips of the lateral branches (*e.g.* Figs 1K & 1L). As recorded by Laurent *et al.* (1999), *Oreostylidium* has a branching venation pattern similar to that found in *Forstera* and many species of *Stylidium* (Fig 1M).

The labellum in *Stylidium* has a simpler pattern of venation than the larger corolla lobes and in many species the trace is unbranched (Table 1; Fig 1D-H). Alternatively, the midvein branches at the base to produce two lateral veins that may divide again (Figs 1I & 1J). Additional branching occasionally occurs along the length of the midvein (Fig 1K). *Stylidium scandens* is unique in having prominent lateral veins that extend along the length of the basal appendages (Fig 1L).

Although the throat appendages typically lack a vascular supply, veins are present in the conspicuous wing-like appendages of species belonging to *Stylidium* subgenus *Forsteropsis* and in subgenus *Tolypangium* sections *Verticillatae* and *Squamosae* (Table 2; Fig 2). The wing-like appendages are attached to the base of the anterior corolla lobes and, where present, the vascular supply originates from the main trace entering the anterior corolla lobe. The additional tooth-like throat appendages attached to the posterior petals of these species do not receive a vascular supply.

Table 2

Species of *Stylidium* in which the throat appendages (paracorolla) have a vascular supply. S = solitary vein; B = branching vein.

Subgenus	Section	Species	Vasculature
Forsteropsis		*S. leeuwinense*	S
Tolypangium	*Verticillatae*	*S. galioides*	S or B
		S. scandens	S or B
	Squamosae	*S. affine*	S
		S. caricifolium	B
		S. hirsutum	S or B
		S. macranthum	B
		S. maritimum	S or B
		S. nungarinense	B
		S. pseudohirsutum	S

Within each of the above-mentioned subgeneric groupings there is often variation in the presence of and the pattern of throat appendage venation. Within subgenus *Forsteropsis*, the wing-like throat appendages in *S. leeuwinense* have a solitary vein and those in *S. semaphorum* and *S. imbricatum* have no vascular supply, whilst *S. preissii* lacks the wing-like appendages altogether. Within section *Squamosae*, the vascular trace may be absent (*e.g. S. crossocephalum, S. leptocalyx, S. pilosum*), remain solitary (*e.g. S. pseudohirsutum*) or branch into two to four traces (*e.g. S. caricifolium, S. macranthum*). Similar variation is also evident within section *Verticillatae* with the vascular trace absent in *S. nonscandens* and *S. verticillatum*, but present and typically branched in *S. scandens*. Interestingly, two yellow-flowering populations of *S. scandens* (JAW 423 and JAW 443) lack basal labellum appendages and have a solitary throat appendage vein. Throat appendage and labellum venation patterns may provide useful characters to taxon delimitation in a revision of this group. However, given that the morphology of the labellum and the throat appendages can be variable within and between populations of the same species (Raulings 2001; personal observations) the venation patterns should be assessed across more populations to determine whether they are taxonomically reliable characters. This is a salient point given that flowers of *S. galioides*, a species known from only one locality, were found here to have throat appendages with either a solitary or a branched vascular trace. This variation was also evident between populations of *S. hirsutum* and within populations of *S. maritimum*.

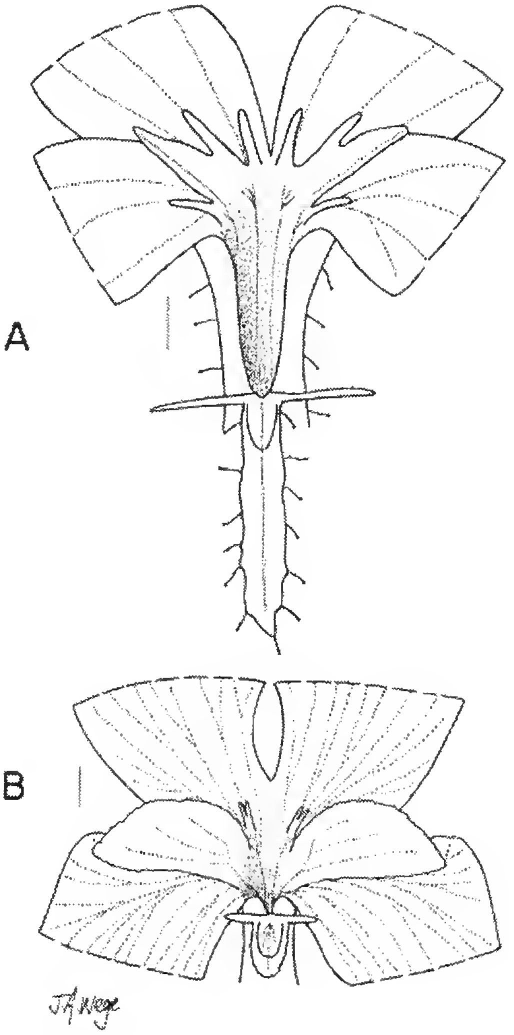

Figure 2. Examples of throat appendage (paracorolla) venation in *Stylidium*. Scale bars at 1 mm. **A:** *S. leeuwinense*; **B:** *S. maritimum*.

The different patterns of corolla venation described here are yet another example of the immense diversity found within Stylidiaceae and particularly within *Stylidium*. Venation patterns may provide useful characters in the study of systematic relationships within the family and potentially in the definition of species boundaries.

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Variation in seed production and germination in 22 rare and threatened Western Australian *Verticordia* (Myrtaceae)

A Cochrane[1], K Brown[2], S Cunneen[3] & A Kelly[4]

[1]Threatened Flora Seed Centre, Department of Conservation and Land Management, Locked Bag 104,
Bentley Delivery Centre, Perth WA 6983
[2]Environmental Weeds Action Network, 108 Adelaide Terrace, East Perth WA 6000
[3]CSIRO Centre for Mediterranean Agricultural Research, Floreat WA 6014
[4]24 Carnarvon St, East Victoria Park WA 6100
email: annec@calm.wa.gov.au

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Abstract

This study investigates the reproductive potential of 22 rare and threatened Western Australian taxa in the genus *Verticordia* (Myrtaceae) over a 5-year period. Considerable inter- and intra-specific variation in both seed production and germinability was demonstrated for the majority of taxa. The seed to flower ratio, or "seed set", ranged from 0% to 68% with an overall mean of 21% in 82 accessions representing seed from 48 populations of the 22 taxa. Percentage germination ranged from 7% to 100% with an average of 49% for 68 accessions. The precariously low annual reproductive capacity of some of the more restricted and critically endangered taxa threatens their survival and unexpected disturbance events may result in population decline or even localised extinction. Mitigation measures such as the reintroduction of plant material into new sites and the enhancement of existing populations through additional plantings may be warranted for many of Western Australia's rare and threatened *Verticordia*.

Keywords: *Verticordia*, seed production, germination

Introduction

Verticordia (family Myrtaceae, sub-family Leptospermoideae) consists of woody perennials largely endemic to the South West Botanical Province of Western Australia. This genus occupies a prominent place in many shrub and heathland communities along with other myrtaceaous genera such as *Beaufortia, Calytrix, Agonis, Leptospermum, Melaleuca, Chamelaucium* and *Calothamnus*. There has been a considerable increase in our taxonomic understanding of the genus in the past decade, and a revision in 1991 identified 3 subgenera, 24 sections, 97 species, and 62 subspecies and varieties (George 1991). Material was later re-examined and 100 species and 43 infraspecific taxa were described for the genus (George & George 1994). Many taxa in the genus are considered of high conservation value. There were 76 taxa of *Verticordia* on the Western Australian Department of Conservation and Land Management's Declared Rare and Priority Flora List (Atkins 1998). Seventeen of these were declared rare (WA Government Gazette 1999), and five of these were ranked under IUCN criteria as Critically Endangered by CALM's Western Australian Threatened Species and Communities Unit (Anon 1998b). Many populations are at risk of local extinction in the near future due to a range of threatening processes. These include disease, weed invasion, salinity, small population sizes, habitat fragmentation and/or continued land clearing.

The genus possesses many species with great potential for ornamental horticulture (George 1990). The often prominently displayed feathery flowers are borne singly but appear as heads or spikes and are generally brightly coloured, ranging from yellow to red to purple. The flowers are long lasting, and can be picked for the cut flower market. Between 1996 and 1998 over 1 million flowering stems of 23 taxa of *Verticordia* were bush picked from private, crown lands and cultivated stands for the cut flower industry (L Rohl, CALM, unpublished data). Over-picking of flowers from the wild has been impacting on wild populations of a number of species (*e.g. V. eryocephala*) with detrimental effects (McEvoy & True 1995).

Although there have been a number of studies on pollen germination and tissue culture propagation in *Verticordia* (McComb *et al.* 1986; Tyagi *et al.* 1992), there has been limited research conducted on the reproductive biology of particular species in the genus. Seed appears to be of the dependent embryo type (small embryos relative to the endosperm) according to classification by Atwater & Vivrette (1987). Tyagi *et al.* (1991) reported that in *Verticordia* only a single seed is set despite ovule numbers of up to 13 in some taxa. Our experience has shown that on rare occasions 2 and 3 seed per flower may form in taxa with multiple ovules (A Cochrane, personal observations). Houston *et al.* (1993) report seed set (based on seed to flower ratio) for *V. nitens* averaging 27% with a range from 0.6% to 54% and 36% for *V. aurea*. Tyagi *et al.* (1991) also reported low seed set for a range of taxa in the genus.

Holm (1988) considered that pollinators for this genus were likely to be unspecialised insects, but postulated that *V. grandis* may be bird pollinated due to the flower structure. Houston *et al.* (1993) reported apparent pollinator mutualism in *V. nitens* and possibly in *V. aurea*. Profuse flowering in some species of *Verticordia* pointed towards intense competition for pollinators (Holm 1988), and given the great range of floral morphology, scent, colour and flowering times, it is possible that many pollinators will be found to be highly specific.

Verticordia have indehiscent fruits (nuts) that usually contain a single seed and are shed annually. They are never discharged but the entire flower dries and breaks off below the receptacle. It is thought that dormancy in some members of the Myrtaceae (for example in *Chamelaucium*, *Verticorida* and *Darwinia*) is controlled by the seed coat inside the fruit that breaks down in time due to weathering and soil disturbance (Beardsell *et al.* 1993a). *Verticordia* plants for the nursery industry have traditionally been propagated vegetatively due to inadequate knowledge of seed collection and germination techniques (Watkins & Shepherd 1984). Relatively few studies have been undertaken on seed germination in this genus, although Ashby (1961) reported some success with *V. picta*, *V. chrysantha* and *V. brownii*. Over the past 5 years considerable developments have been made in the techniques required for successful germination of a range of Western Australian species (see review by Bell *et al.* 1993; Cochrane & Kelly 1996). Smoke responsiveness has been demonstrated in the genus (Dixon *et al.* 1995) and after-ripening requirements can be overcome with the addition of the growth hormone gibberellic acid (Cochrane *et al.* unpublished observations).

Over the past 5 years, seeds of a large range of threatened taxa in the genus *Verticordia* have been collected for conservation in Western Australia's *ex situ* program. The aim of this program is to conserve the genetic diversity of threatened taxa under low moisture and low temperature conditions for long periods of time (> 50 years) until material is required for recovery purposes (Cochrane & Coates 1994).

This present study assessed the reproductive potential of a range of rare and threatened taxa in the genus *Verticordia* through an analysis of seed set and germination data collected over a 5 year period. These data are useful as a basis for recommendations for conservation and management of the populations. Sound knowledge of germination mechanisms will enable adequate monitoring of seed viability in storage and enhances the opportunity to provide whole plants for recovery.

Methods

All *Verticordia* seeds used in this study were collected from wild populations between January 1994 and December 1998. Site names have been abbreviated due to the confidentiality of locational information for conservation flora. Seed stocks are held *ex situ* at the Department of Conservation and Land Management's Threatened Flora Seed Centre, a seed-based genebank for the conservation of genetic material from rare and threatened taxa. Seeds were tested for germinability freshly collected and, in many cases, after moisture content reduction and storage at –20 °C for periods of up to 5 years.

Seed set was assessed by sectioning 3 replicate samples of 100 old flowers (fruits) through the hypanthium to establish the presence or absence of a healthy seed (swollen, moist, white embryo). Calculation of seed set by the cut test method was based on the proportion of seeds to old flowers rather than the seed to ovule ratio. Seed to flower ratio was considered to be a more useful indicator of reproductive potential than seed to ovule ratio as rarely did more than 1 ovule per flower set. "Seed set" was therefore defined as the number of intact and healthy seeds for a given number of flowers. Some predation of developing ovules was observed during cut tests, although the level of predation was not quantified.

Seed germination trials were conducted under laboratory conditions. Seed sample sizes were dependent on the number of old flowers (fruits) collected, as well as the number of seeds obtained by the cut test (seed set) and ranged from 5 to over 1000 seeds ($\bar{x}$ 61). To aid germination, seeds were completely excised from the old flowers with a scalpel under a dissecting microscope. Prior to seed coat removal, flowers were soaked in distilled water for a minimum of 2 hours to soften the seed coat. Seeds were germinated in 90 mm glass Petrie dishes on a 0.75% (w/v) agar solution in temperature and light controlled incubation cabinets, using a 12-hour photoperiod. Cabinets were set at a constant 15 °C. A 2% solution of Previcure fungicide was added to the agar solution to inhibit fungal growth. Seeds were not surface sterilised prior to incubation. Petrie dishes were checked twice weekly and germination was determined by radicle emergence.

Previous research (A Cochrane, unpublished data) has indicated that many species of *Verticordia* are smoke responsive, and the seeds of those species requiring aqueous smoke treatment for optimum germination were soaked for 24 hours in a smoke solution obtained from Perth's Kings Park and Botanic Gardens and produced according to Dixon *et al.* (1995). After soaking, seeds were rinsed with distilled water prior to incubation. Growth promoters have been found to be necessary to cue germination in fresh seed of *Verticordia*, and the growth hormone gibberellic acid (GA_3) was added to the agar medium at either 25 mg L^{-1} or 10 mg L^{-1}.

Results

The number of ovules per flower in the genus *Verticordia* varies between species and ranges from 1 to 8 for the 22 taxa studied (Table 1). Rarely did more than 1 seed per flower reach maturity and as such the seed to ovule ratio ranged from 0.125 to 1 (Table 1). There was a broad range of inter- and intra-specific variation in seed set and germination within the genus (Table 2). The mean seed set for all collections was 21% (± 1.85) with a range from 0 to 68%. Population seed set was never greater than 68%, although seed set for a single individual within a taxon did reach 90% in *V. staminosa* subsp *cylindraceae* var *erecta* (see Fig 1). The mean percentage germination was 49% (± 2.96), range 7-100%, for 68 accessions.

Fourteen taxa are known to be obligate seeders; 4 are respouters, with 3 considered to have the potential to both resprout and seed. Information on the reproductive

Table 1

Fire response, number of ovules per flower, seed to ovule ratio, and percentage seed set and germination for 22 rare and threatened taxa in the genus *Verticordia*.

Species	Fire Response (Seeder/ Resprouter)	Ovules per flower	Seed/ ovule ratio	% seed set (± se, range)	% seed germination (± se, range)
Subgenus Chrysoma					
V. endlicheriana Schauer var *angustifolia* AS George (sect Chrysoma)	Both	2	0.5	11 (11)	24 (24)
V. staminosa ssp *cylindracea* AS George var *cylindracea* (sect Synandra)	Resprouter	2	0.5	58.0 ± 3.6 (53-65)	79.4 ± 11.6 (57-96)
V. staminosa ssp *cylindracea* AS George var *erecta* (sect Synandra)	Resprouter	2	0.5	33.5 ± 25.5 (8-59)	84.5 ± 3.5 (81-88)
V. staminosa C Gardner & AS George ssp *staminosa* (sect Synandra)	Resprouter	2	0.5	32.0 ± 6.1 (20-40)	76.7 ± 12.0 (60-100)
Subgenus Eperephes					
V. albida AS George (sect Pennuligera)	Seeder	7 or 8	0.125-0.14	43.8 ± 5.02 (20-68)	30.4 ± 8.6 (10-87)
V. comosa AS George (sect Pennuligera)	Seeder	8	0.14	17 (17)	47 (47)
V. attenuata AS George (sect Verticordella)	Seeder	6	0.17	22.8 ± 8.9 (8-48)	37.5 ± 5.9 (26-54)
V. bifimbriata AS George (sect Verticordella)	Seeder	6	0.17	33.5 ± 16.5 (17-50)	68 (68)
V. carinata Turcz (sect Verticordella)	Seeder	6	0.17	16.0 ± 2.1 (13-20)	34.7 ± 11.9 (11-48)
V. hughanii F Muell (sect Verticordella)	Both	8	0.143	15.0 ± 9 (6-24)	63.0 ± 6.0 (57-69)
V. spicata ssp *squamosa* F Muell (sect Verticordella)	Seeder	6 or 7	0.17-0.14	8.6 ± 2.1 (0-19)	43.0 ± 8.6 (7-86)
Subgenus Verticordia					
V. densiflora Lindley var *caespitosa* Turcz (sect Corymbiformis)	Seeder	1 or 2	1-0.5	25 (25)	73 (73)
V. densiflora Lindley var *pedunculata* AS George (sect Corymbiformis)	Seeder	1 or 2	1-0.5	25 (25)	78 (78)
V. dasystylis ssp *oestopoia* AS George (sect Penicillaris)	Unknown	2	1-0.5	6 (6)	75 (75)
V. fimbrilepis ssp *australis* Trucz (sect Verticordia)	Seeder	2	0.5	22.7 ± 4.5 (14-29)	56.7 ± 21.5 (15-87)
V. fimbrilepis ssp *fimbrilepis* Trucz (sect Verticordia)	Seeder	2	0.5	24.0 ± 2.5 (15-39)	53.8 ± 6.5 (25-86)
V. harveyi Benth (sect Verticordia)	Seeder	2	0.5	11.5 ± 3.1 (3-25)	33 (33)
V. helichrysantha F Muell Ex Benth (sect Verticordia)	Both	4 or 5	0.25-0.2	19.3 ± 8.4 (4-33)	47.3 ± 9.940 (29-63)
V. pityrhops AS George (sect Verticordia)	Seeder	2	0.5	5 (5)	-
V. plumosa var *ananeotes* (Desf) Druce (sect Verticordia)	Resprouter	4	0.25	5.4 ± 1.6 (2-11)	26.0 ± 7.0 (11-42)
V. plumosa var *pleiobotrya* (Desf) Druce (sect Verticordia)	Seeder	4	0.25	24 (24)	72 (72)
V. plumosa var *vassensis* (Desf) Druce (sect Verticordia)	Seeder	4	0.25	7.7 ± 2.6 (0-17)	46.0 ± 8.7 (25-75)

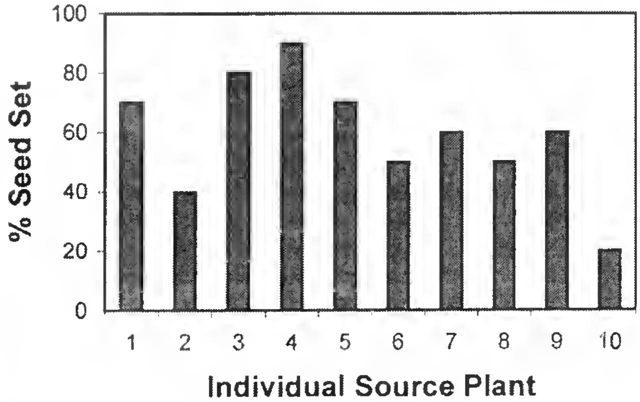

Figure 1. Differences in seed set between individual plants for *V. staminosa* subsp *cylindracea* var *erecta* 1995 Site MG.

strategy for one taxon (*V. dasystylis* subsp *oestopoia*) was not known.

Seed production and germinability for the 82 collections of *Verticordia* exhibited year to year (Fig 2A-C), population to population (Fig 3), plant to plant (Fig 4) and seasonal (Figs 5, 6) variation. The mean seed set and germination for each taxon was calculated (Table 1); however, the wide spatial and temporal variation make these figures somewhat misleading. Nonetheless these data provide a reference point to illustrate the variation between taxa. There were no apparent trends evident for seed set and germination or for reproductive strategy within the different subgenera or sections (Table 1). There was also no correlation between condition of the population as determined by location (road verge versus reserve or bushland) and health of population (degraded or healthy) and reproductive potential (Table 2). In addition, there was no correlation between intra-specific population size and levels of seed set (Table 2).

Discussion

Seed Production

It would appear from this study that rare and threatened taxa within the genus *Verticordia* exhibit excess flower production and a corresponding low seed to flower ratio, in keeping with previous results for common taxa in the genus (Tyagi *et al.* 1991; Houston *et al.* 1993). Lee & Bazzaz (1982) consider it more cost beneficial for plants to produce excess flowers and only allocate energy for seed production to those flowers with a minimal level of surviving embryos. Flower production is less energy draining than the necessary proteins and lipids required for seed production. Surplus flower production may enable plants to exploit favourable conditions such as increased resources or pollinator activity that occur unpredictably. Seasonal and yearly changes in seed set may be due to changes in flower density during the flowering period that may in turn affect pollinator assemblages, abundance and behaviour. It may also give a plant the opportunity to increase its

Table 2

Site location, condition (D=degraded H=healthy RV=road verge P=reserve, park, remnant bush), population size, time of collection, number of plants sampled, percentage seed set, and germination for 22 rare and threatened taxa in the genus *Verticordia*.

Species	Location	Condition	Population size	Time of collection	Plants sampled	% seed set	% germination	Seeds used in germination trials
V. albida	Site L	H RV	16	Jan-96	16	24	19	54
V. albida	Site L	H RV	16	Jan-97	12	20	30	53
V. albida	Site S	D RV	<20	Jan-96	5	50	87	8
V. albida	Site S	D RV	<20	Jan-97	7	56	12	50
V. albida	Site TSE	D RV	<50	Jan-96	10	42	27	15
V. albida	Site TSE	D RV	<50	Jan-97	20	38	10	50
V. albida	Site WW	H P	1000+	Jan-95	8	46	-	-
V. albida	Site WW	H P	1000+	Jan-96	500	68	29	78
V. albida	Site WW	H P	1000+	Jan-97	25	50	29	31
V. attenuata	Site BH	D RV	<100	Mar-94	30	13	36	47
V. attenuata	Site E	D RV	<50	Mar-94	20	22	34	35
V. attenuata	Site E	D RV	<50	Feb-95	30	48	26	66
V. attenuata	Site R	D RV	1000+	Mar-94	50	8	54	28
V. bifimbriata	Site D	H P	<30	Jan-95	12	50	-	-
V. bifimbriata	Site D	H P	<30	Feb-99	15	17	68	28
V. carinata	Site NIT	H P	1000+	Apr-96	100	20	48	23
V. carinata	Site NIT	H P	1000+	Apr-97	400	13	45	38
V. carinata	Site NIT	H P	1000+	Apr-98	100	15	11	36
V. comosa	Site NETS	H RV/P	100+	Jan-97	30	17	47	19
V. dasystylis ssp *oestopoia*	Site BC	D RV	8	Nov-97	8	6	75	16
V. densiflora var *caespitosa*	Site FNR	H P	100+	Feb-99	20	25	73	22
V. densiflora var *pedunculata*	Site WLH	D RV	<50	Feb-99	20	25	78	18
V. endlicheriana var *angustifolia*	Site MB	H P	1000+	Feb-95	50	11	24	17
V. fimbrilepis ssp *australis*	Site KR	H P	500+	Jan-95	200	14	15	13
V. fimbrilepis ssp *australis*	Site KR	H P	500+	Feb-96	200	29	87	45
V. fimbrilepis ssp *australis*	Site KR	H P	500+	Feb-97	100	25	68	63
V. fimbrilepis ssp *fimbrilepis*	Site AT	D P	<50	Mar-97	25	15	30	40
V. fimbrilepis ssp *fimbrilepis*	Site AT	D P	<50	Feb-98	15	20	25	48
V. fimbrilepis ssp *fimbrilepis*	Site AT	D P	<50	Jan-96, Feb-96	8	39	79	168
V. fimbrilepis ssp *fimbrilepis*	Site J4	D RV	<50	Mar-97	40	17	62	29
V. fimbrilepis ssp *fimbrilepis*	Site J4	D RV	<50	Jan-98	30	20	32	54
V. fimbrilepis ssp *fimbrilepis*	Site J4	D RV	<50	Jan-96, Feb-96	30	31	56	168
V. fimbrilepis ssp *fimbrilepis*	Site J7	D RV	100+	Mar-97	50	32	73	81
V. fimbrilepis ssp *fimbrilepis*	Site J7	D RV	100+	Jan-96, Feb-96	150	28	86	99
V. fimbrilepis ssp *fimbrilepis*	Site JNR	H P	300+	Feb-98	250	15	82	71
V. fimbrilepis ssp *fimbrilepis*	Site NH	D RV	13	Jan-96	10	20	46	63
V. fimbrilepis ssp *fimbrilepis*	Site R	D RV	10	Jan-98, Feb-98, Mar-98	10	19	30	23
V. fimbrilepis ssp *fimbrilepis*	Site TR	H P	100	Jan-99	100	37	44	1470
V. harveyi	Site BP	H P	1000+	Apr-94	16	13	-	-
V. harveyi	Site BP	H P	1000+	Apr-96	30	10	-	-
V. harveyi	Site BP	H P	1000+	Apr-97	50	11	-	-
V. harveyi	Site EPT	H P	1000+	Apr-95	200	7	-	-
V. harveyi	Site EPT	H P	1000+	Apr-97	50	3	33	9
V. harveyi	Site SET	H P	1000+	Apr-96	500	25	12	25
V. helichrysantha	Site CR	H P	1000+	Nov-94	200	33	63	104
V. helichrysantha	Site CR	H P	1000+	Oct-95	1000	21	50	54
V. helichrysantha	Site TB	H P	1000+	Nov-98	50	4	29	14
V. hughanii	Site A	H P	1000+	Mar-99	60	24	69	58
V. hughanii	Site HNR	D P	<30	Mar-99	8	6	57	21
V. pityrhops	Site EMB	H P	500+	May-99	200	5	-	-
V. plumosa var *ananeotes*	Site ANR	H P	<100	Mar-94	10	11	11	9
V. plumosa var *ananeotes*	Site ANR	H P	<100	Mar-94	20	3	18	11
V. plumosa var *ananeotes*	Site ANR	H P	<100	Feb-95	30	5	-	-
V. plumosa var *ananeotes*	Site ANR	H P	100+	Feb-98	150	6	42	19
V. plumosa var *ananeotes*	Site ANR	H P	100+	Feb-99	30	2	33	24
V. plumosa var *pleiobotrya*	Site M	D RV	500+	Feb-95	27	24	72	64
V. plumosa var *vassensis*	Site APV	D RV	50+	Feb-97	40	5	53	15

Table 2 (continued)

Species	Location	Condition	Population size	Time of collection	Plants sampled	% seed set	% germination	Seeds used in germination trials
V. plumosa var *vassensis*	Site APV	D RV	50+	Jan-98	30	9	44	27
V. plumosa var *vassensis*	Site E	D RV	<20	Feb-99	10	0	-	-
V. plumosa var *vassensis*	Site FR	H P	1000++	Feb-98	1000	0	-	-
V. plumosa var *vassensis*	Site FR	H P	1000++	Feb-99	90	7	75	8
V. plumosa var *vassensis*	Site GBR	H RV	100+	Feb-98	20	17	48	44
V. plumosa var *vassensis*	Site WLH	D RV	50+	Feb-99	17	16	33	82
V. spicata ssp *squamosa*	Site C	H P	11	Jan-96	5	18	52	46
V. spicata ssp *squamosa*	Site C	H P	11	Jan-97	10	7	29	21
V. spicata ssp *squamosa*	Site C	H P	11	Feb-98	11	19	24	54
V. spicata ssp *squamosa*	Site CR	D RV	1	Jan-97	1	4	60	5
V. spicata ssp *squamosa*	Site CYM	D RV	1	Jan-96	1	0.35	-	-
V. spicata ssp *squamosa*	Site CYM2	D RV	1	Jan-97	1	0	-	-
V. spicata ssp *squamosa*	Site NETS	D RV	1	Jan-97	1	1	-	-
V. spicata ssp *squamosa*	Site S	D RV	2	Jan-96	2	8	36	22
V. spicata ssp *squamosa*	Site S	D RV	1	Jan-97	1	14	50	6
V. spicata ssp *squamosa*	Site TSM	D RV/P	15	Jan-96	15	11	86	7
V. spicata ssp *squamosa*	Site TSM	D RV/P	15	Jan-97	13	12	7	31
V. staminosa ssp *cylindraceae* var *cylindraceae*	Site PG	H P	30	Dec-95	7	53	57	14
V. staminosa ssp *cylindraceae* var *cylindraceae*	Site PR	H P	200	Dec-98	33	65	96	100
V. staminosa ssp *cylindraceae* var *cylindraceae*	Site VR	H P	50	Dec-98	12	56	85	103
V. staminosa ssp *cylindraceae* var *erecta*	Site MG	H P	200+	Dec-95	10	59	88	40
V. staminosa ssp *cylindraceae* var *erecta*	Site MG	H P	200+	Dec-98	50	8	81	21
V. staminosa ssp *staminosa*	Site MH	H P	500+	Oct-95, Nov-95	20	36	60	45
V. staminosa ssp *staminosa*	Site MH	H P	500+	Oct-97	30	40	70	50
V. staminosa ssp *staminosa*	Site MH	H P	500+	Oct-96, Oct-96, Nov-96	50	20	100	24

offspring vigour through selective abortion. Surplus flower production may also provide an ovary reserve in case of mortality of flowers, or may provide a buffer during adverse weather conditions or during competition that may reduce pollen flow (Lee & Bazzaz 1982). The interacting factors of pollination failure, resource deficiency, predation and genetic defects causing developmental failure may cause pre-dispersal seed and ovule mortality (Fenner 1985; Wallace & O'Dowd 1989). A range of biological constraints can also lead to reductions in seed production (Owens 1995). These include (1) periodic or inadequate floral initiation, (2) asynchronous development and flowering, (3) floral abortion, (4) ovule abortion, (5) embryo abortion, and (6) failure of seeds and fruits to mature and our inability to determine maturity. Constraints and their importance will vary among species, sites and years and occur throughout all stages of development. Stephenson (1981) reports that whole fruit abortion is common among outcrossing perennials and that a low fruit to flower ratio (i.e. seed set) is observed in many species. Similarly, Wiens *et al.* (1987) noted that reproductive success as measured by seed to ovule ratio in outcrossing plants was considerably lower (22%) than in inbreeding plants (90%).

A number of researchers have reported that self-incompatibility in the family Myrtaceae contributed to low seed set (*e.g.* Briggs 1962, 1964; Prakash 1969; Rye 1980; Barlow & Forrestor 1984; Griffin *et al.* 1987; Beardsell *et al.* 1993b, Sedgley & Granger 1996). Despite widespread self-incompatibility within the family, recent research into the mating system of the rare *Verticordia fimbrilepis* subsp *fimbrilepis* has established that inbreeding rates are very high (J Samson, CALM, personal communication). Rye (1980) and Tyagi *et al.* (1991) also noted self-compatibility in a number of species in the genus. Tyagi *et al.* (1991) considered that low seed set in field populations of some species of *Verticordia* was determined by factors such as efficiency of pollen transfer, genetic diversity within populations and physiological constraints rather than loss of pollen fertility. They were unable to demonstrate that seed produced by inbreeding was viable, although recent studies (J Samson, CALM, personal communication) have now shown that 78% of seeds of *V. fimbrilepis* subsp *fimbrilepis* produced as a result of self-fertilisation were viable. McEvoy (1995) also reported that seed viability was not reduced by selfing in the common *V. eriocephala*. These data suggest that inbreeding depression is unlikely to be a cause of low seed set in this genus.

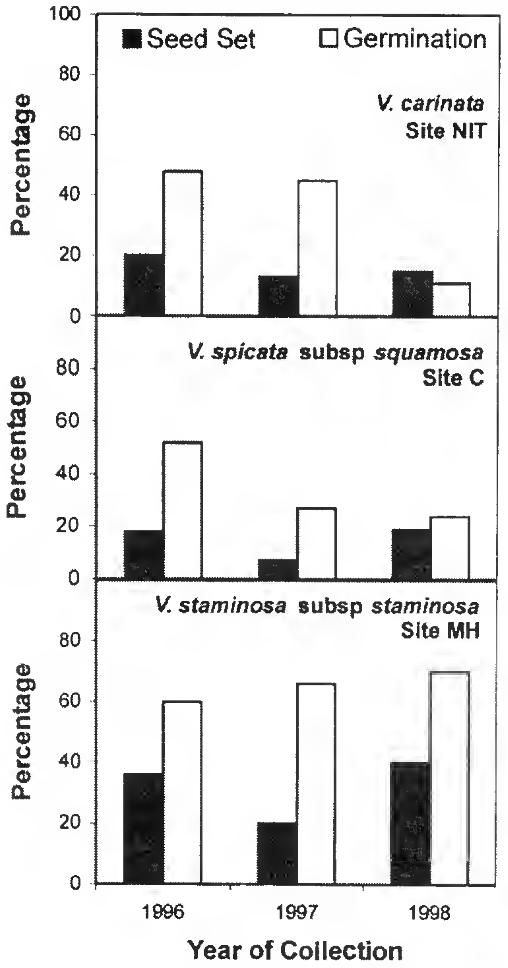

Figure 2. Difference in seed set and germination between years for *V. carinata* Site NIT, *V. spicata* subsp *squamosa* Site C, and *V. staminosa* subsp *staminosa* Site MH.

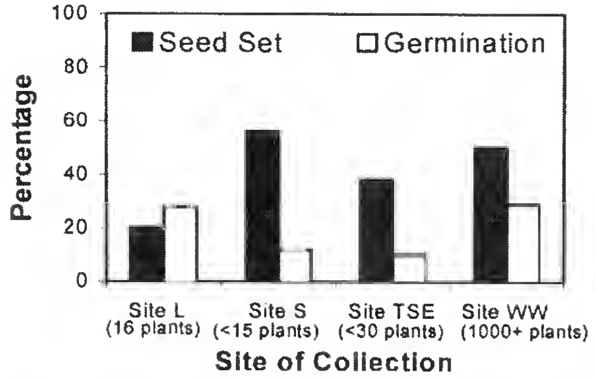

Figure 3. Differences in seed set and germination between sites of collection for *V albida* 1997 collections.

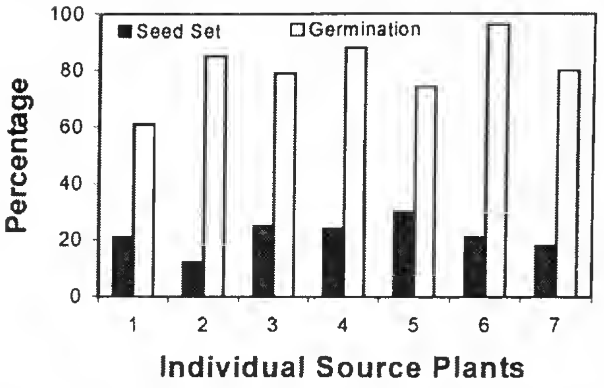

Figure 4. Differences in seed set and germination between individual plants for *V fimbrilepis* subsp *fimbrilepis* Site A, 1998.

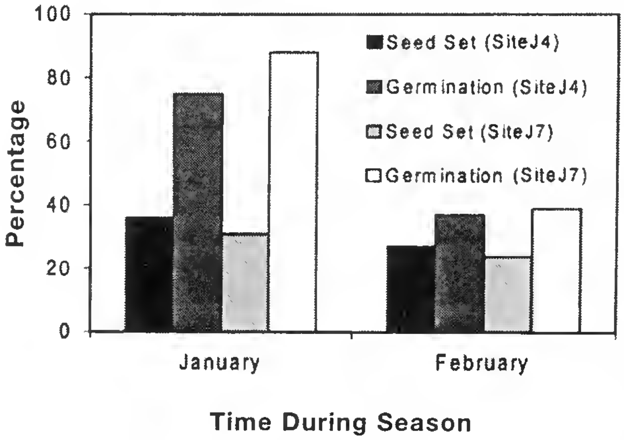

Figure 5. Seasonal differences in seed set and germination for *V fimbrilepis* subsp *fimbrilepis* 1996 collections.

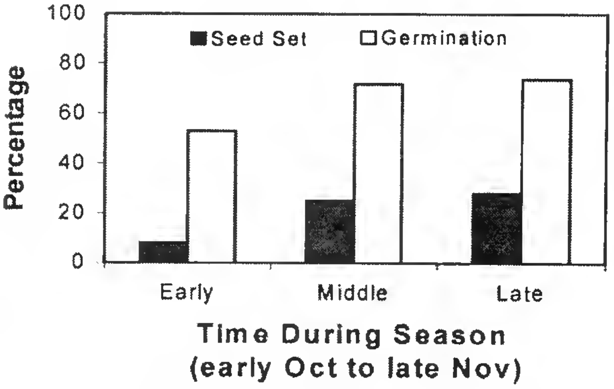

Figure 6. Seasonal differences in seed set and germination for *V staminosa* subsp *staminosa* Site MH 1996 collections.

Environmental stress and demographic structure of the population have also been known to contribute to low seed production (Jordano 1992) and can account for some of the wide variation in seed set noted between individuals, populations and years. However, this study demonstrated that smaller populations of *Verticordia* located on degraded road verges did not necessarily exhibit lower seed set than larger populations occurring in remnant bush or in reserves or bushland (Table 2). There appeared to be no difference in seed set between healthy and degraded sites indicating that environmental stress at a gross level may not be impacting on the reproductive capacity of those taxa studied. It is possible that reproductive success may be a function of plant maturity, although at the time of this study the age structure of each population was unknown. Another significant factor affecting seed set is the presence and health of pollinators, which may in part be related to the health of the site and opportunities for supporting pollinators.

Various studies have reported a relationship between seed set and life history (Wiens 1984; Ehrlen 1991;

Richmond & Chinnock 1994; Meney *et al*. 1997). It appears that reproductive success in some genera may in part be determined by the internal allocation of resources as dictated by the plants' regenerative mode (Carpenter & Recher 1979; Hansen *et al*. 1991; Ladd & Wooller 1997; Meney *et al*. 1997). In this study, there was no evidence to suggest that seed set in *Verticordia* varied between obligate seeding and resprouting species. The wide intra-specific variation in seed set makes it difficult to determine relationship between levels of seed set and regenerative mode and further investigations are required.

Seed Germination

The breakdown of seed dormancy in *Verticordia* appears to require not only the removal of the seed coat, which acts as a barrier to water uptake, but also the addition of growth hormones to overcome an after-ripening requirement. It is possible that the hypanthium and perianth might help protect the seed from weathering, thus maintaining dormancy. This has been observed in *Thrytomene calycina* (Beardsell *et al*. 1993c). Recent work on other genera in the family Myrtaceae (*Darwinia* and *Chamelaucium*) has also established the need for hypanthium removal and the application of growth hormones to aid germination (A Cochrane, unpublished data). Despite considerable inroads into understanding the germination requirements of the genus *Verticordia*, we are not achieving maximum germination in most cases from what appears to be healthy, mature seed. It is obvious that there is still a great deal more to be understood about the germination requirements of particular taxa. Further research is required to determine whether this incomplete germination is due to after-ripening requirements, to maturity of seed, to inadequate dormancy breaking treatments and/or to genetically related defects.

Given that sampling of material for *ex situ* conservation occurs on a random basis to enable the range of genetic characters and reproductive potential to be represented, it is not unexpected to find such intra- and inter-specific variability in germination. Germinability of seed will be affected by the environmental conditions under which the seed developed. It will also be affected by the timing of collection (see Figs 5, 6) and post-harvest conditions prior to germination. Germination differences among individuals have important fitness consequences and germination differences between populations could well be reflecting inbreeding depression (Menges 1991). There have been suggestions that there is a relationship between population size and germinability in species, with larger populations exhibiting higher germination than smaller populations (Menges 1991). Our data on *Verticordia* indicate no such relationship (Figure 3).

This study has demonstrated considerable variation in seed set and germinability in a range of taxa in the genus *Verticordia*. The precariously low annual reproductive success of some of the taxa studied indicates a need for considerable monitoring of the health and biology of these taxa over the long-term. Continued disturbance such as clearing, disease or fire may result in population decline or even localised extinction of some of the more critically endangered taxa. Changes in population size, degree of isolation and fitness are warning signs that populations may be vulnerable (Ellstrand & Elam 1993) and should cause concern to conservation managers. Regeneration plays a major role in the composition and floral diversity of plant communities. The regeneration potential of a population depends on the proportions of germinable seed successfully growing, maturing and attaining reproductive status, as well as the reproductive potential determined by seed set and germination. For most taxa the effective size of the soil seedbank remains unknown. Seedling survival through summer months is also unknown. Further stresses due to post-dispersal factors (seed predation and seedling mortality) in species that already exhibit low pre-dispersal reproductive success will critically restrict the ability of the taxon to reconstitute populations from seed, or to maintain levels of plants in the face of disturbance and senescence.

Seed set in plants occurring in intact vegetation is no greater than in plants located in degraded sites, but the ability of populations to attract and support pollinators may be dependent on the condition of the site and its associated vegetation. Despite the ability of plants to self-pollinate, the impact of reducing population size and health on the survival of plants and their reproductive capacity is unknown. Mitigation measures such as the reintroduction of material into new sites and the enhancement of existing populations may be warranted for many of Western Australia's rare and threatened *Verticordia*. The observed year to year and site to site variations in seed set and germination suggest a cycle of alternating high and low reproductive activity which may be affected by seasonal influences on fruit survival and maturation. Reproductive success in terms of seed to flower ratio may be a function of size, age, condition and genetic make-up of the plants, as well as seasonal factors and pollinator activity. Research into spatial and temporal factors (*e.g*. climatic data, nutrient status of sites, pollinator visitors, pollen loads, age structure and genetic variability within each population) affecting seed production and germinability in *Verticordia* is considered necessary to ensure local extinction of small isolated populations does not occur.

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Microgeographic variation in two relict island populations of the quokka, *Setonix brachyurus* (Macropodidae: Marsupialia), assessed by allozyme electrophoresis

E A Sinclair*

Department of Zoology, The University of Western Australia, Crawley WA 6009
*present address: Department of Zoology, Brigham Young University, Provo UTAH 84602 USA
email: es88@email.byu.edu

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Abstract

Genetic variation was examined in two relict island populations of the quokka, *Setonix brachyurus*, on Rottnest and Bald Islands. Allozyme electrophoresis was used to examine subdivision among the two islands, at a broad-scale population level within Rottnest Island, and a fine-scale subpopulation level within West End, Rottnest Island. Low levels of variation were detected (two loci). However, significant heterogeneity was observed among the Bald and Rottnest Island populations (F_{ST} = 0.288) and among the Rottnest Island populations (F_{ST} = 0.193). No significant fine-scale subdivision was detected within West End (F_{ST} = 0.023). The population level subdivision may be playing an important role in slowing the rate of loss of variation.

Keywords: microgeography, population structure, allozymes, *Setonix*, marsupial, relict, island populations

Introduction

Two fundamentally different views on the structuring of populations have been developed; the classical subpopulation paradigm from genetics and the social structure paradigm from behavioural ecology (Sugg *et al.* 1996). The subpopulation models assume random mating within subpopulations. However, populations are often composed of more than just randomly mating subpopulations; many organisms form small, local breeding groups with gene flow being restricted by the social structure (Liu & Godt 1983; Sugg *et al.* 1996). Therefore, the genetic structure of a species will be influenced by the dispersal, demography, and mating system characterising that species (Shields 1987). In the absence of selection, the interaction of population size, amount of gene exchange, and breeding patterns will also be reflected in the genetic structure (Patton & Feder 1981). Those populations characterised by high gene flow and random mating will be much less structured than those in which the reverse conditions hold. Where social structure is strong within the subpopulations, random mating will not occur among the breeding groups.

The organisation of populations into independent breeding units may have important effects on the short-term evolution of populations (Wright 1980), as well as on the maintenance of genetic polymorphisms (Chesser *et al.* 1980). Genetic drift due to small effective population size could lead to heterogeneity among the groups. Genetic heterogeneity over short geographic distance has been observed among populations of small mammal species (*e.g.* Selander 1970; Wright 1978; Patton & Feder 1981; Chesser 1983; Kessler & Avise 1985).

Although the relationship between mating systems and sexual dimorphism has more commonly been studied in birds (Lack 1968; Orians 1969; Selander 1972), Jarman (1983) suggested that the degree of sexual dimorphism in mammals can be used as an indicator of mating strategy and hence social structure. Among Australian marsupials, sexual dimorphism is greatest in the larger macropod species (see Jarman 1989). In moderate to highly dimorphic species, the males are organised into dominance hierarchies (Jarman 1983; Croft 1989) and the mating system is either promiscuous (Croft 1989; Jarman 1991) or polygamous (*e.g.* Croft 1981; Sander *et al.* 1997). Smaller species show little sexual dimorphism (Jarman 1989) and tend to be monogamous. Moderate sexual dimorphism, based on five morphological measures, was detected in the quokka, *Setonix brachyurus* (Sinclair 1998) and dominance hierarchies have been reported (Kitchener 1970). Adult males form a linear hierarchy and are dominant to females and juveniles. Infrequent changes were observed in the ranking order of adult males during Kitchener's (1970) study, indicating that the hierarchy was relatively stable. The existence of dominance hierarchies among males and prevalence of polygamy would enhance inbreeding and small effective population size (Wilson *et al.* 1975).

In mammals, males show a greater tendency than females for movement between their birth place and first breeding location (Greenwood 1980). Information on dispersal and philopatry is available for nine macropod species, for which dispersal is predominantly by juvenile males (Johnson 1989). Breeding dispersal in macropods is generally rare (Johnson 1989; but see Christensen 1980; Oliver 1986). Natal dispersal was absent in both the tammar wallaby (*Macropus eugenii*) and *S. brachyurus*. Nicholls (1971) concluded that for *S. brachyurus*, the group home ranges were constrained by resource distributions and not social structure on Rottnest Island. Three capture-mark-release-recapture studies failed to find any evidence for dispersal in any age class on Rottnest Island (Dunnet 1962; Holsworth 1967; Kitchener 1970). Few studies have examined levels of microgeographic genetic variation in marsupials (although see Moritz *et al.* 1997; Taylor *et al.* 1997; Pope *et al.* 2000), where behavioural traits such as territoriality and mating systems may also give rise to genetic subdivision. Behavioural and morphological studies of *S. brachyurus* on Rottnest Island provide testable hypotheses for a genetic analysis of population structure. As there is some sexual dimorphism and a dominance hierarchy in males, *S. brachyurus* is predicted to have a promiscuous or polygynous mating system.

Here, I use allozyme electrophoresis to examine genetic structure at three geographic levels within *S. brachyurus*. Firstly, to compare two island populations, Bald and Rottnest Island, which have been isolated since the late Pleistocene. Secondly, to examine broad-scale population structure on Rottnest Island; Dunnet (1962) showed that *S. brachyurus* could be grouped into five fairly discrete populations, among which there was virtually no mixing of animals. If this is true, then it would be expected that there is genetic differentiation among these populations. And thirdly, to examine fine-scale group territories; within one population (West End), individuals were found to have home ranges, and groups of 25 to 150 individuals had overlapping home ranges called 'group territories' (Holsworth 1967). These group territories were stable and non-overlapping; animals rarely moved from one to another, and boundaries were generally coincident with topographic features. Kitchener (1973) suggested that *S. brachyurus* occupied the same home ranges throughout their lives, as quokkas of both sexes and a wide range of ages had died within their own home ranges, while Nicholls (1971) used radio-tracking to show that there was movement of individuals between these group territories. If the social groups observed in the field represent the breeding groups, then some genetic structure may be observed. Alternatively, if either sex preferentially mates with individuals from a different social group, little or no genetic differentiation would be observed.

Materials and Methods

Sampling

S. brachyurus was sampled from two continental islands off the Western Australian coastline (Fig 1). Sampling was carried out at two spatial scales on Rottnest Island, the broad-scale population level and fine-scale group territory level. For the broad-scale population level, samples were collected from five sites between July 1994 and January 1995; (1) West End (n = 47), (2) Rubbish Tip (n = 54), (3) Government House Lake (n = 50), (4) west side of Lake Bagdad (n = 49), and (5) Golf Course (n = 53). Sites were selected based on work by Dunnet (1962) and Holsworth (1967). To examine variation at the fine-scale, samples were collected from eight locations at West End. Seven individuals were excluded since these represented sites where fewer than three quokkas were captured. Sample sizes from these locations ranged between 3 and 14 for a total of 40 individuals. The sites at West End represented 5 out of the 15 group territories determined by Holsworth (1967). Twenty-one quokkas were sampled from Bald Island in November 1994.

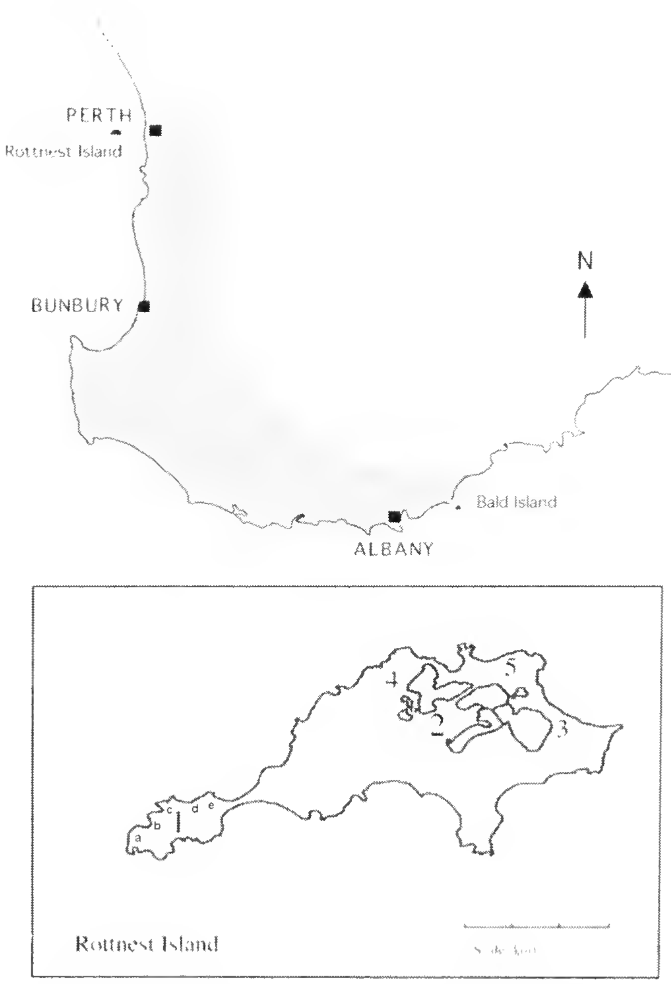

Figure 1. Map showing the distribution of *Setonix brachyurus* in south-western Western Australia (shaded) and the location of Rottnest and Bald Islands. Inset shows the sites sampled on Rottnest Island: 1) West End, 2) Rubbish Tip, 3) Government House Lake, 4) west side of Lake Bagdad, 5) Golf Course, and subsampling at West End: a) Grass Patch, b) Mabel Cove, c) Haywood Cape, d) Marjorie Bay and e) Edeline Beach.

Three methods were used to catch *S. brachyurus*, cage trapping, hand-netting, and by hand. Juveniles and sub-adults were avoided where possible. A 1 ml blood sample was collected from the tail vein of each animal, which was then individually tagged for future identification. Animals were released at the site of capture. The blood was added to 150 µL acid-citrate-dextrose (ACD) and kept on ice in the field. The blood was centrifuged in the laboratory, and the plasma and red blood cells were stored separately at -70°C until required.

Electrophoresis

Red blood cells were lysed in an equal volume of distilled water containing 1 mg mL^{-1} NADP and then centrifuged for 5 min to remove the cell debris. Variation was examined using Titan gel electrophoresis (Helena Laboratories, USA). Standard electrophoretic procedures were used, as outlined by Richardson *et al.* (1986). Two polymorphic loci, adenylate kinase (EC 2.7.4.3; *Ak*) and pyruvate kinase (EC 2.7.1.40; *Pk*) were examined for variation using 0.01 M citrate phosphate buffer. These were the only consistently scoreable, polymorphic loci found in an earlier survey of 28 loci across the full range of *S. brachyurus* (Sinclair 2001), and analyses are based on these two loci unless otherwise indicated.

Analysis

Variation at the two polymorphic allozyme loci was summarized by allele frequencies and observed heterozygosities using the program GENEPOP version 3.1 (Raymond & Rousset 1995). The probability test of Guo & Thompson (1992), available in GENEPOP, was used to test for locus conformity to Hardy-Weinberg equilibrium (HWE). A Markov chain algorithm was used to obtain an unbiased estimate of the exact probability. Genic differentiation (allele frequencies) and genotypic differentiation (genotype frequencies) among populations were tested using exact tests, with a Markov chain method used to generate probabilities.

F-statistics (F_{ST}) were used to determine the degree of differentiation among islands, among populations at the broad-scale population (within Rottnest Island), and fine-scale subpopulation (within West End) levels, using the program FSTAT (Goudet 1995). The method of Weir & Cockerham (1984) was used, as this corrects for small sample sizes and departures from Hardy-Weinberg equilibrium. The possible values for F_{ST} range from 0 to 1, with larger values indicating greater genetic subdivision of the sampled populations. 95% confidence limits and an exact G-test (Goudet *et al.* 1996) were used to determine whether F_{ST} values were significantly greater than zero.

Finally, genetic distances between sampled populations were estimated using Nei's (1978) unbiased distance measure. A hierarchical cluster analysis was performed using the unweighted pair-group method with arithmetic mean averaging (UPGMA; Sneath & Sokal 1973).

Results

Mean genetic variability measures were low in all populations (Table 1). Of the two polymorphic loci used in this study, each had only two alleles, of which one was generally uncommon. Three out of the five Rottnest Island populations had a frequency greater than 0.95 for the most common allele at one of the two loci. The *Ak-b* allele was more common on Rottnest Island, while *Ak-c* was the more common allele on Bald Island. A third allele, *Ak-a*, was not present in either of the island populations (Sinclair 2001). There were significant deficits in heterozygosites across all populations and across both loci. The Rubbish Tip and Golf Course populations showed deficits at the *Ak* locus; West End, Government House Lake, and West Bagdad had deficits at the *Pk* locus; while Bald Island had deficits at both loci ($P < 0.001$). Only one heterozygote was detected in the Bald Island population.

There was significant differentiation among allele frequencies and genotypes across populations for both loci ($p < 0.001$). Analysis of pairwise differentiation indicated that many of the significant values were attributed to Bald Island, however, some differences were also attributed to differences among Rottnest Island populations. F-statistics showed significant heterogeneity between Rottnest and Bald Island populations (F_{ST} = 0.288) and among the Rottnest Island populations (F_{ST} = 0.193; Table 2). The subdivision on Rottnest Island was largely due to the *Pk* locus. The Rubbish Tip population had a much higher frequency of the *Pk-a* allele than any other population. A separate analysis without this population gave an F_{ST} value nearly five times lower, 0.048, but still significantly greater than zero, indicating that there was some genetic subdivision among the four remaining populations on Rottnest Island. For an analysis of fine-scale subdivision within West End, there was very little variation in allele frequencies (Table 3), with an F_{ST} not significantly greater than zero (F_{ST} = 0.023).

The UPGMA cluster analysis is shown in Fig 2. All Rottnest Island populations clustered together, reflecting a more recent common history with each other than to Bald Island. Pairwise genetic distance among populations within Rottnest Island ranged from 0.001 (West Bagdad and Goverment House) to 0.184 (Golf Course and Rubbish Tip). Distance measures between Bald Island and the five Rottnest Island populations (range = 0.290 to 0.580) were larger than the distances among Rottnest Island populations.

Table 1

Sample sizes, allele frequencies, and observed heterozygosities (Het) at two polymorphic loci for six island populations of *S. brachyurus*. Significant deficits of heterozygotes from H-W expected values: * P < 0.05, ** P < 0.01, *** P < 0.001.

Locus	Allele	Rottnest Island populations					Bald Island
		West End	Rubbish Tip	Govt House	West Bagdad	Golf Course	
	n =	47	54	50	49	53	21
Ak	*b*	0.968	0.889	0.910	0.949	0.783	0.190
	c	0.032	0.111	0.090	0.051	0.217	0.810
	Het	0.064	0.074***	0.140	0.061	0.170**	0.000***
Pk	*a*	0.160	0.537	0.100	0.031	0.047	0.214
	b	0.840	0.463	0.900	0.969	0.953	0.786
	Het	0.106***	0.481	0.080**	0.020*	0.094	0.048***
Overall Het (28 loci)		0.006	0.020	0.008	0.003	0.009	0.002

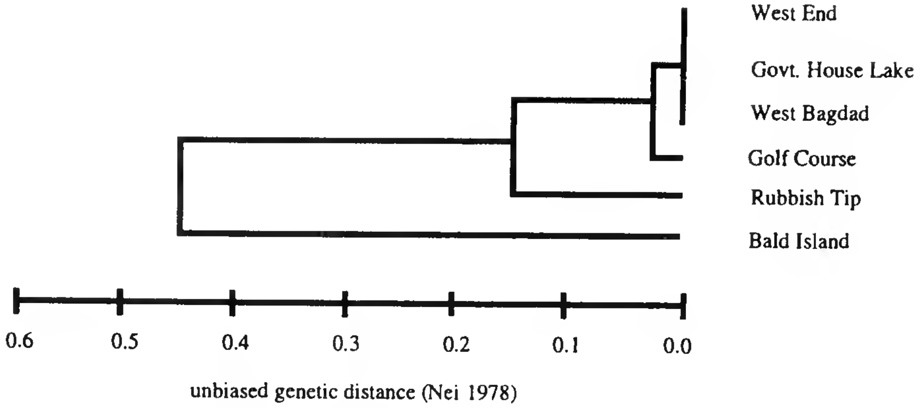

Figure 2. UPGMA cluster analysis of Nei (1978) genetic distance measure among sampled island populations of *S. brachyurus*.

Discussion

There are limitations to the use of allozyme data in examining microgeographic variation in sexually reproducing organisms, as nuclear-encoded allozyme genotypes segregate and recombine (Kessler & Avise 1985). Therefore, genotypes of the offspring can be different to either parental genotype. Population subdivision is then inferred indirectly from heterogeneity in allele frequencies. When considering small numbers of individuals in social groups, the sampling variance may be as great as the variance in allele frequencies, a problem that applies to the calculation of *F*-statistics (Chesser 1983). Also, in most studies using allozymes, *F*-statistics are calculated from more than two polymorphic loci, so the results from this study should be interpreted with some caution.

The significant heterogeneity among Rottnest Island quokka populations suggests broad-scale subdivision across the Island and hence low gene flow between populations. These genetic findings are consistent with the study by Dunnet (1962), who thought there were five fairly discrete populations on the island, among which there was virtually no mixing of quokkas. The highly seasonal conditions on Rottnest Island play an important role in the behaviour of *S. brachyurus*. While populations remain very sedentary during the winter months when food and water are abundant across the island, the drought conditions over summer force animals in the eastern parts of the island to move towards very limited food and water around lake margins (Dunnet 1962). Quokkas at West End tend to move towards the western tip, where succulent vegetation provides some moisture, but little nourishment.

The apparently high degree of subdivision may have been an artefact of the allele frequencies at the *Pk* locus in the Rubbish Tip population. However, analysis without the Rubbish Tip population indicated that there was still significant heterogeneity among the four remaining populations. The Rubbish Tip population differs from the other populations in that it has a constant food source throughout the summer months. Large numbers of *S. brachyurus* also continue to feed there during the winter months, suggesting that these quokkas may not disperse to utilise their natural food resources, as is observed in other parts of the island. If these quokkas remain at the Rubbish Tip site throughout the year, then their behaviour may limit opportunities to mix with other animals. Therefore, lower gene flow between these quokkas and the other sampled populations might be expected. Heterozygosity of the Rubbish Tip population is an order of magnitude higher than the other populations. Other Rottnest populations may undergo frequent (or seasonal) bottlenecks during the summer, leading to lower heterozygosities.

Deficits of heterozygotes were detected in all five populations on Rottnest Island for one of the two loci,

Table 2

Estimates of levels of subdivision as measured by F_{ST} across different sampling levels for *S. brachyurus*. The 95% confidence intervals are given; * indicates value significantly greater than zero. Results for the exact G-test are also given.

	Among Islands	Rottnest Island			Overall
Number of populations	6 450 km	All sites 5 up to 11 km	excluding Rubbish Tip 4 up to 11 km	within West End 5 < 2 km	Geographic range[1] 7 450 km
Locus					
Ak	0.328	0.043	0.065	-0.044	0.210
Pk	0.252	0.283	0.028	0.039	0.457
Over all loci	0.288*	0.193*	0.048*	0.023	0.363*
95% confidence interval	0.252 - 0.328	0.043 - 0.283	0.028 - 0.065	-0.044 - 0.039	0.210 - 0.457
exact G-test	0.0001	0.0001	0.0001	0.1530	0.0001

[1] from Sinclair (2001)

Table 3

Sample sizes, allele frequencies, and observed heterozygosities (Het) for sampled subpopulations of *S. brachyurus* on West End. Significant deficits of heterozygotes from H-W expected values: * $P < 0.05$.

		West End, Rottnest Island				
Locus	Allele	Grass Patch	Mabel Cove	Haywood Cape	Marjorie Bay	Edeline Beach
	n =	14	6	7	9	3
Ak	*b*	0.964	0.917	1.000	0.944	1.000
	c	0.036	0.083	-	0.056	-
	Het	0.071	0.167	0.000	0.111	0.000
Pk	*a*	0.179	0.333	-	0.167	0.500
	b	0.821	0.667	1.000	0.833	0.500
	Het	0.071*	0.000*	0.000	0.333	0.333
Overall Het (28 loci)		0.005	0.006	0.000	0.016	0.012

and at both loci on Bald Island. These deficits may be the result of a Wahlund Effect (where homozygosity decreases as a result of sampling across more than one subpopulation), selection, or inbreeding. The F_{ST} value was not significantly greater than zero when subdivision was examined within West End, indicating that a Wahlund Effect was not responsible for the heterozygote deficits at this site. The apparent absence of fine-scale genetic subdivision within West End, however, supports radio-tracking data by Nicholls (1971). He observed frequent and extensive movement of individuals outside the group territories initially defined by Holsworth (1967). These movements may be only short visits, but enough to maintain gene flow among territories.

Inbreeding occurs as a consequence of the geographic subdivision of a population into a number of subpopulations or through the choice of mates according to phenotype or genetic relationship (Selander 1983). The limited dispersal of individuals and isolation from the mainland suggest that inbreeding may contribute to the deficit in heterozygotes. However, as the assumption is made that allozyme variation is largely neutral, one would expect that if inbreeding were responsible, then there would be deficits in heterozygotes at both loci and across all populations. Selection is unlikely to play a significant role in divergence among subpopulations as they occur over very small distances and selection pressures would be similar. None of these explanations adequately accounts for the deficits in heterozygotes of quokkas on Rottnest Island. Two further possibilities may account for these deficits, incorrect scoring of polymorphisms and X-linkage. However, genotypes from a captive bred colony (Sinclair, unpublished data) showed both loci were inherited as expected under a Mendelian mode of inheritance, that is, heterozygous males were observed. Therefore, the cause for heterozygote deficits in Rottnest Island populations could not be determined. However, highly significant deficits in heterozygotes on Bald Island for both loci are consistent with inbreeding.

Breeding group models provide the opportunity to examine which aspects of an organism's biology influence the maintenance of genetic variation (Sugg *et al.* 1996). In *S. brachyurus*, the social groups observed on West End do not show any evidence of reflecting the breeding groups, despite an apparently well maintained social group structure (Dunnet 1962; Nicholls 1971). Environmental conditions may be contributing to the homogeneity. In a study by Oliver (1986) the incidence of breeding dispersal in *Macropus rufus* and *M. eugenii* increased as environmental conditions deteriorated. A similar situation may occur in *S. brachyurus*. Both island populations of *S. brachyurus* experience extremely harsh conditions during the summer months. If group home ranges were constrained by resource distributions, and not social structure, then it would be expected that there is less structure at the fine-scale level. To examine further the microgeographic structure in both islands, the development of highly variable microsatellite markers and more extensive sampling would be required.

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Notes on ....

Decline of the riverine trees of the Harvey River delta following the opening of the Dawesville Channel

N Gibson

Science Division, Department of Conservation and Land Management, Wildlife Research Centre, PO Box 51
Wanneroo WA 6065
email: neilg@calm.wa.gov.au

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Abstract. The three dominant tree species, *Casuarina obesa*, *Eucalyptus rudis* and *Melaleuca rhaphiophylla*, of the riverine vegetation of the Harvey River delta showed a general decline in canopy condition over the four years following the opening of the Dawesville Channel. *M. rhaphiophylla* also showed significant depression in diameter increment for the population closest to the river mouth. The most likely explanation of the tree decline on the Harvey delta is in changes to the salinity regime of the lower Harvey estuary following the opening of the Channel. Further decline of the vegetation is expected.

Key words: vegetation change, salinity, growth rates, canopy decline

Introduction

The Dawesville Channel south of Mandurah was constructed to increase tidal flow within the Peel-Harvey estuary and decrease the occurrence of toxic algal blooms resulting from excess inputs of nutrients from the catchment. Following the opening of the Channel to the sea in April 1994, the tidal amplitude of the Harvey estuary has increased 55% with a significant influx of marine waters and decreased residence time within the estuary (Anon 1998). A study was instigated in late 1994 to monitor the tree health of the lower 4 km of the Harvey River to ascertain if the changes in the salinity regime of the lower Harvey estuary and the greater penetration of salt water up the Harvey River (JAK Lane, CALM, personal communication) were adversely impacting on the riverine vegetation (Fig 1).

Methods

Tree species appear to segregate along the lower Harvey River in response to salinity levels, with the most tolerant species, *Casuarina obesa* Miq (Casuarinaceae, Saltwater Paperbark) restricted to the lower 1.5 km of the river, and the least tolerant species *Eucalyptus rudis* Endl (Myrtaceae, Flooded Gum) appearing as dense stands 2 km above the river mouth and continuing far upstream. *Melaleuca rhaphiophylla* Schauer (Myrtaceae, Swamp Paperbark) is widely distributed along the 4 km length of the lower Harvey.

Thirty individuals of each species were marked at the lower and upper ends of their range in the lower Harvey River. Each individual was marked with a steel tag and girth at breast height over bark (GBHOB) was measured and condition of the tree was scored on a one to five scale (1 < 20% canopy alive, to 5 > 80% canopy alive). The first 30 individuals encountered within 5 m of the river bank were selected for measurement. *Melaleuca rhaphiophylla* is a typical paperbark which sheds bark in long strips every year. Measurement of GBHOB was considered unreliable for this species and basal diameter over bark (BDOB) was measured instead. GBHOB measurements of *C. obesa* and *E. rudis* were undertaken in November 1994 and November 1995, 1996 and 1997. Canopy condition was scored in November 1994, May 1995, and November 1995, 1996 and 1997. Measurements of *M. rhaphiophylla* were undertaken in June 1995, and November 1995, 1996 and 1997.

Influence of year of sampling (seasonal effect) and position of population along river on change in tree diameter were analyzed by a repeat measure two way analysis of variance for each of the three canopy species. To achieve normally distributed data it was necessary to omit from the analysis several atypical individuals that showed increases of eight to ten times the mean values. Analysis of both data sets showed essentially similar results. Differences in tree condition between sampling times and between populations for each species were analyzed separately by Kruskal-Wallis one way analysis of variance since it proved impossible to normalize the data.

Results

The only species that showed no significant decrease in canopy condition during the study period was the upstream population of *Eucalyptus rudis* (Fig 2A). The downstream population showed a small but significant decline in canopy condition. Both *Casuarina obesa* and *Melaleuca rhaphiophylla* showed more dramatic declines in canopy condition over the four years of the study, with the downstream populations being the most affected (Fig 2A). *Melaleuca rhaphiophylla* showed a greater decline (>40% for the population near the river mouth) than was apparent in *Casuarina obesa*.

There was a significant difference in growth increment of upstream (4.0 km from the river mouth) and downstream (0.5 km) populations of *Melaleuca rhaphiophylla* ($F_{1,24}$ = 19.66, P = 0.0002), with no significant difference between times or the interaction between time and distance. At all time periods during the study, the population near the river mouth recorded no increase in basal diameter (the small decrease recorded probably reflects bark shedding or measurement error; Fig 2B).

Casuarina obesa showed no significant difference in growth increment between the population near the river mouth (0.5 km) and the population 1.5 km upstream. There were significant differences between sampling times ($F_{2,50}$ = 3.23, P = 0.048), with a non-significant time distance interaction. Negative growth was recorded at both populations during the 1995-96 period (Fig 2C). These negative values probably result from small variation in the location of girth measurements on the stems between years and should be regarded indicating zero growth over the measurement period. Standard errors support this interpretation.

Eucalyptus rudis, which occurred further up the river system than the other two species, generally had larger growth increments (Fig 2D). There was both a significant difference between the downstream population (2.0 km from river mouth) and the upstream population (4.0 km) ($F_{1,26}$ = 8.60, P = 0.007) and sampling periods ($F_{2,52}$= 10.44, P < 0.0002). There was no significant interaction effect.

Figure 1. Harvey River delta from the southern end of the Harvey estuary looking south. Photograph G Pearson, CALM.

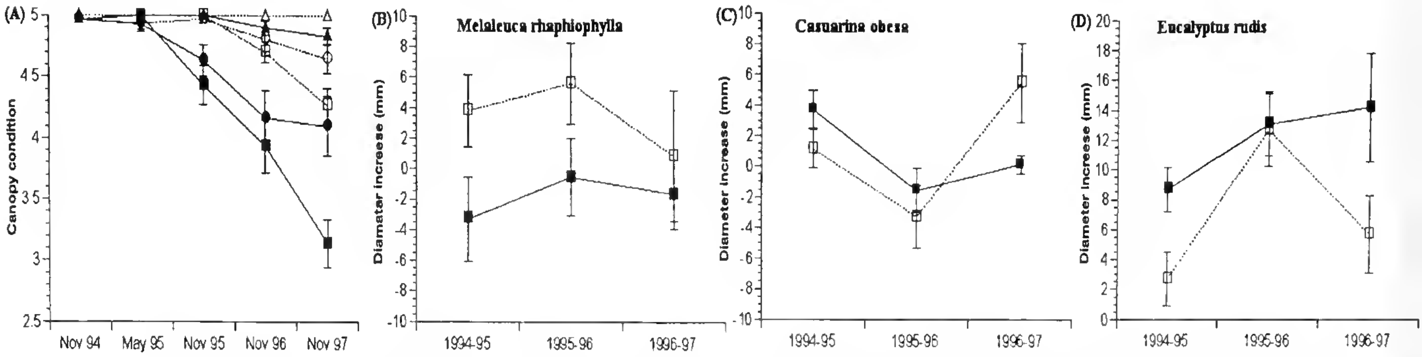

Figure 2. **A**: Changes in canopy condition over time. Canopy condition scored on five point scale (1 < 20% canopy alive, to 5 > 80% canopy alive). Triangles – *Eucalyptus rudis*, Circles – *Casuarina obesa*, Squares – *Melaleuca rhaphiophylla*. Dotted line and open symbols indicate upstream populations, solid lines and solid symbols downstream populations. **B**: Growth increment over three measuring periods for *Melaleuca rhaphiophylla*. Solid symbols indicate downstream population (0.5 km from river mouth), open symbols indicate upstream population (4.0 km). **C**: Growth increment over three measuring periods for *Casuarina obesa*. Solid symbols indicate downstream population (0.5 km from river mouth), open symbols indicate upstream population (1.5 km). **D**: Growth increment over three measuring periods for *Eucalyptus rudis*. Solid symbols indicate downstream population (2.0 km from river mouth), open symbols indicate upstream population (4.0 km).

Discussion

There has been a significant decline in the canopy condition of five of the six populations of the dominant riverine tree species monitored since the opening of the Dawesville Channel (Fig 2A). The decline has not been uniform across the species studied with *Melaleuca rhaphiophylla* showing a greater degree of decline than the other two species. While no direct causal relationship between the opening of the Channel and the decline of the trees has been demonstrated, the period of decline exactly correlates with the opening of Harvey Estuary to more direct marine influences, as does the death of fringing vegetation along much of the western shore of the Harvey Estuary (JAK Lane, CALM, personal communication). The pattern of canopy decline in *Eucalyptus rudis* was not consistent with a leafminer outbreak which have been reported from elsewhere in south west Western Australia (Abbott *et al.* 1999).

Melaleuca rhaphiophylla showed clear a depression in growth rate at the river mouth population compared with the upstream population. No increase in diameter was recorded for the river mouth population during any of the three growth periods (Fig 2B). Very low or zero growth rates were also generally recorded in both populations of *Casuarina obesa* which occupies the lower 2 km of river. The low growth rates, except for the upstream population at the last sampling period, are consistent with populations under stress (Fig 2C).

Eucalyptus rudis that occurs above 2 km from the mouth generally showed higher growth rates than the other two species. In contrast to the pattern seen in the other two species the downstream population grew significantly faster, although as noted above this population showed greater degree of canopy decline. These results are somewhat unexpected as glasshouse and field experiments of seedlings planted into saline soils indicate that *Eucalyptus rudis* is a salt sensitive species (Pepper & Craig 1986; van der Moezel *et al.* 1991). The hydrology of the root zone of *Eucalyptus rudis* along the Harvey River is likely to be complex as the intruding salt wedge lies below a freshwater lens whose characteristics change throughout the year (JAK Lane, CALM, personal communication).

Eucalyptus rudis also showed significant differences in the growth rates between time periods. This was also true for *Casuarina obesa* and, although there was no significant difference between times for *Melaleuca rhaphiophylla*, the trend was consistent with the pattern shown in *Eucalyptus rudis* (Fig 2B,C). It is interesting to note that the pattern in growth over time for *Casuarina obesa* is opposite to that recorded for the other two species.

These data are consistent with a stress-induced response of the canopy to an increase in the penetration of salt water up the lower Harvey River as a result of an increased marine influence in the Harvey Estuary. Significant canopy decline was noted for all populations except for the *E. rudis* population 4 km from the river mouth, with the downstream populations being the most severely affected. Surprisingly there was a large decline in the canopy condition of *M. rhaphiophylla* even as far as 4 km above the river mouth. Growth rates were low or zero for the *M. rhaphiophylla* population near the river mouth and for both populations of *C. obesa* found in the lower 2 km of the river. While the trends in the data are consistent with general tree decline in the lower Harvey there are substantial differences in the responses of individual species especially *E. rudis* which was recorded only above 2.0 km of the river mouth. The long term rainfall average for Pinjarra (20 km north west of the study area) is 951 mm, rainfall over the study period was below average and not correlated with the observed patterns (1995, 807 mm; 1996, 848mm; 1997 676 mm).

There is no indication of a decrease in the rate of decline of the canopy condition and further deterioration should be expected. It is likely that over the next decade the composition of the canopy species along the lower reaches of the Harvey River will change substantially.

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Notes on ....

A method for measuring the ECG and ventilation rate in bats

G R Zosky

Department of Zoology, University of Western Australia, Crawley WA 6009
email: gzosky@cyllene.uwa.edu.au

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Abstract. A new method is described for the simultaneous measurement of ventilation rate and the parameters of the electrocardiogram (ECG) for bats. The ECG was measured using mildly adhesive electrode pads that were placed on the forearms of the animal. Ventilation rate was simultaneously measured by recording the bat's thorax movements with a human pulse transducer placed beneath the bat while it was housed in a specialised chamber. These methods reduced the risk of permanent injury to the bat and, unlike other methods used, did not cause any physical damage to the bat's body. The clarity of the signal found using this new method was demonstrated for Western Australian bats at heart rates ranging from 120 b min^{-1} up to 720 b min^{-1}.

Key words: bat, ECG, ventilation, methodology

Introduction

Measurement of the electrocardiogram (ECG) was first demonstrated in 1909 by Augustus Waller using a dog standing in jars containing salt that were linked to two galvanometers (Levick 1995). The methods used, and our understanding of the information contained in an ECG, have improved considerably since then. The requirements for measurement of the ECG of animals, particularly small mammals, has undergone a dramatic change in recent times as it has become increasingly important to use methods that minimise stress and intrusion.

Most physiological studies measuring the ECG of small mammals have used sub-dermal insertion of thin metal electrodes at various points around the body (e.g. Chatfield & Lyman 1950; Twente & Twente 1978; Milsom *et al.* 1993; Harris & Milsom 1995). While this technique maximises the clarity of the signal, there is a risk to the animal associated with the anaesthesia required and an increased risk of permanent damage due to post-surgery infection. Recently, studies involving one of the smallest mammals (*Suncus etruscus*) have utilised a non-intrusive method of ECG measurement involving an electrode grid which the animal stands on to provide contact between the skin and the leads that record the ECG (Fons *et al.* 1997).

While significant progress has been made in this respect for recording of ECGs in most small mammals, it appears there has been little change in the methods used to measure the same parameters in bats. The only method employed has been one that is similar to that described previously involving sub-dermally inserted electrodes (Twente & Twente 1978; Cook *et al.* 1987). In the case of bats, these electrodes were inserted through the wing membrane in a number of places. Again, while this ensures good quality of the ECG signal, there is a risk of death during the insertion of the electrodes under anaesthesia, and of the possibility of permanent damage to the delicate wing membrane.

I describe here a new non-invasive technique for monitoring the ECG and ventilation rate in bats, and demonstrate its effectiveness over a range of activity levels.

Materials and Methods

Four different species of bat ranging in size from 5 to 21 g were used to investigate the effectiveness of this technique across a range of size classes. These species included lesser and greater long-eared bats (*Nyctophilus geoffroyi* and *Nyctophilus timoriensis*), Gould's long-eared bat (*Nyctophilus gouldi*) and Gould's wattled bat (*Chalinolobus gouldii*). Recordings of the ECG and ventilation rate were made during euthermia and during torpor at an ambient temperature of 15 °C

For the measurement of the ECG and ventilation rate, bats were placed in a 'holder' consisting of a vertically suspended, 15 cm length of 30 mm dia PVC pipe lined with hessian to provide a surface from which the bats could hang. The lid consisted of a removable, modified cap for the PVC pipe with holes cut in either side to allow the ECG leads (described below) to move freely as the animal moved in the tube. The opposite end had a similar cap with a hole in the centre to allow airflow into the holder. This end of the holder was also lined with hessian to prevent the animal from trying to force its way out of the hole.

The ECG electrodes were placed on the bat to measure a Lead I signal (the hardware and software were only capable of measuring one ECG signal). In humans, a Lead I ECG measures cardiac activity by recording the difference in potential between the left and right arms. Similarly, in the case of the bats, the positive and negative electrodes were placed on the bat's forearms just distal to the elbow. These electrodes, with the leads attached, were placed on the bat while outside the chamber. The bat was then placed near the entrance to the chamber and allowed to crawl in before sealing the end of the chamber with the cap.

While this electrode system is commonly used in humans, the leads and the electrodes themselves required modification for ECG measurement of bats weighing less than 25 g. The leads themselves consisted of a length of insulated electrical wire (0.65 mm dia) with a plug at one end that was insulated and crimped to fit the input sockets of a 3 lead Bio Amp cable (ADInstruments). The other end of the lead was a modified miniature clip for attachment to electrode pads that adhered to the bat. To fashion a miniature clip, a brass safety pin was cut in half, leaving the spring with two ends measuring approximately 0.5 cm. The tips of the ends were flattened and twisted around each other to form a clip that shut under its own spring tension. The modified clip, except for the tips that were in contact with the electrode pads, was then coated in a clear lacquer to ensure maximum insulation and minimise interference. These leads, and the associated clips, were sufficiently strong to ensure that a continuous circuit was maintained between the electrode pads and the hardware, but were also light enough so that the animals could move with a minimum of hindrance. The electrode pads were strips cut from adhesive Bio Tab (ADInstruments) silver chloride electrodes that were then clipped to the end of the electrode leads. These electrodes could be placed on the bat without the need for anaesthetia and appeared to cause minimal disturbance to the bat once they were attached. The mildly adhesive nature of the electrodes meant that they could be removed without damaging the delicate wing membrane.

The ventilation detector consisted of a MLT1010 pulse transducer (ADInstruments) placed beneath the hessian strip in the 'bat holder'. This transducer is typically used to measure heart rates from a finger pulse in humans. For application as a ventilation detector, the only modification that was required was the removal of the strap that usually secured the transducer in place around the finger. The transducer was placed beneath the hessian before the bat entered the chamber. Its sensitivity was such that any movement of the bat's thorax could be monitored with

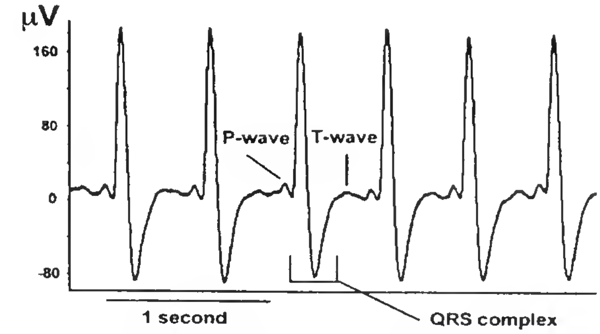

Figure 1. ECG recording from a lesser long-eared bat (*Nyctophilus geoffroyi*) during torpor with a heart rate of approximately 120 b min^{-1}. The atrial contraction (P-wave) ventricular depolarisation (QRS complex) and ventricular repolarisation (T wave) can be clearly distinguished.

minimal disruption to its normal mobility. From these thorax movements it was possible to calculate ventilation rate.

The Bio Amp cable was connected to a ML132 Bio Amp (ADInstruments). The amplified ECG signal and pulse transducer signal were interfaced to a MacLab (ADInstruments, v 4/s) and Macintosh personal computer (LC630), allowing the inputs to be recorded using Chart (ADInstruments, v 3.5.6). This system allowed simultaneous recording of ventilation rate and heart rate and had sufficiently high sampling rates (1 to 100 kHz) such that the major components of the ECG could be identified.

Results and Discussion

This system was highly effective over a wide range of activity levels for all bat species tested. At low heart rates, it was possible to distinguish the depolarisations of both the atrial (P wave) and ventricular (QRS complex) chambers from the ECG (Fig 1). At higher heart rates, however, this distinction became less clear (Fig 2). This was mostly due to the limitations of the hardware and software rather than a limitation of the technique. The most common sampling rate used was 1 kHz. At high heart rates this sampling rate was not sufficient to distinguish the components of the ECG (Fig 2). At higher sampling rates, however, it was only possible to record one channel at a time, so for the purposes of simultaneously measuring heart rate and ventilation rate the resolution was compromised.

Despite this, even at relatively low sampling rates the system demonstrated a clarity that was equal to, if not better, than that using the method of sub-dermal electrode insertion (see Twente & Twente 1978; Harris & Milsom 1995) and was certainly more effective than the method used on other mammals weighing less than 25 g (see Fons *et al.* 1997). Similarly, the sensitivity of the pulse transducer ensured that ventilation rate could be easily monitored (Fig 3) allowing an immediate comparison to be made between heart rate and ventilation rate.

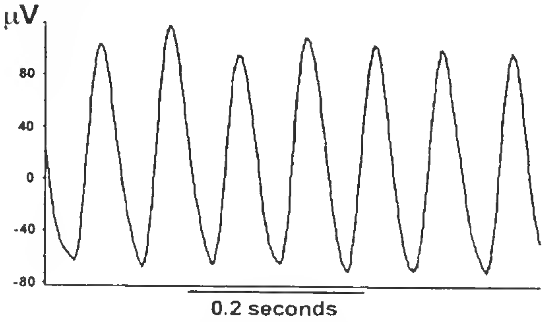

Figure 2. ECG recording from a Gould's long-eared bat (*Nyctophilus gouldi*) with a heart rate of nearly 720 b min^{-1}. The only part of the ECG that was recorded at a sampling rate of 1 kHz was the QRS complex.

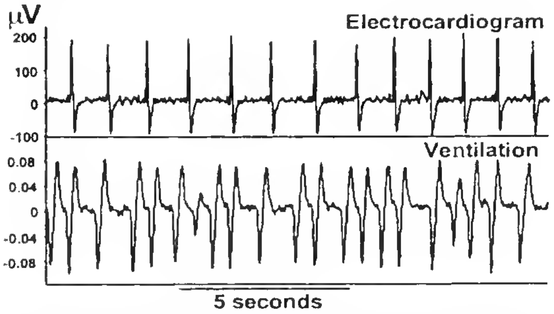

Figure 3. Simultaneous recording of an ECG and ventilation events from a lesser long-eared bat (*Nyctophilus geoffroyi*).

On occasions, due to their design the electrode pads were dislodged as the bat entered the chamber. However, it was essential that the pads were only mildly adhesive so that they could be removed without damaging the delicate wing membrane. This also allowed the bat the ability to free itself from entanglement and was seen as an advantage over the method involving sub-dermal insertion of wire electrodes.

This method of ECG measurement eliminated the risk associated with anaesthesia and did not cause any damage to the bat's body. Given that there was minimal intrusion on the bats, this methodology has significant implications for further research into the cardiorespiratory physiology of bats. This subject is of particular interest given that bats represent an extreme in terms of cardiac neuronal control (O'Shea & Evans 1985; O'Shea 1987; O'Shea 1993) over a range of heart rates from less than 10 b min^{-1} during torpor (Twente & Twente 1978) up to 1000 b min^{-1} during flight (Thomas & Suthers 1972).

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Flora and vegetation of the Eastern Goldfields ranges: Part 5. Hunt Range, Yendilberin and Watt Hills

N Gibson & M N Lyons

Science Division, Department of Conservation and Land Management, Wildlife Research Center,
PO Box 51 Wanneroo, WA 6065
email: neilg@calm.wa.gov.au; mikel@calm.wa.gov.au

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Abstract

A study was undertaken of the flora and plant communities of the Watt and Yendilberin Hills and the Hunt Range on Jaurdi Station. The area has a complex geology which includes Archaean mafics, ultramafics and banded ironstones, and Tertiary laterites. A total flora of 287 taxa and one hybrid was recorded from the uplands, of which 273 were native and 15 were weeds. Fifty three quadrats were established along the range system and used to define seven community types, which were most highly correlated with soil chemistry and an inferred soil moisture gradient. None of the Bungalbin vegetation system is presently in any National Park or Nature Reserve, although the northern section of the Hunt Range has been recommended for inclusion into the Mt Manning Range Nature Reserve. Mining activity in the study area has the potential to severely impact on the restricted breakaway community type. Impacts of past wood harvesting for mining operations and for the water pipeline boilers are still evident decades after these operations ceased.

Keywords: flora, vegetation, Goldfields, Hunt Range, Yendilberin Hills, Watt Hills

Introduction

Greenstone and banded ironstone ranges are common landforms of the Eastern Goldfields and extend from the Highclere Hills in the west to the Roe Hills some 300 km further east and stretch north-south over 800 km. These ranges systems have been heavily exploited for minerals for over a hundred years although a detailed knowledge of their vegetation and flora is far from complete. Earlier botanical work has concentrated on broad scale structural vegetation mapping (*e.g.* Beard 1972, 1978) and regional vegetation surveys (*e.g.* Newbey & Hnatiuk 1985), and few detailed botanical surveys have been undertaken on individual range systems.

The aim of this series is to report on detailed floristic studies on individual ranges to address this deficiency (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2000). This work has shown high beta-diversity in species composition between adjacent ranges, highly localized distribution patterns for some elements of the flora and a number of new taxa not previously known. This paper extends these detailed studies and reports recent survey work undertaken on the greenstone plain north of Jaurdi homestead, the Watt and Yendilberin Hills and the Hunt Range (collectively referred to as the uplands of Jaurdi Station).

Study Locality

The study area occurs on Jaurdi Station some 60 km east of Koolyanobbing and 135 km west of Kalgoorlie. Running north-northwest from the homestead are a series of uplands of contrasting geologies which include mafic and ultramafic ridges (these formations are commonly termed greenstones), banded ironstones and extensive Tertiary laterites. The uplands of Jaurdi Station form part of the western most greenstone belts (Fig 1).

Jaurdi was purchased by the Department of Conservation and Land Management in 1989 using Sandalwood Conservation and Regeneration Project funding. In the Goldfields region management plan (CALM 1994) it is proposed that the northern section of Jaurdi station (covering the Hunt Range) be incorporated into the Mt Manning Range Nature Reserve, while the southern section (including the Yendilberin and Watt Hills and associated greenstones) be vested as State Forest for sandalwood and flora and fauna conservation. None of the station is grazed. Much of the southern section of Jaurdi has been cut over for timber to feed the pumping stations supplying water to the goldfields earlier last century.

The climate of the region is semi-arid mediterranean with warm winters and hot summers. Mean annual rainfall at Southern Cross (100 km south-west) is 288 mm although seasonal variation is high. The driest year on record was 1940 with 117 mm and the wettest was 1943 with 542 mm. Most rain falls in winter generally associated with frontal activity from May through August. Summer falls (to 100 mm) are highly erratic and result from thunderstorms. Heaviest falls are associated with rain bearing depressions forming from tropical cyclones (Newbey 1985; Anon 1988).

The temperature data from Southern Cross shows mean maximum temperatures are highest in January

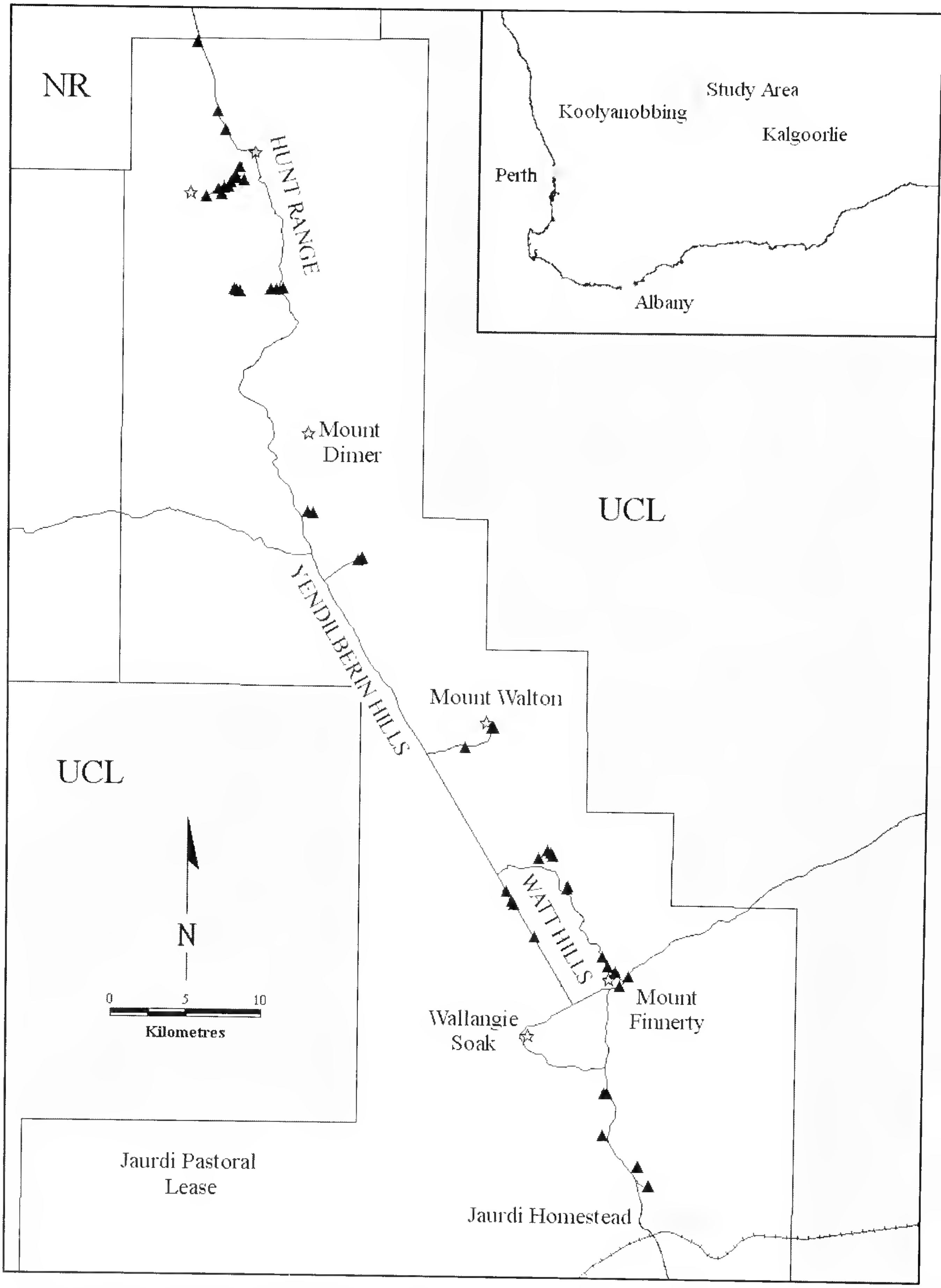

Figure 1. Location survey sites (solid triangle) within the study area. (UCL, Unallocated Crown Land; NR, Nature Reserve)

(34.5 °C) with December through March all recording mean annual temperatures above 30 °C and the highest daily temperature on record of 45.6 °C. Lowest mean minimum temperatures of below 5 °C are recorded in July and August. Lowest daily minimum temperature on record was −3.8 °C.

The geology of the study area has been mapped and described in detail in Jackson and Kalgoorlie 1: 250000 sheets (Chin & Smith 1983; Wyche 1993) and the geology and landforms have been summarized by Newbey (1985). The study area has been tectonically stable since the Proterozoic (600 - 2500 MY old). The major landscape features are controlled by the Archaean (2500 - 3700 MY old) granites, which underlie most of the study area and have weathered into gently undulating plains and broad valleys covered by Tertiary soils (< 65 MY old). Immediately north of the Jaurdi homestead are a series of Archaean mafic and ultramafic ridges. These give way to the Watt and Yendilberin Hills which have a core of resistant Archaean banded ironstones (formed from lacustrine deposits of iron oxides and quartz sand) and chert surrounded by Tertiary laterites. Further to the north, the Hunt Range is largely greenstone and a narrow band of banded ironstone. The upland areas and around the base of the range have been extensively laterised. The net result is a subdued landscape set in extensive outwash plains of Tertiary colluvium.

Jaurdi Station lies in the Coolgardie interzone, which is generally dominated by eucalypt woodlands and shrublands on yellow sandplains. The interzone marks the transition in vegetation from the species-rich southwest to the more arid communities of the desert regions (Beard 1990). Beard (1972, 1978) first described the major structural formations of this area, which he grouped into vegetation systems. He defined the vegetation of the Watt and Yendilberin Hills and the Hunt Range as forming part of the Bungalbin System. This system also encompasses the ironstone and greenstone areas of the Helena and Aurora Range, the Koolyanobbing Range and Mt Jackson area. The undulating greenstone plain north of Jaurdi homestead is described as part of the very widespread Jackson system.

The Bungalbin system is most well developed on the massive banded ironstone ranges (Helena and Aurora, Mt Jackson and Koolyanobbing Ranges). The system is a low thicket composed of *Acacia quadrimarginea*, *A. tetragonophylla*, *Allocasuarina acutivalvis* with trees of *Brachychiton gregorii* and on massive outcrops *Dryandra arborea*. This system typically has an understorey of *Dodonaea* spp, *Eremophila clarkei*, *Eriostemon brucei*, *Grevillea paradoxa* and a range of annual species (Beard 1972). On Mt Finnerty *Allocasuarina acutivalvis* dominates rather than *Acacia quadrimarginea*. On the lower slopes *Eucalyptus corrugata* and *Brachychiton gregorii* are present merging below with woodlands of *E. corrugata*, *E. longicornis*, *E. loxophleba* and *Casuarina pauper* (= *C. cristata*) (Beard 1978).

The Jackson system around Jaurdi homestead is described (Beard 1978) as woodlands principally composed of *E. sheathiana*, *E. salubris*, *E. transcontinentalis* and *Casuarina pauper* with an understorey of either broombush (*Eremophila*) or saltbush (*Atriplex*). Elsewhere on the Jackson sheet Beard describes *Acacia* shrublands and breakaways in this vegetation system (Beard 1972).

Beard's pioneering work was followed up some years later with a major regional survey of the biota of the Eastern Goldfields (Dell *et al.* 1985). Newbey & Hnatiuk's (1985) description of the vegetation of the study area was essentially similar to that provided by Beard. Both Beard's survey and the later biological survey of the eastern goldfields were undertaken to provide regional overviews. Consequently the individual ranges were not sampled extensively.

The aim of the present work was to undertake a detailed flora and vegetation survey of the greenstone areas north of Jaurdi homestead and the Watt and Yendilberin Hills and the Hunt Range (Fig 1).

Methods

Fifty three 20 m x 20 m quadrats were established on the greenstone areas north of Jaurdi homestead, and on the foot slopes and the outwash plains of the Hunt Range and the Yendilberin and Watt Hills (Fig 1). These quadrats attempted to cover the major geographical, geomorphological and floristic variation found in the study area. Care was taken to locate quadrats in the least disturbed vegetation available in the area being sampled. Additional records from the Hunt Range and the Yendilberin and Watt Hills were compiled from collections held in the Western Australian Herbarium.

All vascular plants within each quadrat were recorded and data on topographical position, slope, aspect, percentage litter, percentage bare ground, percentage exposed rock, and vegetation structure were collected from each quadrat. Most of the Hunt Range quadrats were established in July 1995 and all quadrats were scored in September 1995. Topographical position was scored on a subjective seven point scale (ridge tops (1); upper slopes (2); midslopes (3); lower slopes (4); valley flats (5); small rises in valley (6); washlines (7)). Slope was scored on a one to three scale from flat to steep. Aspect was recorded as one of 16 cardinal directions. Vegetation structure was recorded using Muir's (1977) classification.

All quadrats were permanently marked with four steel fence droppers and their positions determined using a GPS unit. Twenty four soil samples from the upper 10 cm were collected from each quadrat. These were bulked and analyzed for electrical conductivity, pH, total N, total P, percentage sand, silt and clay, exchangeable Ca, exchangeable Mg, exchangeable Na, and exchangeable K (McArthur 1991).

Quadrats were classified according to similarities in species composition of perennial taxa to facilitate comparisons with classifications from other ranges in the area (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2000). The quadrat and species classifications were undertaken used the Czekanowski coefficient and followed by "unweighted pair-group mean average" fusion method (UPGMA; Sneath & Sokal 1973). Semi-strong hybrid (SSH) ordination of the quadrat data was undertaken to show spatial relationships between groups and to elucidate possible environmental correlates with the classification (Belbin 1991).

Climate estimates (mean annual temperature, annual temperature range, mean annual rainfall, rainfall coefficient of variation) were obtained from BIOCLIM (Busby 1986), a prediction system that uses mathematical surfaces fitted to long term climate data. Relationships among and between soil and physical site parameters and climate estimates were examined using Spearman rank correlation coefficient. Vectors for soil, physical site parameters, and climatic estimates were fitted to the ordination along axes of highest correlation using the principal axis correlation routine in the PATN package (Belbin 1993) (also known as rotational correlation analysis). Statistical significance of these vectors was determined using random permutations of the values of the variable among sites (Faith & Norris 1989). Statistical relationships between quadrat groups for factors such as soil and physical site parameters and climate estimates were tested using Kruskal-Wallis non-parametric analysis of variance (Siegel 1956). To reduce the probability of type I errors given the number of intercorrelations and cross comparisons made, significance differences were reported at a level of $P<0.01$.

Nomenclature generally follows Paczkowska & Chapman (2000). Manuscript names are indicated by "ms", introduced weeds by "*". Selected voucher specimens have been lodged in the Western Australian Herbarium.

Results

Flora

A total of 287 taxa (species, subspecies and varieties) and one hybrid were recorded from the Jaurdi greenstones, Watt Hills, the Yendilberin Hills and the Hunt Range. The flora list was compiled from taxa found in the 53 plots or the adjacent area, from other opportunistic collections and collections held in Western Australian Herbarium (Appendix 1). Of these 288 taxa, 273 are native and 15 are weeds.

The best represented families were the Asteraceae (41 native taxa and 3 weeds), Myrtaceae (32 taxa), Poaceae (12 native taxa and 6 weeds), Chenopodiaceae (16 taxa), Myoporaceae (16 taxa), Mimosaceae (17 taxa), and Proteaceae (13 taxa). This pattern is typical of the flora of the South Western Interzone (Newbey & Hnatiuk 1985). Good rains were experienced in the winter and early spring of 1995, reflected by the large numbers of annuals and geophytes on the flora list (Appendix 1). The most common genera were *Eucalyptus* (20 taxa), *Acacia* (17 taxa) and *Eremophila* (16 taxa).

Six taxa (*Acacia acanthoclada* subsp *glaucescens*, *Elachanthus pusillus*, *Eremophila caerulea* subsp *merrallii* ms, *Grevillea erectiloba*, *Grevillea georgeana*, *Trymalium urceolare*) were recorded during the survey that are under consideration for listing as threatened flora (K Atkins, CALM, personal communication). *Grevillea georgeana* was widespread on banded ironstone along the entire range from near Jaurdi homestead to close to the Mt Manning Range Nature Reserve boundary (Fig 1). *Acacia acanthoclada* subsp *glaucescens*, *Elachanthus pusillus*, *Eremophila caerulea* subsp *merrallii* ms, *Grevillea erectiloba* and *Trymalium urceolare* were all located near the northern end of the Hunt Range (Fig 1). The *Acacia* and *Elachanthus* were growing on greenstone soils near the base of the range.

Elachanthus pusillus is a small annual daisy that has been poorly collected. Only four other collections are lodged in Western Australian Herbarium, one collected by Spencer Moore in the WA goldfields in 1895, another by WV Fitzgerald from Kalgoorlie in 1898, and a third by GJ Keighery 16 km east of Cocklebiddy in 1981. The fourth collection lacks locality details. Further work is required to determine the extent of this species north of the Hunt Range.

Grevillea erectiloba was found on yellow sands over laterite, a similar habitat to where it has been located at the Helena and Aurora Ranges and the Mt Manning Range (Gibson *et al.* 1997; Gibson & Lyons, unpublished data). The *Trymalium* was located on a yellow sand sheet in the saddle of the Hunt Range between Pittosporum and Kurrajong Rock Holes. This represents a range extension of some 350 km from the Bindoon – Calinigiri area.

A large new population of *Eremophila caerulea* subsp *merrallii* ms was located on red clay flats over decomposing granite at the base of the Hunt Range. This taxon is also known from a number of populations from the Hunt Range and south to Southern Cross area and west to Bruce Rock.

Three other taxa were recorded that have been very poorly collected. *Leucopogon* sp Marvel Loch (RJ Cranfield & P J Spencer 7790) was collected on the top of a breakaway in the Watt Hills; this taxon had only previously been recorded from a breakaway about 50 km SSW of the study area. Further collections of this taxon have subsequently been made in similar habitats at the southern end of the Watt Hills (M Hislop 2092 & 2093).

A *Gnephosis* sp related to *G. brevifolia* was collected from *Eucalyptus salubris* woodland near Jaurdi homestead. This collection matches *Gnephosis* sp Norseman (KR Newbey 8096), which was collected 12 km north-east of Norseman.

Austrostipa blackii was collected twice, once below the Watt Hills and again below the Hunt Range. This taxon is widespread in South Australia, New South Wales and Victoria, but had only been collected three times previously in Western Australia, most recently in 1959 (Vickery *et al.* 1986). It has recently been relocated in the nearby Highclere Hills (NG & ML 2504) and in the Dalwallinu town reserve, some 300 km east of the study area (M Hislop 1815 & 1852).

Vegetation

Only material that could be identified to species level was included in the analysis (*ca* 99% of records). In the 53 quadrats established on the greenstones north of Jaurdi homestead, Watt and Yendilberin Hills, and Hunt Range, 236 taxa were recorded of which 148 were perennial (Appendix 1). Forty three perennials occurred at only one quadrat. Preliminary analyses showed these singletons had little effect on the community classification and therefore were excluded. As a result the final data set consisted of 105 perennial taxa in 53 quadrats. Species richness ranged from one to 24 taxa per quadrat, with individual taxa occurring in between two and 37 of the 53 quadrats.

The dendrogram shows the 53 sites divide into two primary groups, based on soil type with the eucalypt

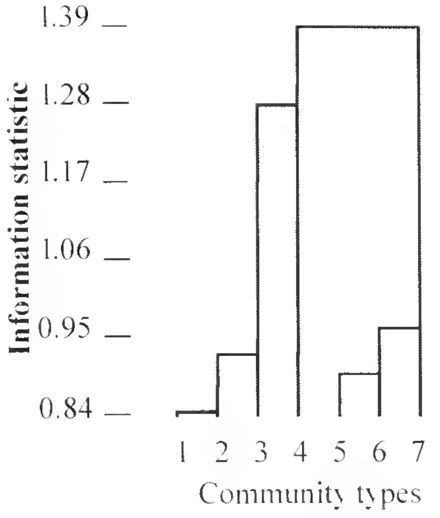

Figure 2. Dendrogram of the floristic quadrats from the uplands of Jaurdi Station showing the seven group level classification.

woodlands (community type 1, 2, 3 & 4) of the deeper more fertile soils separating from the *Acacia* and *Allocasuarina* shrublands (community types 5, 6 & 7) of the less fertile sites (Fig 2). This division can also be clearly seen in the sorted two-way table of the sites and species classification (Table 1).

- **Community type 1** is generally dominated by *Eucalyptus clelandii, E. griffithsii* or *E. longicornis*. Species in species group B are typical of this community as is the lack of species in species group J (Table 1). Common species in the understorey include *Olearia muelleri, Acacia erinacea* and *Maireana georgei*. Community type 1 can be split into two subgroups. Type 1a typically includes taxa such as *Acacia acuminata, Ptilotus obovatus, Dodonaea lobulata, Eremophila oldfieldii, Sclerolaena densiflora* and other taxa in species group C, while type 1b is well represented by species in species group D including *Eucalyptus salmonophloia, E. salubris* and *Melaleuca pauperiflora* subsp *fastigiata*. Community type 1b represents deeper and or more fertile soils lower in the landscape. Average species richness was similar (18.3 *cf* 14.4 perennial taxa per plot) between subgroups.
- **Community type 2** shared many species in species group B but also had high representation of species in the chenopod-rich species group C. Sites in this type were typically low in the landscape and dominated by *Eucalyptus ravida* or *E. longicornis*. Average species richness was 13.0 taxa per plot.
- **Community type 3** was dominated or co-dominated by *Eucalyptus transcontinentalis* and *E. clelandii*. Both sites in this group were species poor (average richness of 8.5 taxa per plot) and both sites had been extensively cut over for timber.
- **Community type 4** was also species poor with an average species richness of only 3.3 taxa per plot. This community type occurred on breakaways and was dominated by *Eucalyptus capillosa* subsp *capillosa* or *E. capillosa* subsp *polyclada*. The difference between the subspecies was that the first was a tree and the second a mallee. The understorey was typically *Ptilotus helichrysoides* (species group F) but on one site on the Hunt Range it was totally lacking. It is not clear if the growth form of the eucalypt is genetically fixed or if the tree habit develops with old age.
- **Community type 5** occurs on sandy soils developed over laterites or banded ironstone. This community type is characterized by species in species group J, some of which are shared with community type 6. Those largely restricted to and generally co-dominant in community type 5 include *Allocasuarina campestris, Baeckea elderiana, Grevillea obliquistigma, Acacia ?sibina,* and *Grevillea paradoxa*. This community was found in the north of the study area on Hunt Range and on the Yendilberin Hills. On the Hunt Range it occurred as a dense thicket on the top of the range on sands developed on a laterite sheet and on laterites on change in slope at the base of the range. On the Yendilberin Hills the community was more open and occurred on north and north-northwest facing slopes. Average species richness was 13.8 taxa per plot.
- **Community type 6** generally occurred on shallower soils than community type 5 and was more widespread occurring from the Hunt Range to near Jaurdi homestead. Species groups J and B were typical of this community type, but as noted above some taxa in species group J were absent or occurred at low frequency. This community type was generally dominated or co-dominated by *Acacia acuminata*, with or without a variable eucalypt component. *Eriostemon brucei, Eremophila clarkei*, the rock fern *Cheilanthes austrotenuifolia* and *Allocasuarina acutivalvis* were common understorey components. On massive banded ironstone the *Acacia acuminata* was replaced by *Acacia hemiteles*. Average species richness in community type 6 is high at 16.5 taxa per plot.
- **Community type 7** comprised a single site occurring on deep yellow sands in the saddle on the Hunt Range between Pittosporum and Kurrajong Rock Holes. These sands are presumed colluvial deposits derived from weathered laterites higher in the landscape. This community type was considerably different from all other sites sampled with 10 shared taxa and a further nine recorded only from this one site.

Physical correlates

Soil parameters showed generally high levels of intercorrelation (Table 2) except for total P and percentage clay. The highest levels of intercorrelation were seen between pH and exchangeable Ca and exchangeable K. Similarly the climate estimates and latitude were all highly intercorrelated, while physical site parameters (*e.g.* topographic position, slope, aspect, etc) were more independent (Table 2). Soil parameters showed significant differences in mean values of electrical conductivity, exchangeable Na, pH, exchangeable Ca, exchangeable K, exchangeable Mg, total N and percentage sand between floristic groups (Table 3).

Soils of community types 1, 2 and 3 had a higher pH and higher levels of exchangeable Ca and K than the other four community types. A similar pattern is seen for exchangeable Mg but community type 4 also had elevated levels compared with the remaining community types. Community types 2 and 3 were found on the most

Table 1

Sorted two-way table of Jaurdi greenstone, Yendilberin and Watt Hills, and the Hunt Range sites showing species occurrence by community type. Sites appears as columns, species as rows.

	COMMUNITY TYPE							
	1A	1B	2	3	4	5	6	7
SPECIES GROUP A								
Acacia acanthoclada subsp *glaucescens*	* *							
Eucalyptus corrugata	***							
Eucalyptus transcontinentalis	*		*	**				
Maireana radiata	**		**					
Acacia hemiteles	**	*					** ***	
Eremophila caperata ms	*	* *						
Halgania andromedifolia	* *	*						
Bossiaea walkeri	* *		*					
Dodonaea stenozyga	* *	*	**	*				
Eucalyptus ravida			***					
SPECIES GROUP B								
Acacia acuminata	** ***					****	*********** *	
Scaevola spinescens	**** *****	******	*			*	* *** * * *	
Austrostipa elegantissima	**********	* **	**** **			****	* ******** ****	*
Acacia tetragonophylla	***	**		*		*	** * ** ** *	
Alyxia buxifolia	* ****	* *			*		** **********	
Santalum spicatum	* * ****	*					* * ***	*
Dodonaea lobulata	* *** *					*	* * *	
Eremophila oldfieldii subsp *angustifolia* ms	** *** *						**** * *	
Ptilotus obovatus	** *******						*** *	
Eucalyptus griffithsii	** * *		* *				** ***	
Senna artemisioides subsp *filifolia*	******	*	**	*		*	***	
Austrostipa trichophylla	****	** *	**	**			** ***** * ***	
Acacia erinacea	** ***	* *****	** **		*			
Eremophila scoparia	* ****	***	* *****	*				
Maireana trichoptera	******* **	** * *	*******					
Sclerolaena diacantha	******* *	* *** *	*******					
Eucalyptus clelandii	**** ***	** **	**	*				
Maireana georgei	***** *	*** * *	*				**	
Olearia muelleri	****** **	******	*** ***	**			****	
Eremophila oppositifolia var *angustifolia* ms	* *	******	*	*		* *	* ** *	
Grevillea acuaria	**	*****	*		**		* *	
Exocarpos aphyllus	*	*	* *	*			* *	
Eucalyptus yilgarnensis	**	* *						
Solanum orbiculatum	* *		*			*	*	
SPECIES GROUP C								
Acacia pachypoda	*		**					
Sida spodochroma			**					
Atriplex nummularia	** *		** ** *					
Atriplex vesicaria	* *		**** **	*				
Eremophila ionantha		**	*****				*	
Eremophila interstans	**	*	*					
Eucalyptus longicornis	**		*** *					
Sclerolaena densiflora	** **	*	****					
Austrostipa platychaeta	***		*					
Atriplex paludosa	*		*					
Maireana pentatropis	* *		***					
Maireana triptera	*		*** *					
Beyeria brevifolia			* *					
Enchylaena tomentosa	* *							
Pittosporum phylliraeoides	* *							
Rhagodia drummondii	* *							
Eremophila glabra subsp *glabra*	* * *							
SPECIES GROUP D								
Eucalyptus salmonophloia		***	* *					
Lawrencia repens		* *	*					
Santalum acuminatum	*	*** *						*

Table 1 (continued)

	COMMUNITY TYPE							
	1A	1B	2	3	4	5	6	7
Sclerolaena fusiformis	****	*** *						
Eucalyptus sheathiana		**						
Melaleuca pauperiflora subsp *fastigiata*		* **		*				
Templetonia sulcata		* * *						
Eucalyptus salubris		* *	*					
SPECIES GROUP E								
Acacia andrewsii	*	*			*		**	
Eucalyptus capillosa subsp *polyclada*					*		*	
Eremophila granitica							**	
Melaleuca leiocarpa							* ** *	
Xerolirion divaricata							** *	
SPECIES GROUP F								
Eucalyptus capillosa subsp *capillosa*					* *			
Ptilotus helichrysoides					**			
SPECIES GROUP G								
Eucalyptus ewartiana							**	
Austrostipa blackii							* *	
SPECIES GROUP H								
Acacia quadrimarginea							* *	
Eucalyptus oleosa							**	
Dodonaea microzyga var *acrolobata*						*	* * ***	
Olearia pimeleoides						*	*****	
Eucalyptus loxophleba subsp *lissophloia*				*		*	* * * *	
SPECIES GROUP I								
Acacia ramulosa		*				*		*
Phebalium canaliculatum		*		*			*	*
Acacia resinimarginea							*	*
Phebalium tuberculosum							*	*
Amphipogon strictus						* **	* *	*
Lepidosperma sp (NG & ML 2056)							**	
Prostanthera campbellii						*	** *	
Rinzia carnosa						*	*	
SPECIES GROUP J								
Acacia ?sibina						******		
Baeckea elderiana						******	* *	
Grevillea obliquistigma						** ***	***	
Allocasuarina campestris						* * **	** *	
Grevillea paradoxa						****	** *	
Hibbertia rostellata complex						** ***	* **	
Prostanthera grylloana						***	*** * **	
Allocasuarina acutivalvis						** *	* ** ** *******	*
Leucopogon breviflorus						*****	*** * * ****	
Cheilanthes austrotenuifolia						* *	****** *******	
Philotheca brucei	*					* ***	** *************	
Eremophila clarkei						* *	** **** ** ** *	
Calycopeplus paucifolius						*	*	
Melaleuca nematophylla						** *	* * *	
Brachychiton gregorii						*	* *	
Dryandra arborea						*	*	
Rhyncharrhena linearis		*				*		
Dianella revoluta						* *	* * **	
Sida atrovirens ms						*	* *	
Olearia stuartii							* ** *	
Grevillea georgeana							* * *	
Hibbertia eatoniae							* **	
Westringia cephalantha							* *	
Hibbertia exasperata							****	*

Table 2

Matrix of Spearman rank correlation coefficents between soil and physical site parameters and climate estimates. Only correlations significant at $P < 0.01$ shown ($r > 0.351$). See methods for parameter codes.

	EC	pH	N	P	Sand	Silt	Clay	Ca	Mg	Na	K	Topog	Slope	Aspect	%rock	%litter	%bare	Lat	Tann	Trange	Rann	Rcv
Soil parameters																						
EC	1.000																					
pH	.484	1.000																				
Total N	.626	.530	1.000																			
Total P	.	.	.	1.000																		
% Sand	-.462	-.434	.	.	1.000																	
% Silt	.558	.544	.559	.	-.760	1.000																
% Clay	.	.	.	.	-.806	.	1.000															
Ca	.535	.916	.674	.	-.532	.625	.	1.000														
Mg	.738	.692	.542	.	-.604	.621	.355	.733	1.000													
Na	.771	.	.356	.	-.526	.470	.379	.	.692	1.000												
K	.519	.915	.607	.	-.469	.591	.	.884	.731		1.000											
Physical site parameters																						
Topography	.	.	.	.	.	.	.	.	.	.	.416	1.000										
Slope	.	-.503	.	.	.	.	.	.	.	.	-.508	.	1.000									
Aspect	-.398	-.399	.	.	.	-.391	.	.	-.362	.	-.423	.	.	1.000								
%Rock	.	-.524	.	.	.	.	.	.	.	.	-.538	-.533	.459	.	1.000							
%Litter	.	.365	.	.	.	.	.	.352	.	.	.377	.	.	.	-.497	1.000						
%Bare	.	.366	.	.	.	.	.	.	.	.	.	.416	-.421	.	-.758	.	1.000					
Latitude																		1.000				
Climate estimates																						
Tann	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-.375	.	.389	.916	1.000			
Trange	.	.	.	.	.	.	.	.	.	-.363	.	.	.	.	.	.	.	.989	.917	1.000		
Rann	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.371	-.363	-.401	-.932	-.982	-.926	1.000	
Rcv	.	.	.	.	.	.	.	.	.	.394	.	.	.	.	.	.	.	-.753	-.603	-.749	.629	1.000

alkaline soils (pH > 8.2) with community type 2 also having high levels of exchangeable K. While communities types 1, 2 and 3 all tended to occur on low slopes, they were not restricted to positions low in the landscape; community types 1 and 2 were recorded from most topographic positions, implying that these sites were not simple colluvial deposits low in the landscape or that calcrete accumulation occurs only in erosional regimes (*cf* Anand *et al.* 1997). The breakaway community (type 4) shows greatly elevated levels of exchangeable Na and electrical conductivity than the other communities, probably resulting from the release of salts from the pallid zone clays.

Of the major elements, total N was higher in the soils of the eucalypt woodlands (especially community type 3) and lower in the soils of the units on laterites, banded ironstone and sands (community types 5, 6 and 7) although total N in soils of community type 6 were quite variable (Table 3). Soils of community types 4 to 7 were acidic ranging from pH 4 to pH 6.7 with the breakaway soils being the most acidic. Total P levels were largely uniform across all soils but were elevated in soils of community type 4 (eroding breakaway) and lower in the sands of community type 7. Insufficient number of plots were available to allow tests of significance of this trend. Community types 1, 2 and 3 tended to occur low in the landscape with community type 3 in washlines. Soils of community types 1 and 2 showed significantly lower percentage sand.

Of the site parameters only percentage surface rock and litter cover showed significant differences between the mean of the floristic groups with community types typical of steeper slopes (types 5 and 6) having significantly higher surface rock cover. Conversely litter cover was generally low in these sites. Some geographic segregation in distribution of floristic groups was seen, with significant differences in mean latitude, temperature range and annual rainfall estimates (Table 3).

Both the three (stress 0.18) and four dimensional (stress 0.14) ordinations of the data-set showed essentially the same patterns, except for an increase level of correlations with climatic variables on the fourth axis. The simpler three dimensional solution is depicted in Fig 3. Abiotic vectors were fitted to the ordination, with the most highly correlated soil, physical site parameters and climatic estimates being superimposed on the ordination (Fig 3A,B). Correlations could not be improved by standard data transformations, implying no simple non-linear responses in the data.

Table 3

Jaurdi upland community type means for soil and physical site parameters and climate estimates. Differences between means for community types 1, 2, 5 and 6 (in bold) tested using Kruskal-Wallis non-parametric analysis of variance (ns indicates not significant, ** indicates P < 0.01, *** indicates P < 0.001, **** indicates P < 0.0001).

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Soil parameters							
EC (mS m^{-1}) ****	**12.23**	**15.75**	24.00	116.33	**2.33**	**3.50**	2.00
pH ****	**7.80**	**8.63**	8.35	4.57	**5.53**	**5.92**	5.80
Total N (%) **	**.083**	**.101**	.142	.087	**.039**	**.066**	.0270
Total P (%) ^{NS}	**126.6**	**128.9**	125.5	273.0	**138.3**	**145.2**	64.0
% Sand **	**71.8**	**66.8**	80.3	75.8	**80.5**	**74.2**	93.5
% Silt **	**12.1**	**15.9**	11.5	10.7	**8.4**	**10.1**	1.5
% clay ^{NS}	**16.1**	**17.3**	8.3	13.5	**11.1**	**15.7**	5.0
exch Ca (me%) ****	**12.7**	**18.3**	13.2	1.1	**1.6**	**4.0**	1.0
exch Mg (me%) ****	**3.92**	**4.15**	6.07	2.77	**0.39**	**1.16**	0.16
exch Na (me%) **	**0.28**	**0.38**	0.28	3.60	**0.03**	**0.07**	0.02
exch K (me%) ****	**0.74**	**1.18**	0.95	0.16	**0.19**	**0.31**	0.11
Physical site parameters							
Topography ^{NS}	**3.2**	**3.9**	4.0	2.0	**2.8**	**2.4**	1.0
Slope ^{NS}	**1.7**	**1.6**	1.5	2.7	**2.2**	**2.1**	2.0
Aspect ^{NS}	**3.3**	**2.1**	2.0	3.3	**4.7**	**4.6**	6.0
% rock **	**51.8**	**28.8**	27.5	93.3	**76.7**	**75.0**	0.0
% litter **	**35.6**	**32.5**	35.0	31.7	**27.5**	**13.8**	50.0
% bare ^{NS}	**16.5**	**22.5**	35.0	0.0	**10.0**	**6.9**	50.0
Latitude ^{NS}	**-30.439**	**-30.383**	-30.645	-30.533	**-30.325**	**-30.583**	-30.200
Climate estimates							
Mean annual temp (°C) **	**18.7**	**18.8**	18.5	18.5	**18.7**	**18.5**	18.8
Annual temp range (°C) ^{NS}	**29.7**	**29.8**	29.5	29.6	**29.9**	**29.6**	30.0
Mean annual rainfall (mm) **	**261**	**260**	266	266	**260**	**266**	258
Rainfall coefficient of variation (%) ^{NS}	**31.9**	**31.7**	32.0	31.9	**31.7**	**31.7**	31.6
Number of quadrats	**17**	**8**	2	3	**6**	**16**	1

While none of the abiotic vectors paralleled the primary ordination axis, the eucalypt woodlands (types 1 to 4, top left quadrant) clearly separate from the shrublands (types 5 to 7, bottom right quadrant). Strong correlations with soil pH, exchangeable Ca, exchangeable K and exchangeable Mg are consistent with this separation (Fig 3A). These parameters were highly intercorrelated as noted above. Gradients in exchangeable Na and electrical conductivity (both highly intercorrelated) and percentage rock cover are consistent with the separation of the breakaway community (type 4) on axis 3 (Fig 3B, Table 3). Significant correlations with estimated climatic parameters (mean annual temperature and mean annual rainfall) result from the restriction of community types 3 and most occurrences of type 6 to the southern part of the study area while types 5 and 7 occur in the north. These regional gradients become more obvious in the four dimensional solution (not shown).

Discussion

The Jaurdi greenstones, the Watt and Yendilberin Hills and the Hunt Range have a rich flora, with 287 taxa and one hybrid having been recorded. This includes six taxa under consideration for listing as threatened flora. In addition three further poorly-surveyed taxa were identified, which should also be considered for listing.

The flora is comparable with that of the Helena and Aurora Range (50 km to the west, Gibson *et al.* 1997) and the Highclere Hill (100 km west-southwest, Gibson & Lyons 2000) (Table 4). The uplands of Jaurdi station (which include the Jaurdi greenstones, the Watt Hills, the Yendilberin Hills and the Hunt Range) are less extensive

Table 4.

Comparison of the floras of the uplands of Jaurdi station with the Helena and Aurora Range, and the Highclere Hills.

	Upland of Jaurdi Station	Helena and Aurora Range	Highclere Hills
Total flora	288	325	242
Weeds	15	21	25
Endemic taxa	-	4	-
Eucalyptus spp	20	19	12
Eremophila spp	16	14	8
Acacia spp	15	17	9
Melaleuca spp	4	5	2

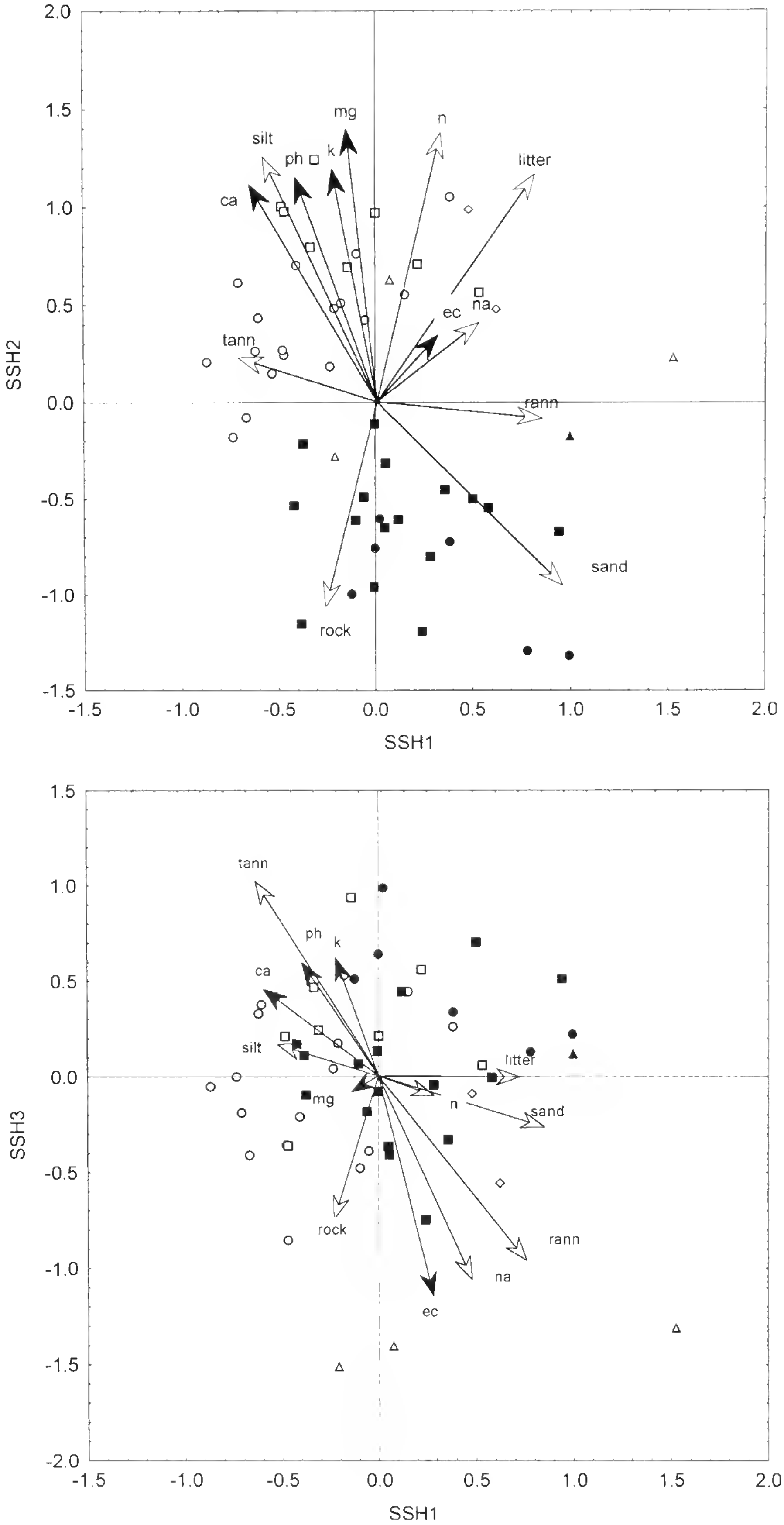

Figure 3. Ordination of Jaurdi Station uplands floristic quadrats coded by community type (1 open circles, 2 open squares, 3 open diamonds, 4 open triangles, 5 solid circles, 6 solid squares, 7, solid triangles). Arrows show the direction of the best fit linear correlation for the most significant (solid arrows, P< 0.001; open arrows P< 0.01) soil and site parameters. The longer the lines the less projection into other dimensions. **A:** Ordination axes 1 versus 2. **B:** Ordination axes 1 versus 3.

in area than the Helena and Aurora Range, and this is likely to contribute to the lower number of taxa recorded, with the reverse being true in the comparison with the Highclere Hills. Both the Helena and Aurora Range and the uplands of Jaurdi station have similar numbers of the eucalypts, *Acacia* spp, and *Eremophila* spp. However, there is a significant changeover of species between the range systems. Five of the 20 eucalypts, five of the 16 *Eremophila* spp and seven of the 15 *Acacia* spp recorded in the present study were not recorded on the Helena and Aurora Range.

While none of the measured soil, physical site parameters or climate estimates corresponded closely with the primary axis of the ordination, the site descriptions are strongly suggestive of a soil moisture gradient running from the eucalypt woodlands on deep more clayey soils on the left of the ordination to the shrublands on skeletal sandier soil to the right, with the single site on deep yellow sand lying in the middle of the ordination. Very strong correlations were found between the site ordination scores and some of the soil parameters. The eucalypt woodlands (types 1 to 3) occurred on more alkaline sites with higher levels of total N, while the breakaways produced highly acidic soil with higher levels of exchangeable Na, electrical conductivity and total P than other habitats. These differences presumably related to the mobilization of elements associated with the active erosion of these areas. Differences between soil parameters between community types within the major floristic division tended to be gradational.

The primary split between community types 1, 2, 3, and 4 from community types 5, 6 and 7 also largely conforms with the division between Beard's Jackson and Bungalbin systems (Beard 1972, 1978). Species typical of the Bungalbin system are found in species groups E, G, H, I and J. Our data show that the Bungalbin system on Jaurdi Station can be subdivided into three community types. Beard (1972, 1978) although recognizing variation within the Bungalbin system did not describe the patterns reported here.

The Bungalbin system is typical of the outcrops of banded ironstone (Beard 1972,1978). What is clear from the present survey is that this system also encompasses vegetation of decomposing laterites and that these laterites occur both on the tops of ranges and also at the change in slope at the base of the ranges. What is not clear is if these laterites are solely derived from banded ironstones or were derived from a several different lithologies.

The banded ironstones on Jaurdi station are much smaller and less extensive outcrops than on the Helena and Aurora Ranges or the Koolyanobbing Range to the west. Consequently somewhat different plant associations are recorded. Gibson *et al.* (1997) record three floristic communities on the banded ironstones of the Helena and Aurora Ranges. One was an upland community on massive ironstone variously dominated or co-dominated by *Dryandra arborea*, *Calycopeplus paucifolius*, *Acacia quadrimarginea*, *Grevillea zygoloba*, *Melaleuca nematophylla* (=*M. filifolia*) and *Allocasuarina acutivalvis*. The second community that occurred on the upper slopes and breakaways was dominated by *Eucalyptus ebbanoensis* or *E. capillosa* subsp *capillosa*. The third community occurred on the mid slopes and was generally dominated by *Eucalyptus ebbanoensis* over *Neurachne* sp Helena & Aurora (KRN 8972). With the possible exception of the breakaway community type, direct analogues of these three communities do not occur on Jaurdi ironstones. *Dryandra arborea* and *Calycopeplus paucifolius* (common and widespread on the Helena and Aurora Range) were rarely recorded on Jaurdi and *Eucalyptus ebbanoensis* and *Neurachne* sp Helena & Aurora (KRN 8972) were entirely lacking.

There are however some similarities in species composition between the ironstone floras of the two range systems. Species group J from the current analysis shares many taxa in common with species group H from the Helena and Aurora analysis. The smaller size of the outcrops and the more extensive development of laterite on the Jaurdi uplands are the most likely explanations of the shift in floristic composition although a climatic gradient and Tertiary climatic history (Hopper 1979) may also be involved.

These data imply that while broad agreement exists between Beard's vegetation systems (based on structural mapping, dominant species and geology) and the floristic classification presented here (based on perennial species presence/absence), significant variation does occur within a vegetation system and not all components of this variation are present on all ranges. None of the Bungalbin vegetation system is presently in any National Park or Nature Reserve, although the northern section of the Hunt Range and the Helena and Aurora Range have been recommended for inclusion into the Mt Manning Range Nature Reserve (CALM 1994). Our results support these recommendations.

Small scale mining has and continues to occur on Jaurdi station. While the greenstone community types appear to be widespread, mining activity is also impacting on the much more restricted breakaway community (type 4). Any future expansion into this community type will need to be very carefully assessed. Jaurdi was also extensively cut over to supply wood for mines and the boilers of the pumping stations for the goldfields water pipeline. The most severely impacted areas were avoided in the present study although community type 3 may be a result of this cutting.

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Appendix 1

Flora List for the Jaurdi greenstones, the Yendilberin and Watt Hills, and the Hunt Range. Nomenclature follows Paczkowska & Chapman (2000); ms denotes a manuscript name, * an introduced taxon.

- Adiantaceae
  - *Cheilanthes austrotenuifolia*
  - *Cheilanthes lasiophylla*
  - *Cheilanthes sieberi* subsp *sieberi*

- Aizoaceae
  - * *Mesembryanthemum nodiflorum*

- Amaranthaceae
  - *Ptilotus aervoides*
  - *Ptilotus carlsonii*
  - *Ptilotus exaltatus*
  - *Ptilotus gaudichaudii*
  - *Ptilotus helichrysoides*
  - *Ptilotus holosericeus*
  - *Ptilotus obovatus*

- Anthericaceae
  - *Thysanotus manglesianus*
  - *Thysanotus patersonii*

- Apiaceae
  - *Daucus glochidiatus*
  - *Hydrocotyle rugulosa*
  - *Trachymene cyanopetala*
  - *Trachymene ornata*
  - *Uldinia ceratocarpa*

- Apocynaceae
  - *Alyxia buxifolia*

- Asclepiadaceae
  - *Rhyncharrhena linearis*

- Asteraceae
  - *Actinobole uliginosum*
  - *Angianthus tomentosus*
  - * *Arctotheca calendula*
  - *Asteridea athrixioides*
  - *Blennospora drummondii*
  - *Brachyscome ciliaris*
  - *Calotis hispidula*
  - *Cephalipterum drummondii*
  - * *Centaurea melitensis*
  - *Ceratogyne obionoides*
  - *Chthonocephalus pseudevax*
  - *Elachanthus pusillus*
  - *Erymophyllum ramosum* subsp *ramosum*
  - *Gilruthia osbornei*
  - *Gnephosis* sp Norseman (KRN 8096)
  - *Gnephosis tenuissima*
  - *Hyalosperma demissum*
  - *Hyalosperma zacchaeus*
  - * *Hypochaeris glabra*
  - *Isoetopsis graminifolia*
  - *Lawrencella rosea*
  - *Leucochrysum fitzgibbonii*
  - *Millotia myosotidifolia*
  - *Millotia tenuifolia*
  - *Olearia exiguifolia*
  - *Olearia muelleri*
  - *Olearia pimeleoides*
  - *Olearia stuartii*
  - *Podolepis canescens*
  - *Podolepis capillaris*
  - *Podolepis lessonii*
  - *Podotheca angustifolia*
  - *Pogonolepis stricta*
  - *Rhodanthe laevis*
  - *Rhodanthe oppositifolia*
  - *Rhodanthe rubella*
  - *Rhodanthe stricta*
  - *Schoenia cassiniana*
  - *Senecio glossanthus*
  - *Streptoglossa liatroides*
  - *Trichanthodium skirrophorum*
  - *Triptilodiscus pygmaeus*
  - *Waitzia acuminata*

- Boraginaceae
  - * *Echium plantagineum*
  - *Halgania andromedifolia*

- Brassicaceae
  - * *Brassica tournefortii*
  - *Harmsiodoxa brevipes*
  - *Lepidium muelleri-ferdinandii*
  - *Lepidium rotundum*
  - *Stenopetalum filifolium*

- Caesalpiniaceae
  - *Senna artemisioides* subsp *filifolia*
  - *Senna cardiosperma* subsp *cardiosperma*

- Campanulaceae
  - *Wahlenbergia tumidifructa*

- Casuarinaceae
  - *Allocasuarina acutivalvis*
  - *Allocasuarina campestris*
  - *Allocasuarina corniculata*
  - *Casuarina pauper*

- Centrolepidaceae
  - *Centrolepis pilosa*

- Chenopodiaceae
  - *Atriplex nummularia*
  - *Atriplex paludosa*
  - *Atriplex vesicaria*
  - *Enchylaena tomentosa*
  - *Maireana carnosa*
  - *Maireana georgei*
  - *Maireana pentatropis*
  - *Maireana radiata*
  - *Maireana trichoptera*
  - *Maireana triptera*
  - *Rhagodia drummondii*
  - *Sclerolaena densiflora*
  - *Sclerolaena diacantha*
  - *Sclerolaena fusiformis*
  - *Sclerolaena parviflora*
  - *Threlkeldia diffusa*

- Chloanthaceae
  - *Lachnostachys coolgardiensis*

- Colchicaceae
  - *Wurmbea tenella*

- Crassulaceae
  - *Crassula colorata*

- Cupressaceae
  - *Callitris glaucophylla*
  - *Callitris tuberculata*

- Cyperaceae
  - *Isolepis cernua*
  - *Lepidosperma* aff *angustatum*
  - *Lepidosperma* sp (NG & ML 2056)
  - *Schoenus nanus*

- Dasypogonaceae
  - *Lomandra effusa*
  - *Xerolirion divaricata*

- Dilleniaceae
  - *Hibbertia eatoniae*
  - *Hibbertia exasperata*
  - *Hibbertia rostellata* complex

- Droseraceae
  - *Drosera macrantha* subsp *macrantha*

- Epacridaceae
  - *Leucopogon* sp Marvel Loch (RJC & PJS 7790)
  - *Leucopogon breviflorus*

- Euphorbiaceae
  - *Beyeria brevifolia*
  - *Calycopeplus paucifolius*
  - *Euphorbia drummondii*
  - *Monotaxis occidentalis*
  - *Poranthera microphylla*

- Frankeniaceae
  - *Frankenia* sp

- Geraniaceae
  - * *Erodium cicutarium*
  - *Erodium cygnorum*

- Goodeniaceae
  - *Brunonia australis*
  - *Dampiera eriocephala*
  - *Dampiera stenostachya*
  - *Goodenia berardiana*
  - *Goodenia krauseana*
  - *Goodenia mimuloides*
  - *Goodenia occidentalis*
  - *Scaevola spinescens*
  - *Velleia rosea*

- Haloragaceae
  - *Gonocarpus nodulosus*
  - *Haloragis gossei*

- Juncaceae
  - *Juncus aridicola*

- Juncaginaceae
  - *Triglochin calcitrapum*

- Lamiaceae
  - *Prostanthera althoferi* subsp *althoferi*
  - *Prostanthera campbellii*
  - *Prostanthera grylloana*
  - *Prostanthera incurva*
  - *Westringia cephalantha*
  - *Westringia rigida*

- Lobeliaceae
  - *Isotoma petraea*

Appendix 1 (continued)

Loganiaceae
Phyllangium paradoxa

Loranthaceae
Amyema benthamii
Amyema preissii
Lysiana casuarinae

Malvaceae
Lawrencia repens
Sida atrovirens ms
Sida spodochroma

Mimosaceae
Acacia acanthoclada subsp *glaucescens*
Acacia acuminata
Acacia andrewsii
Acacia assimilis subsp *assimilis*
Acacia colletioides
Acacia daviesioides
Acacia erinacea
Acacia hemiteles
Acacia merrallii
Acacia pachypoda
Acacia quadrimarginea
Acacia ramulosa
Acacia resinimarginea
Acacia rhodophloia
Acacia ?sibina
Acacia steedmanii
Acacia tetragonophylla

Myoporaceae
Eremophila caerulea subsp *merrallii* ms
Eremophila ?caperata ms
Eremophila clarkei
Eremophila decipiens subsp *decipiens* ms
Eremophila drummondii
Eremophila glabra subsp *glabra*
Eremophila granitica
Eremophila interstans
Eremophila ionantha
Eremophila latrobei subsp *latrobei* ms
Eremophila maculata
Eremophila oldfieldii subsp *angustifolia* ms
Eremophila oppositifolia var *angustifolia* ms
Eremophila rugosa ms
Eremophila scoparia
Eremophila serrulata

Myrtaceae
Baeckea elderiana
Eucalyptus brachycorys
Eucalyptus capillosa subsp *capillosa*
Eucalyptus capillosa subsp *polyclada*
Eucalyptus celastroides subsp *celastroides*
Eucalyptus clelandii
Eucalyptus corrugata
Eucalyptus cylindrocarpa
Eucalyptus ewartiana
Eucalyptus griffithsii
Eucalyptus hypochlamydea subsp *hypochlamydea*
Eucalyptus leptopoda subsp *subluta*
Eucalyptus longicornis
Eucalyptus loxophleba subsp *lissophloia*
Eucalyptus oleosa
Eucalyptus ravida
Eucalyptus salmonophloia
Eucalyptus salubris
Eucalyptus sheathiana
Eucalyptus transcontinentalis subsp *transcontinentalis*
Eucalyptus yilgarnensis
Euryomyrtus maidenii ms
Leptospermum roei
Malleostemon roseus
Malleostemon tuberculatus
Melaleuca nematophylla
Melaleuca leiocarpa
Melaleuca pauperiflora subsp *fastigiata*
Melaleuca uncinata
Micromyrtus imbricata
Rinzia carnosa
Thryptomene urceolaris

Ophioglossaceae
Ophioglossum lusitanicum

Orchidaceae
Pterostylis aff *nana*
Pterostylis aff *picta* (NG & ML 3690)
Thelymitra aff *macrophyllum*

Orobanchaceae
* *Orobanche minor*

Papilionaceae
Bossiaea walkeri
Mirbelia aff *densiflora* (NG & ML 3560)
Mirbelia sp (NG & ML 2055)
Templetonia sulcata

Phormiaceae
Dianella revoluta

Pittosporaceae
Pittosporum phylliraeoides

Plantaginaceae
Plantago aff *hispidula* (NG & ML 1732)
Plantago drummondii

Poaceae
* *Aira caryophyllea*
Amphipogon strictus
Aristida holathera
Austrodanthonia caespitosa
Austrostipa blackii
Austrostipa elegantissima
Austrostipa platychaeta
Austrostipa trichophylla
* *Bromus rubens*
Elymus scaber
Eragrostis dielsii
Eragrostis eriopoda
Eriachne flaccida
* *Hordeum leporinum*
Monachather paradoxus
* *Pentaschistis airoides*
* *Rostraria pumila*
* *Vulpia myuros*

Polygalaceae
Comesperma volubile

Portulacaceae
Calandrinia corrigioloides
Calandrinia eremaea
Calandrinia ptychosperma

Primulaceae
* *Anagallis arvensis* var *caerulea*

Proteaceae
Dryandra arborea
Grevillea acuaria
Grevillea erectiloba
Grevillea georgeana
Grevillea haplantha subsp *haplantha*
Grevillea huegelii
Grevillea obliquistigma subsp *obliquistigma*
Grevillea paradoxa
Grevillea zygoloba
Hakea minyma
Hakea preissii
Hakea recurva subsp *recurva*
Persoonia sp

Rhamnaceae
Stenanthemum stipulosum
Trymalium myrtillus subsp *myrtillus*
Trymalium urceolare

Rutaceae
Phebalium canaliculatum
Phebalium canaliculatum x megaphyllum (NG & ML 3685)
Phebalium megaphyllum
Phebalium tuberculosum
Philotheca brucei subsp *brucei*

Santalaceae
Exocarpos aphyllus
Leptomeria preissiana
Santalum acuminatum
Santalum spicatum

Sapindaceae
Dodonaea lobulata
Dodonaea microzyga var *acrolobata*
Dodonaea stenozyga
Dodonaea viscosa subsp *angustissima*

Solanaceae
Nicotiana occidentalis
Solanum lasiophyllum
Solanum orbiculatum

Stackhousiaceae
Tripterococcus brunonis

Sterculiaceae
Brachychiton gregorii

Stylidiaceae
Levenhookia leptantha
Stylidium induratum

Zygophyllaceae
Zygophyllum aff *tesquorum*
Zygophyllum apiculatum
Zygophyllum eremaeum
Zygophyllum glaucum
Zygophyllum ovatum

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The Botanists Diels and Pritzel in Western Australia: A Centenary

J S Beard

6 Fraser Road, Applecross WA 6153
e-mail jsbeard@global.net.au

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Keywords: history, botanist, Diels, Pritzel, Western Australia

Ludwig Diels and his companion Ernst Pritzel arrived in Western Australia on Oct 30 1900 on a botanical expedition that was to last 14 months. During that time they travelled as widely as possible in the limited state of development of the Colony, collecting specimens (Pritzel 1016 specimens, Diels 4700) and making observations of the vegetation. On leaving in Dec 1901 they proceeded to the Eastern States and New Zealand. After returning to Germany they at first collaborated on writing up their botanical collections, published in Engler's *Botanische Jahrbücher* in 1904 and 1905 (Diels & Pritzel 1904-05) which included the description of 235 new species. In 1906 Diels published his observations in a book *Die Planzenwelt von West-Australien südlich des Wendekreises* (The Plant World of Western Australia south of the Tropic). This was of 416 pages and a landmark, publishing new information on the flora, descriptions of the vegetation, and a small coloured vegetation map of Australia.

The book was only published in German, which few people in Western Australia could read at that time, and was not translated for publication in English. After the establishment of the University of Western Australia, the Botany Department undertook to translate Diels' book but only typed copies were made. D J Carr (1981) published a translation of an introductory chapter, pp 41-72 of the book, which gives details of previous botanists who had worked in Western Australia.

Few details of Diels' travels and his career are available in the book, but an obituary by H Ziegenspeck (1952) was published in German in the South American journal *Revista Sudamericana de Botanica*. A translation of this is given as an appendix to this paper. The account of the expedition which Diels gave in an address in Berlin on his return (Diels 1902) does not contain any information additional to the later book.

Ludwig Diels

Friedrich Emil Ludwig Diels (Fig 1) was born in Hamburg, Germany, in 1874 to a family of distinguished academics. He took early to botany and studied taxonomy under Engler, and geography under von Richthofen, at Berlin. His doctoral thesis was titled "Vegetation Biology of New Zealand". He had not at that time visited that country but after graduating began to prepare plans for a tour of the southern hemisphere, visiting South Africa, western and eastern Australia, and New Zealand, with principal emphasis on Western Australia. In January 1900, at the age of 25, he proposed this journey to the Humboldt Foundation for Nature Research and Travel, and obtained approval and funding. With a travelling companion Ernst Pritzel (see below) he left Germany in the same year via South Africa where between August and mid-October 1900 they visited the Western Cape and adjoining area of the Karoo near Calvinia. On Oct 30 1900 they disembarked at Fremantle, and started work in mid-November.


Figure 1. Friedrich Ludwig Emil Diels, 1874-1945. Photograph supplied by Botanic Garden & Museum, Berlin-Dahlem.

Diels and Pritzel left Fremantle at the end of December 1901 for eastern Australia and New Zealand, but we have found no record of where they went and how long they stayed there. They were back in Berlin by October 1902. Diels had already been appointed to the staff of Berlin

University in 1900, and he worked there on the results of his expedition. In 1906 he accepted an appointment as Professor at the University of Marburg, a position which he enjoyed, developing also a happy home life with a wife and four children. Later the family moved to Berlin when Diels was appointed Assistant Director of the Botanical Museum in Berlin-Dahlem as successor to Urban, and working under Engler. In 1929 he became Director-General of the Museum, and in 1933 a member of the Academy, thus reaching the peak of his career. In 1933 he undertook a journey to Ecuador, repeating his experiences in Western Australia and in the same way writing a book and papers to follow. Shortly after this he renewed his connection with Western Australia through Charles Gardner who had been appointed Government Botanist in the State in 1929, and acted as Australian Botanical Liaison Officer at the Royal Botanic Gardens at Kew from March 1937 to January 1939. During this period Gardner visited Berlin where Diels allowed him to examine his collections and to remove small pieces of specimens which are now in the Western Australian Herbarium. It is likely that Diels inspired Gardner to extend his earlier treatment of the vegetation of the State to include the tropical north and desert interior. Gardner did this in a lengthy paper to the Royal Society of Western Australia in 1941 which owing to the war was not published until 1944 (Gardner 1944) and the appropriate map even later (Gardner & Bennetts 1956). Gardner added a Northern Province and numerous new Botanical Districts to Diels' previous work.

The outbreak of war in 1939 brought disaster with the destruction of the herbarium and library at Berlin-Dahlem by allied bombing. Diels was very disheartened by this. He died at the end of the war in 1945 at the age of 71. Fortunately his and Pritzel's collections were not all lost, as specimens are recorded as held today in 30 of the world's herbaria (Orchard 1999). The Western Australian Herbarium holds 239 specimens collected by Diels in the State, 398 by Pritzel and 540 under their joint names, a total of 1177. These include those few obtained by Gardner in 1939 (N Marchant, WA Herbarium, personal communication).

Ernst Pritzel

Of the life and career of Ernst Pritzel, who was less eminent, we have fewer details. No obituary or biography has been located. He was born in Germany on 15 May 1875 and died, probably in Berlin, on 6 April 1946, so that his life span was similar to Diels'. He was a noted phytogeographer and taxonomist, his best-known contributions being Lycopodiaceae and Psilotaceae in Engler & Prantl's *Die Natürlichen Pflanzenfamilien* in 1901 and Pittosporaceae in 1930. According to Hall (1978) he collected at Coolgardie in 1907, implying a second visit to Western Australia, but this is thought to be a mistake for 1901. Pritzel's specimens in the W A Herbarium are all dated 1900-01. The genus *Pritzeliella* P C Hennings was named after him in 1903, and he was specially honoured by his colleagues at a celebration of his 60th birthday in 1935. No portrait-photograph of him is known to be available, but it is possible that he is shown as the scale-object in the photograph Plate XXXIV of the book of Diels (1906).

Vegetation Studies

In approaching their work in Western Australia, Diels made it clear from the start that he intended a wider scope than just botanical collection. His prime interest would be in the vegetation, stated in the very first sentence of the foreword to the 1906 book:

"In our knowledge of the plant world of Western Australia there has for a long time been a strange incongruity. The floristic elements were well known: on the other hand one knew nothing as to how they fitted into the picture as vegetation".

Diels and Pritzel therefore travelled as widely as possible, collecting as they went, but Diels must have made exhaustive notes on the vegetation, and Pritzel took photographs. There is a map on p 68 of Diels (1906) that indicates the areas botanically explored up to that time and shows their journeys by dotted lines (reproduced as Fig 1.4 by Beard 1990). A slightly better map accompanied their joint paper of 1904-05 and is reproduced here as Fig 2. No details are available as to

Table 1

Time-table of the travels of Diels and Pritzel in Western Australia, including collecting localities.

1900	30 October	Arrived Fremantle.
	November	Toodyay-Northam-York, Coolgardie.
	December	Serpentine River, Geographe Bay.
1901	January	Champion Bay, Watheroo, Toodyay-Northam-York, Collie River, King George Sound.
	February	Mogumber-Moora-New Norcia, Toodyay-Northam-York, Bridgetown, Bunbury.
	March	Bunbury, Bridgetown,Busselton, Cape Leeuwin, Lake Muir, Albany. Depart for the Pilbara by sea.
	April	Nickol Bay, Roebourne.
	May	Serpentine River, Tammin, Southern Cross, Toodyay-Northam-York, eastern hills of Darling Range, Stirling Range.
	June	Serpentine River, Mogumber-Moora-New Norcia, Watheroo, Mingenew, Irwin River, Champion Bay.
	July	Cue, Champion Bay, Greenough River, Watheroo, Tammin, Stirling Range, Cape Riche.
	August	Carnarvon, Champion Bay, Watheroo, Greenbushes, Toodyay-Northam-York, Mogumber-Moora-New Norcia.
	September	Champion Bay, Greenough River, Irwin River, Mingenew, Watheroo, Toodyay-Northam-York, Stirling Range, Swan River.
	October	Pallinup River and east to the Phillips River, Stirling Range (ascending Toolbrunup and Mt Trio, Collie River, Tammin, Bullabulling, Menzies.
	November	Coolgardie, Esperance, Karalee, Southern Cross, Watheroo, Champion Bay, towards the Murchison River.
	December	Mogumber-Moora-New Norcia, Bunbury, eastern hills of Darling Range. End of December left Western Australia.

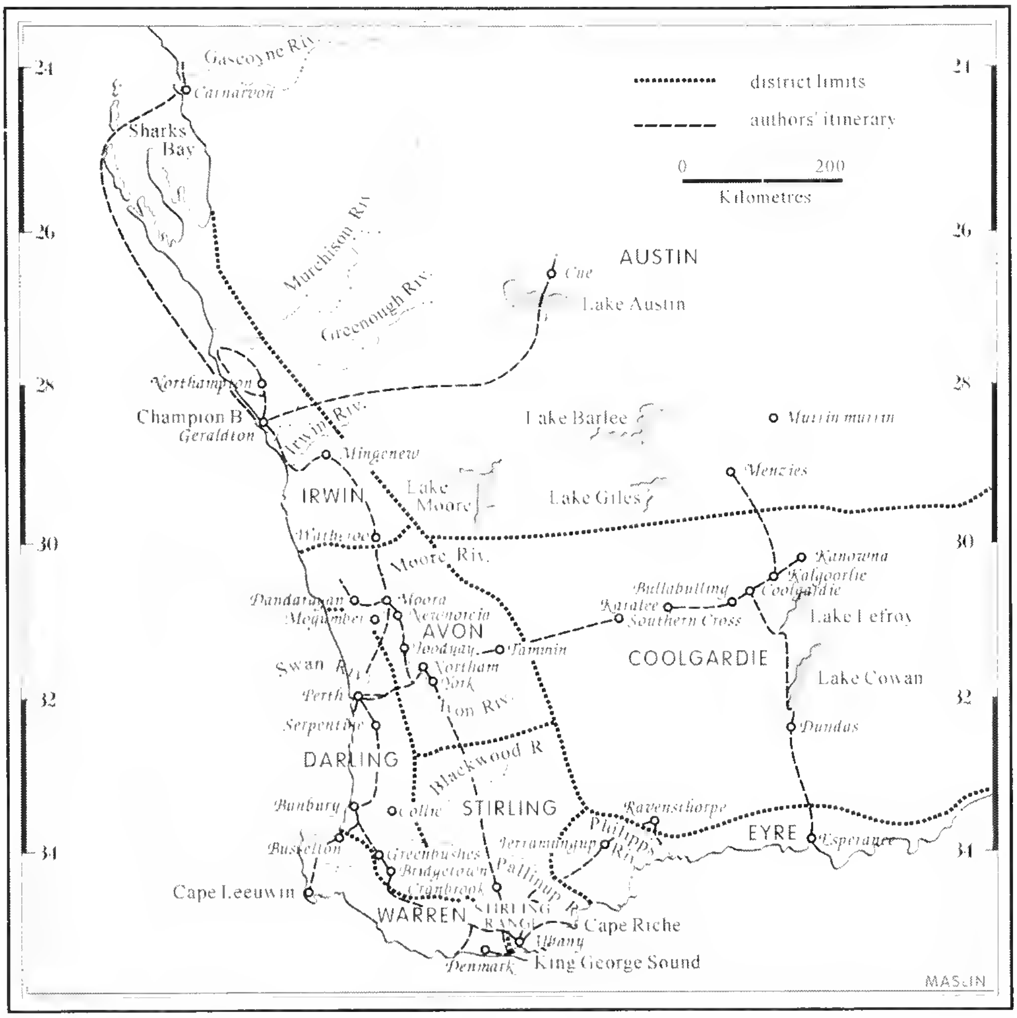

Figure 2. Travels of Diels & Pritzel in Western Australia 1900-01. Redrawn from Diels & Pritzel 1904-05 by John Maslin.

how they travelled, where they stayed en route, camping or otherwise, nor how they dried their specimens. Handling such a large quantity, an average of 100 specimens a week when they were constantly on the move, must have been a major problem. A table is appended showing where they went, compiled from the 1905 paper with some amendments using data from the 1906 book. In addition to these sorties they mentioned collecting around the Swan River in all months and around King Sound in almost all months. It is clear that they must have travelled principally by train as most of the travel shown on the map coincides with the railways which already existed, enabling them to reach the Goldfields *e.g.* Kalgoorlie, Menzies and Cue. However in March 1901 they travelled by road from the Blackwood River via Lake Muir to the south coast. They also travelled by road from Albany through the Stirling Range and as far east as the Phillips River, and from the eastern goldfields to Esperance. In March-April 1901 they made a sortie by sea up to the Pilbara at Roebourne, and to Carnarvon in August.

The results of their taxonomic work were published jointly in 1904-05 (Diels & Pritzel 1904-05) at Berlin in Engler's *Botaniche Jahrbücher*, in a volume of over 600 pages. This lists and describes all of their collections, including a great deal of ecological data, and illustrates many species. A catalogue of Pritzel's specimens is included, apparently in the order collected from 1 onward. Diels' collecting numbers in W A were 1500-6160.

Diels' book of 1906 consisted of 413 pages, written essentially from an ecological viewpoint. It is divided into an introduction and five chapters. The Introduction is headed "The Main Features of the Plant World of Australia" with general descriptions of the vegetation classified under 9 formations, and a section on floristics. This is accompanied by a small coloured vegetation map of Australia, the whole of Australia not just the west, scale 1:27 000 000, at the back of the book, using the same plant formations as in the chapter except for Riverain Woodlands left out owing to scale. A table on p 26 of the book gives a detailed key to the formations mapped, but there is no other mention of the map in the text, so that we do not know how or when Diels compiled it nor what sources of information were available to him. The map is of particular interest in that it appears to have been the first vegetation map of Australia to be published. A facsimile reproduction of this map has been published elsewhere (Beard 2001; Fox *et al.* 2001).

Chapter 1 of the book is headed "History and Literature of the Botanical Exploration of Extra-tropical Australia" and is the portion translated by D J Carr

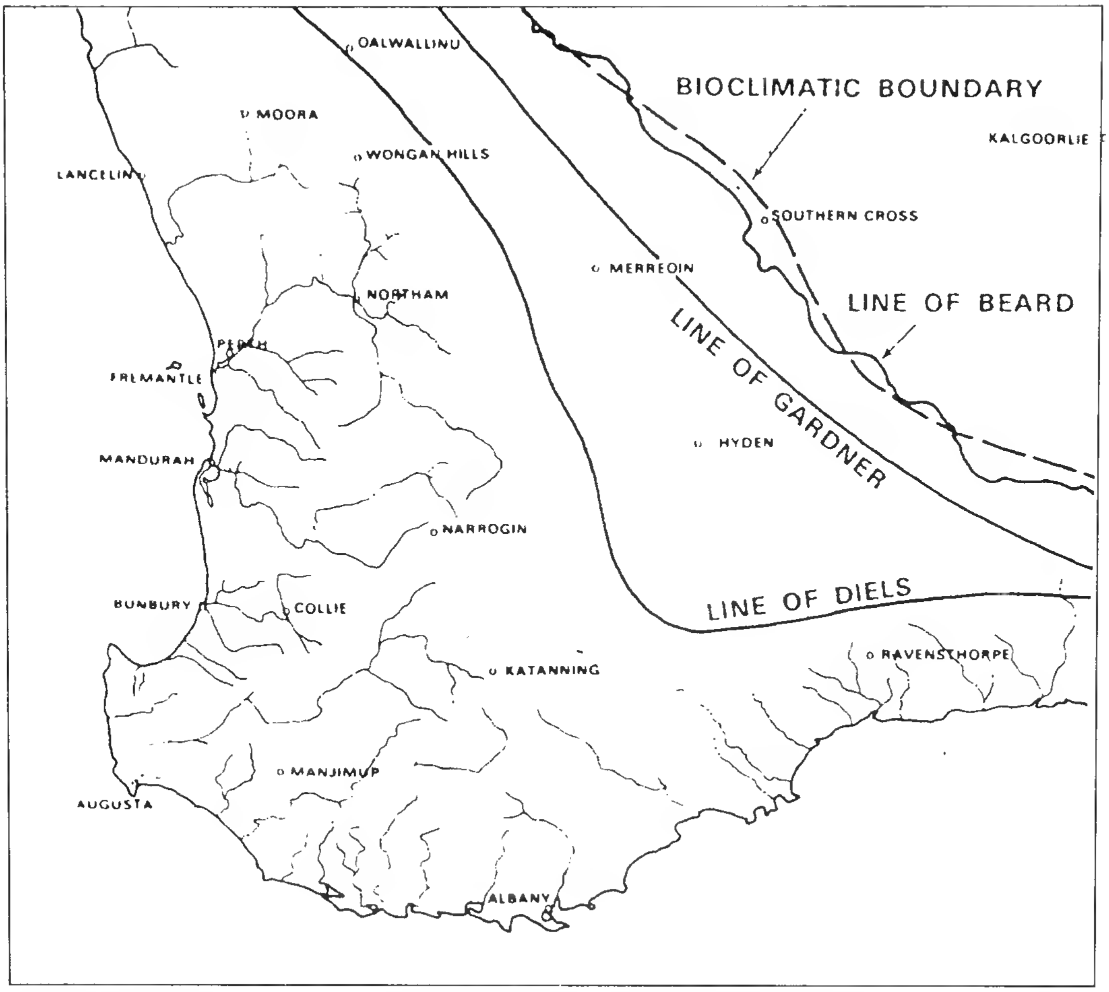

Figure 3. Comparison of the positions of the boundary of the South-West Botanical Province according to Diels (1906), Gardner & Bennetts (1956) and Beard (1980), with the bioclimatic boundary (Beard 1980).

(1981). It is followed by another short general chapter, "Summary of the Physical Geography of Extra-tropical Australia". Chapters 3 and 4 are devoted to detailed descriptions of the vegetation of the South-West and Eremaean Provinces, both floristic and ecological, using a physiognomic classification of plant formations. Curiously, these bear no relation to the classification used for the vegetation map, and with other discrepancies give the impression that the introductory chapters including the map were written separately and at a different time from the chapters dealing specifically with Western Australia. The final chapter of the book establishes Diels' famous biogeographical classification of the southern part of Western Australia into two Botanical Provinces, subdivided into Botanical Districts. The South-West Province was divided into six Districts and the Eremaean Province (as far as known to him) into two. Gardner (1944) expanded this to cover the whole State with the addition of a Northern Province and numerous new Districts, and the system has been later refined by Beard (1980), Beard & Sprenger (1984) and Thackway & Cresswell (1995). This recognition of ecological regions has been one of Diels' most enduring legacies. The boundary between the two Provinces, he said, coincided approximately with the 300 mm rainfall line, separated the internal drainage area of the country from the portion draining to the sea, was of importance to human settlement in being the boundary of cereal cultivation and had also at that time been picked up in zoogeography (Woodward 1900). Modern rainfall maps show the 300 mm isohyet further east. Diels information was influenced by a relatively dry cycle during the years before his visit. His observation on the drainage pattern is true up to a point as his line coincides with that chosen by Jutson (1914, 1934) as the boundary between his Swanland and Salinaland Physiographic Divisions, and is also the Meckering Line of Mulcahy (1967). More recent work has revised our views of the drainage systems (Beard 1999, 2000). Cereal cultivation has moved out much further east since Diels' time. Woodward's zoogeographic map of 1900 can no longer be traced for comment. C A Gardner (in Gardner & Bennetts, 1956) redrew the State's Botanical Provinces and Districts and moved the boundary of the South-West Province somewhat further east. Beard (1980) moved it a little further still, basing his line on vegetation mapping. These contrasting treatments are shown in Fig 3.

Any work of this kind is likely to be subject to later revision, which does not obviate recognition of the pioneer basis. The expedition of Diels and Pritzel was unique. They came equipped for quite a long stay with the intention of making as far as possible a comprehensive survey of the southern half of the Colony. It was entirely on Diels' own initiative, he had not been invited or commissioned by the Colonial Government to do this, and he had obtained his own funding from the Humboldt Foundation in Germany. On return home he made his own arrangements to publish a very comprehensive book of over 400 pages, including a vegetation map of the whole of Australia (not just the west) which appears to have been the first of its kind. It was certainly a unique achievement.

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Appendix

Obituary of Ludwig Diels (1874-1945) by H Ziegenspeck (1952)

Translated by Pamela Beard

Ludwig Diels was born on Sept 24 1874 in Hamburg, the eldest son of the modern language philologist Hermann Diels. Seldom has a family experienced such a stimulating influence as that exerted on the sons, as happened to the botanist Ludwig Diels and his brothers, the Slav expert Paul and the chemist and Nobel prizewinner Otto.

Their father as well as their mother came from Nassau, and he had as a young grammar school teacher answered the prize questionnaire of the Berlin Science Academy so brilliantly that he was called to Berlin where he spent 33 years on the Academy staff, soon became a University Professor and was finally appointed permanent secretary to the Academy. It was here that the young Ludwig grew up, completing his studies as head boy at the grammar school where he showed a special talent for botany.

He conscientiously studied systematics with Engler and geography with von Richthofen. His dissertation "The Vegetation-biology of New Zealand" showed the direction of his life's work. While the morphological and anatomical aspects may be a principal response to environmental factors, the floristic history in the absence of competition on an island may be the explanation of contradictions. The enormous diversity from the coastal flora to the moist forest areas excited the delight in diversity of the systematists as well as of the vegetation biologists. There followed papers such as the treatment of the ferns in "Natural Plant Families", the "Flora of Central China, Juvenile Forms and Mature Flora in the Plant Kingdom" and above all "The Plant World of Western Australia", the outcome of a long journey taken with Pritzel.In South America reference should be made to his study of the Annonaceae, Myrtaceae, Oxalidaceae and Proteaceae, as also the Weberbauer collections and finally the study of the Droseraceae, Menispermaceae and Iridaceae in Engler's Plant Kingdom.

Recognised as a University Lecturer in Berlin in 1900, Diels became busy at the Berlin University. In 1906 he accepted an appointment in Marburg where he worked in plant geography and systematics. The "Marburg years" were the joy of his life. Here he was happily married, here his four children were born, one son and three daughters. Here he was able to live his scientific and teaching career to the full, free from administrative and academic duties.

This happy time came to an end because of an offer of an appointment as Asst Director of the Botanical Museum in Berlin-Dahlem, as successor to Urban. To work with such a demanding boss as Engler was not easy. Diels managed to continue his goals, which were never of a self-seeking kind, by slipping them into his other work. Those who did not know him very well took him to be a reserved, highly qualified person which was not at all his true self. He was far more sensitive than he appeared, though he knew how to hide his innermost feelings. Diels worked until 1921 under Engler; in 1929 he was promoted to Director-General, and in 1931 he was appointed a member of the Academy. In this way he reached the summit of his career, but remained the same selfless person. Imperceptibly he altered the way the institution was run, during which Pilger, the Asst Director, stood loyally at his side. His colleagues were given much freedom. He operated according to his own standard and his totally scholarly approach.

In 1933 he undertook a long desired journey to Ecuador, about which he reported in his book "Contributions to the understanding of the vegetation and flora of Ecuador", and also in the monographs "New species from Ecuador I-V". After his return to Europe an unfortunate time began for Diels, which was only relieved by the marriage of his daughters and the birth of a grandchild. His much loved son was the victim of an air disaster. The destruction of the herbarium and of the library, which went up in flames during the night of March 1-2 [year not stated] during an air raid, was a blow from which he never recovered. Outwardly he remained composed. Because of the coal shortage the stock in the greenhouses was frozen, and during the final stages of the fighting around Berlin the outdoor parks were destroyed. After the war the black market appeared but he would have nothing to do with it. He struggled tenaciously against the gradual decline of his strength, and continued to fulfil his duties until shortly before his death. On Dec 30 1945 he died peacefully in his official residence. He is buried in the Botanic Garden alongside Schweinfurth and Engler.

Ziegenspeck H 1952 Necrologia: Ludwig Diels 1874-1945 [in German] Revista Sudamericana de Botanica 10:53-54.

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Little Minnie Creek, an L4(S2) ordinary chondritic meteorite from Western Australia

A W R Bevan[1], P J Downes[1] & M Thompson[2]

[1] Department of Earth and Planetary Sciences, Western Australian Museum
Francis Street, Perth WA 6000
[2]Red Dog Prospecting, PO Box 402, South Perth WA 6151
e-mail: bevana@museum.wa.gov.au

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Abstract

The Little Minnie Creek meteorite, weighing 357 g, was found in 1997 at co-ordinates 24° 08' 16.9" S, 115° 52' 17.5" E in the Gascoyne District of Western Australia. Equilibrated ferromagnesian silicates with the compositions olivine ($Fa_{25}Fo_{47}$) and low-Ca orthopyroxene ($Fs_{21.6}En_{77.4}Wo_{1.0}$) show that the meteorite belongs to the L-group of ordinary chondrites. Prominent chondrules, the presence of abundant polysynthetically twinned clinopyroxene, and the wollastonite content of orthopyroxene show that the chondrite is petrologic type 4. Moderate weathering (grade W2) of the meteorite has locally, preferentially attacked troilite over metal and produced a small amount of pentlandite as a secondary weathering product. Preferential attack of troilite may be characteristic of weathering of chondritic meteorites in an arid climate.

Keywords: meteorite, Little Minnie Creek, L4(S2)

Introduction

A small, crusted stony meteorite weighing approximately 357 g was found by one of us (MT) in March 1997 lying on the surface near Little Minnie Creek in the Gascoyne District of Western Australia at co-ordinates 24° 08' 16.9"S, 115° 52' 17.5"E (Fig 1). Subsequently, the name Little Minnie Creek has been approved by the Nomenclature Committee of the Meteoritical Society (Grossman & Zipfel 2001). To confirm that it was a meteorite, the stone was broken in the field into two fragments weighing approximately 305 and 51 g. Beneath a fresh, warty fusion crust, the grey interior is locally stained brown by the rusting of metal particles, and chondrules are clearly visible to the naked eye. On cut surfaces, together with chondrules up to a maximum of 2 mm in diameter, abundant metal particles up to 2 mm across are visible and are evenly distributed throughout the meteorite.

Reconstructed, the meteorite (WAM 15207) is roughly cuboid in shape measuring 7 x 5 x 5 cm (Fig 2). The smaller fragment of the stone was cut, and three polished thin sections prepared for petrographic examination and electron microprobe analysis. Analyses were performed with a Cameca SX50 WDS electron microprobe analyser, at an accelerating potential of 15 kV with an operating current of 30 nA. Standards employed included natural minerals (*e.g.* olivine and pyroxene) as well as glasses and pure metals (Fe, Ni).

Petrology and mineralogy

The Little Minnie Creek meteorite is a chondritic stony meteorite. In thin section, abundant well-defined chondrules ranging from 0.2-0.6 mm across with an average diameter of 0.4 mm are set in a fine-grained matrix. Porphyritic chondrules containing either olivine, or both olivine and pyroxene, and radiating pyroxene chondrules are the most abundant. Chondrule mesostases are devitrified and microcrystalline yielding a composition, under broad beam analysis, close to albitic plagioclase feldspar. Barred olivine chondrules and microporphyritic chondrules are also present in the meteorite. The essential mineralogy of the meteorite is dominated by forsteritic olivine (Fa_{25}) and low-Ca orthopyroxene ($Fs_{21.6}$) although grains of polysynthetically twinned, Ca-poor clinopyroxene also occur both in chondrules and matrix.

Grains of diopside ($Fs_{7.4}En_{46.7}Wo_{45.9}$) together with kamacite, taenite, troilite, chromite, phosphate, and rare grains of native copper enclosed in metal make up the accessory and trace mineralogy of the meteorite. Kamacite typically contains 6 wt % Ni and 0.8 wt % Co, while taenite is strongly zoned with cores of grains ranging from 28.5-35 wt % Ni and less than 0.2 wt % Co. Representative analyses of some of the essential and accessory minerals in the meteorite are given in Table 1 and shown graphically in Fig 3.

Under crossed polars, the ferromagnesian silicates show generally uniform and sharp extinction although some grains of olivine display planar fractures and weakly undulose extinction. Kamacite contains abundant Neumann bands and, under crossed polars, troilite displays deformation bands and localised incipient recrystallisation. Other than in the fusion crust and heat-affected zone below the crust, evidence for shock-melting was not observed throughout the fabric of the meteorite.

Despite a reasonably fresh appearance, at the microscopic level the meteorite displays extensive weathering (Fig 4). Troilite grains have been partially (5-70% by volume) converted to iron oxide, and where they

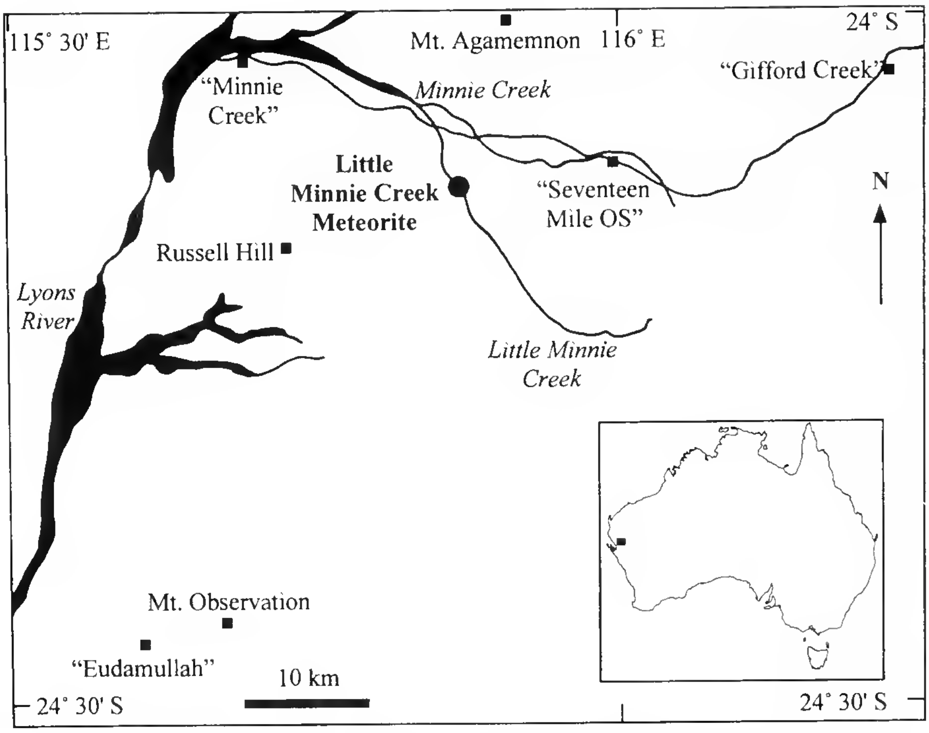

Figure 1. Location map for the find-site of the Little Minnie Creek L4 chondritic meteorite.

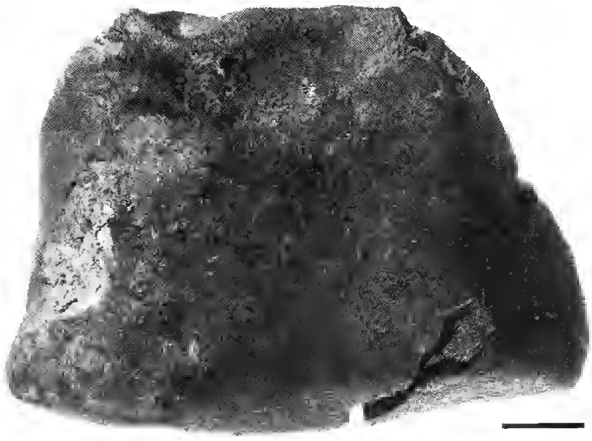

Figure 2. Reconstructed mass of the Little Minnie Creek meteorite (centimetre scale bar)

Table 1.

Representative analyses (wt %) of minerals in the Little Minnie Creek L4 chondrite.

	olivine	orthopyroxene	chromite
SiO_2	38.0	56.1	-
TiO_2	-	-	2.25
Al_2O_3	-	-	6.1
Cr_2O_3	-	-	56.3
V_2O_3	-	-	0.76
FeO*	22.7	13.9	31.5
MnO	0.57	0.55	0.62
MgO	38.5	29.2	2.07
CaO	-	0.52	-
Na_2O	-	-	NA
K_2O	-	-	NA
Totals	99.77	100.27	99.6
moles%	$Fa_{25.3}$ $Fo_{74.7}$	$Fs_{21.6}$ $En_{77.4}$ $Wo_{1.0}$	

*All Fe as FeO; NA = not analysed for; - = not detected. Analyst P Downes

are in association with weathered metal particles grains show rare, incipient secondary alteration to pentlandite $(FeNi)_9S_8$. In general, metal particles show less (5-30% by volume) alteration to iron oxide than troilite.

Discussion and conclusions

The compositions of the ferromagnesian silicates and the cobalt content of kamacite show that Little Minnie Creek belongs to the L-group of ordinary chondrites. Chromite in the meteorite (Table 1) lies within the range of compositions reported by Bunch *et al.* (1967) for L-group ordinary chondrites. The clarity of chondritic texture of the meteorite, the wollastonite content of the low-Ca orthopyroxene (1 mol %), the abundance of polysynthetically twinned clinopyroxene, and the microcrystalline nature of the chondrule mesostases show that the meteorite belongs to the petrologic type 4 of the Van Schmus & Wood (1967) classification of chondrites.

Minor fracturing associated with weak undulose extinction in silicates, Neumann banding in kamacite, and deformation bands in troilite are all consistent with a history of weak shock-loading. The level of shock alteration is appropriate to S2 according to the shock classification of chondrites given by Stöffler *et al.* (1991) and indicates peak shock pressures of < 10 GPa.

Overall the extent of oxidation of the opaque phases in the meteorite shows that it belongs to weathering group

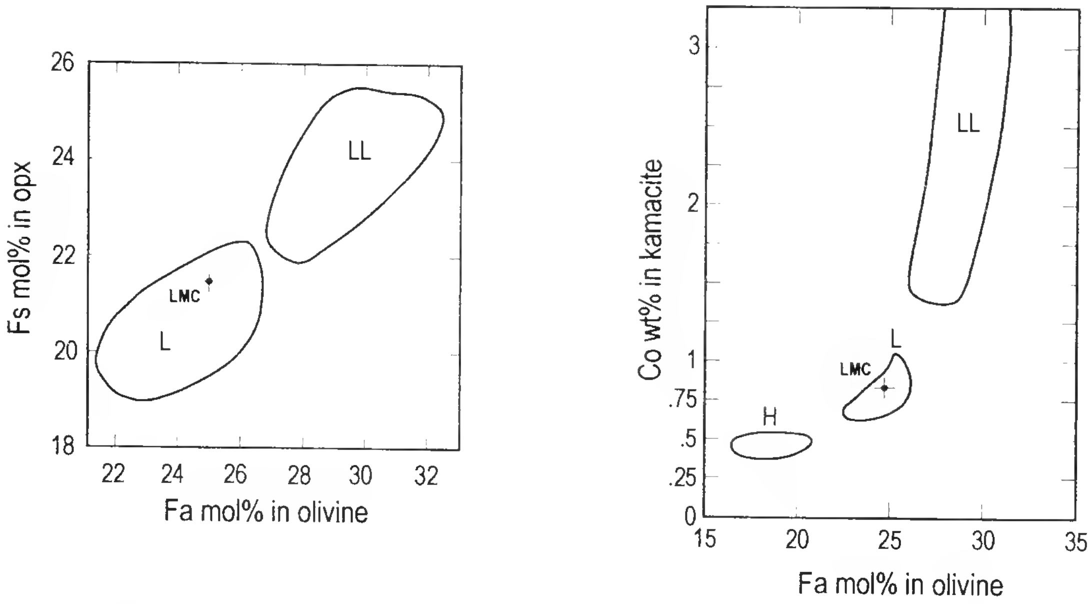

Figure 3. A: Mean compositional fields of olivine (Fa mol%) and low-Ca orthopyroxene (Fs mol%); **B:** Co wt% in kamacite versus olivine composition for the L-, LL- and H-groups of ordinary chondrites (after Ruzicka 1995). Olivine, pyroxene and kamacite compositions of the Little Minnie Creek (LMC) chondrite plot clearly within the L-group field.

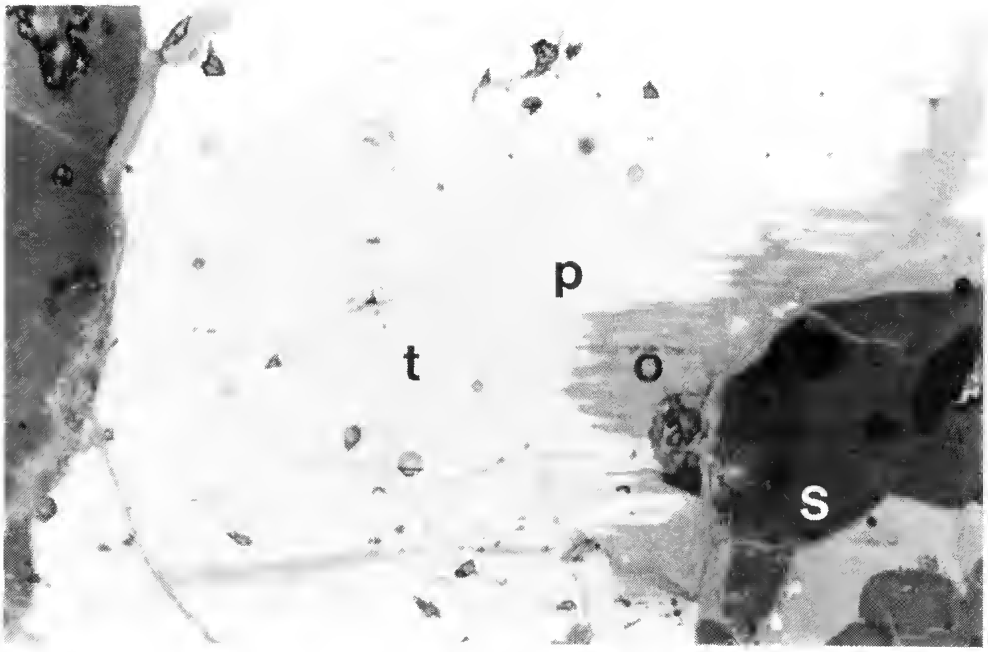

Figure 4. Extensively weathered particle of troilite (t) with dark grey iron oxides (o) surrounded by silicates (s). Weathering of troilite has progressed along (0001) parting planes and there is incipient development of pentlandite (p). Field of view 0.2 mm.

B, or weathering category W2 of Wlotzka (1993). Metal is usually more susceptible to terrestrial oxidation than troilite, with kamacite typically weathering faster than taenite (Ikeda & Kojima 1991). Localised, preferential weathering of troilite over metal has previously been noted by Ruzicka (1995) in an L6 chondrite (Nullarbor 018) that was found on the Nullarbor Plain. Ruzicka (1995) suggests that this may be the result of weathering in an arid climate, although the critical conditions are poorly understood. In the Nullarbor example, Ruzicka (1995) found that S had been preferentially leached from the meteorite. Oxidation and hydration reactions for troilite generally produce S-bearing weathering products that are relatively soluble in water, whereas Fe-bearing weathering products such as hematite are relatively insoluble, thus providing an explanation for why S is selectively leached under such conditions (Ruzicka 1995). Evidently, in Little Minnie Creek more than one weathering reaction involving sulphide has taken place. Nickel liberated from oxidising Fe-Ni metal locally reacted with troilite to cause incipient alteration to secondary pentlandite.

Ruzicka (1995) suggested two thermodynamically favourable reactions for troilite alteration, although he did not consider the involvement of oxidation products (NiO) from decomposing metal. Essentially, troilite is converted to hematite in the presence of water and oxygen with sulphur flushed from the system in aqueous solution. With the additional presence of carbonate (as in the case of the Nullarbor), a similar reaction occurs but with the evolution of gaseous CO_2 and both sulphur and calcium removed in solution. Ruzicka (1995) notes that mineral precipitates from such solutions include both anhydrite and gypsum.

The Little Minnie Creek meteorite was found sitting on a thin (< 30 cm) veneer of red soil over subcropping fresh granite. The site lies within 100 m of a river marked by a sheet wash of quartz/iron scree subject to periodic inundation. In the vicinity, calcrete has developed on the edge of small drainages leading into the river, but was mostly absent at the find-site. Because it was derived from the granite, the soil is not particularly iron- or manganese-rich but instead is strongly potassic. This environment is in stark contrast to the Nullarbor and its calcareous clay soil, yet a similar pattern of weathering has developed in the opaque minerals in the meteorite to that seen in some Nullarbor chondrites. The climatic conditions of generally high ambient temperatures, prolonged aridity with occasional inundation, may be more important controls on troilite versus metal weathering than the substrate on which the meteorite is lying.

When Fe-Ni metal and troilite react, pentlandite is formed. In this reaction, during the decomposition of troilite and metal to iron oxides in the presence of water and oxygen, Ni is released from metal to react with residual troilite to form a small amount of pentlandite with the excess sulphur flushed from the system in aqueous solution.

Bland *et al.* (1998, 2000) have considered the weathering rates of ordinary chondrites from several desert areas of the world, including the Nullarbor of Australia. Typically, pristine L-group ordinary chondrites contain around 8% metal and 6% troilite by weight. In meteorites that have suffered prolonged weathering the ferric iron alteration products include magnetite, maghemite, ferrihydrite, lepidocrocite, goethite and principally, akaganéite (Bland *et al.* 1998; Buchwald & Clarke 1989). From a study of terrestrially age dated ordinary chondritic meteorites, Bland *et al.* (2000) have shown that initial weathering of chondritic meteorites (< 1 ka after fall) appears to be rapid before oxidation is retarded and weathering abates. Arrested weathering rates appear to be related to a reduction in the porosity of the meteorite caused by mobilised corrosion products filling the available pore space and so preventing the subsequent percolation of fluids. Bland *et al.* (2000) suggest that the environment during the initial post fall period generally controls the extent of weathering. Once the porosity is reduced and the weathering rate arrested, even a moderately weathered meteorite may avoid significant alteration during subsequent humid periods. The extent of weathering in Little Minnie Creek, with the presence of abundant oxyhydroxides of iron, suggests that it is not a recent fall and may have a significant terrestrial age.

Other ordinary chondrites found in the vicinity of Little Minnie Creek include several stones of Dalgety Downs (25° 20' S, 116° 11' E), another L4 chondrite (Grady 2000). However, Dalgety Downs is more deeply weathered than Little Minnie Creek and shows a higher level of shock alteration (S4) indicating that they are distinct falls.

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Behaviour and spatial ecology of Gilbert's dragon *Lophognathus gilberti* (Agamidae: Reptilia)

G G Thompson [1] & S A Thompson [2]

[1] Edith Cowan University, [2] Centre for Ecosystem Management, Edith Cowan University,
100 Joondalup Drive, Joondalup WA 6027
email: g.thompson@ecu.edu.au

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Abstract

We examined the behavioural and spatial ecology of *Lophognathus gilberti,* a medium-sized, diurnal, dragon lizard that is commonly found in urban areas of north-western Australia. Males defend daily activity areas against other males, but not females. Both males and females shift their daily activity area on sequential days. *Lophognathus gilberti* use sight and perhaps auditory cues to locate prey, which consists mostly of invertebrates. They catch a prey item every 92 minutes, or 6-7 items each day, most often by sprinting from an elevated perch, but they do not actively search in leaf litter for prey. Three different stationary postures were observed; defensive, vigilant and aggressive. Males also have a courting posture that involves head bobbing, body pressing and tail twitching. These lizards often wave a forelimb and bob their heads after each short sprint. Movement is most often bipedal, with males moving greater distances (37.8 m h^{-1}) than females (13 m h^{-1}). When active, *L. gilberti* are most often found in full shade, and within 5 m of vegetation cover. They are constantly vigilant and are capable swimmers, diving to the bottom to avoid capture.

Keywords: Gilbert's dragon, *Lophognathus gilberti,* behaviour, ecology

Introduction

Lophognathus gilberti, Gilbert's dragon or "Ta Ta" lizard, is abundant in north-western Australia. The name "Ta Ta" lizard also applies to other species in this genus. This medium-size dragon lizard is readily observed because of its conspicuous colouration, active behaviour, and abundance in urban environments. One of the most distinctive features of this lizard, from which it derives its common name, is the rapid waving (circumduction) of its forefeet after each short sprint. Given its abundance there is surprisingly little information about this agamid lizard. James & Shine (1985) indicate they are reproductively active from September to February. Christian *et al.* (1999) report that the ecologically and morphologically similar *Lophognathus temporalis* are more active around Darwin (wet-dry tropics) during the wet season than the dry season, resulting in them being more visible and having significantly higher energy expenditure and water fluxes during the wet season.

Blamires (1998) reported that *L. temporalis* use circumduction as a distraction display to potential predators. Head bobbing and circumduction are most often performed by juvenile *L. temporalis,* and mainly when they were on the ground; these movements are independent of the presence of conspecifics. Large adult male *L. temporalis* employ head bobbing exclusively during the breeding season; this movement generally follows fleeing from a potential predator. Our observations of *L. gilberti* before this study suggested that males may defend territories, head-bobbing and forelimb waving may be a means of communicating with conspecifics, and that colour changes might be part of male's threat display and/or used to regulate body temperature.

Lophognathus gilberti is particularly abundant along the edges of permanent waterways (lakes, rivers, irrigation channels) around Kununurra. During September and October of 1999 we systematically observed these lizards in their natural environment with the specific objectives of examining a) their movement and activity patterns, b) interactions between males, between females, and between males and females, and c) association between body colour and behaviour.

Methods

The study site was a cleared rectangular area 18 m x 50 m along the northern edge of Lake Kununurra (UTM 0470068, 8253996). There was a steep bank of about a metre to the water. The water's edge contained a number of trees, a narrow band of thick vegetation, reeds and open areas. Three large trees, 3-5 m in from the water's edge, provided large areas of shade for most of the day in a cleared area beyond the vegetation at the lake's edge. People and vehicles moved through the area on a regular basis so that *L. gilberti* were habituated to their presence. Nevertheless, these lizards were constantly vigilant and would rapidly move to avoid being threatened.

Lophognathus gilberti emerged, basked and were active in the study area before 0730 each day. Observations prior to the study indicated that *L. gilberti* very seldom ventured toward the northern boundary of the study area

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during the middle of the day because it was mostly in the sun and there was little vegetation cover. *Lophognathus gilberti* were observed for a total period of approximately 19 hours; one hour each day between 0955 and 1630 hours for most days between 26 September and 16 October, 1999. Observations were made by either of the authors who sat in a shady elevated position beyond the northern boundary of the study area. Seven of the observations commenced before noon; the remainder were in the afternoon. The location of lizards in the study area could be observed from this position, except when they climbed the far side of a tree, moved into thick vegetation along the banks of Lake Kununurra, or moved over the edge of the bank down toward the water.

At the beginning of each observational period, every *L. gilberti* present within the area was allocated a number and its sex was gauged by its shape and colour; adult males are generally darker grey or black, and have a larger head. There were no juveniles or sub-adults present in the area during the study period. Ambient air temperature was recorded in the shade approximately one metre above the ground at the commencement of each observation period, using a digital thermometer. The location, posture, movement, colour, behaviour and feeding of every *L. gilberti* present in the study area were recorded for each 5 minute period during a one hour observation.

A detailed map of the study site was prepared and overlayed with a 1 x 1 m grid so the exact location of each lizard and its movements could be accurately recorded. Every time a lizard moved, its new location was recorded. To determine the distance that a lizard moved, we presumed each lizard started and finished in the centre of a 1 x 1 m grid. We calculated the minimum distance that a lizard moved as the distance between the centre of the two grids *i.e.* where the lizard began and where it finished. We only included data where we had continuous visual contact with the lizard for a minimum of 25 min. If the lizard was disturbed by the presence of people or a vehicle, then all of its data were excluded. Total distance moved during a period of continuous observation (greater than 25 min) was divided by observation time in minutes, and is reported as distance moved in m h^{-1}. Body colour was described as dark, medium or light, and the location of the lizard in the sun, partial shade or complete shade was recorded every 5 minutes. Every time that a lizard caught a prey item was recorded; if prey could be identified then this was also recorded.

We made notes on all observations that might assist us to explain *L. gilberti's* behaviour and use of space. Incidental notes of the behaviour of specimens outside the study area were also used to supplement behavioural descriptions of lizards monitored in the study area.

Results

The mean ambient temperature at the commencement of each observation period was 34.2 (± se 0.65) °C. The sky was overcast for only one entire observation period (6 October), and no lizards were observed between 1530 and 1630 hours in the study area on this occasion. Surface soil temperature in the sun was measured at the commencement of an observation session on eight occasions. For those occasions, mean surface soil temperature in the sun was 53.3 (± se 3.19) °C, and ambient air temperature in the shade, one metre above the ground, was 35.0 (± se 1.07) °C. Other than on 6 October, there was always some portion of the study site that was exposed to direct sunlight.

There was no difference (*t* test, $P = 0.71$) in the number of males and females observed within our study site boundaries during an hour observation period. The mean number of females observed was 2.4 (± se 0.30, range 0–5 at any one time) and the mean number of males observed was 2.6 (± se 0.32, range 0–5 at any one time).

Body colour

Female *L. gilberti* never attain the very dark/black body colour apparent for males. In shade, 53% of the observations of male lizards were dark grey/black, 19% were medium brown and 28% were light brown (Fig 1). For females in shade, 39% were light brown and 61% were dark brown. The dense tree canopy meant there were few areas with partial shade; as a consequence there was little opportunity for lizards to be found in these conditions. *Lophognathus gilberti* preferred to stay out of direct sunlight, with only 11% of observations for males and 8% of observations for females occurring in direct sunlight. When in direct sunlight, 42% of males were light coloured and 39% were medium coloured. The remaining 19% were dark brown or black. For females in direct sunlight, 81% had a medium brown body colour, and 19% were light brown.

Feeding

During 3040 lizard minutes of observation, *L. gilberti* were seen to catch 33 prey items; this is equivalent of one item of prey every 92 min. It was not always possible to discern what was caught, as many of the items were small and swallowed quickly. We only observed invertebrates being caught. The general feeding strategy was to remain motionless on an elevated perch (*e.g.* tree stump, elevated surface tree root, low branch, pile of vegetation) watching for potential prey. Prey were generally detected visually but we saw lizards looking in the direction of noises in the leaf litter suggesting that they might also use auditory cues. Having detected potential prey the lizard would sprint to the location from its observation post. These sprints were rarely longer than 2 m, but we did observe sprints of up to 5 m to catch prey. Two males were seen to jump unsuccessfully in an attempt to catch flying insects. An adult male *L. gilberti* which captured a large grasshopper took 20 min to subdue and devour it; another male took 40 min to subdue and devour a dragonfly. Much of the time taken to eat these large prey items appeared to be associated with aligning prey in their mouth so that it was eaten head first. Most of the invertebrates captured were in leaf litter or close to leaf litter.

Posture

Only a small range of stationary postures were adopted;

- defensive – arched (convex) back and tail along the ground, inflated abdomen;
- vigilant – head up with arched (concave) back, tail down and head tilted or moved in accordance with what the animal was observing;

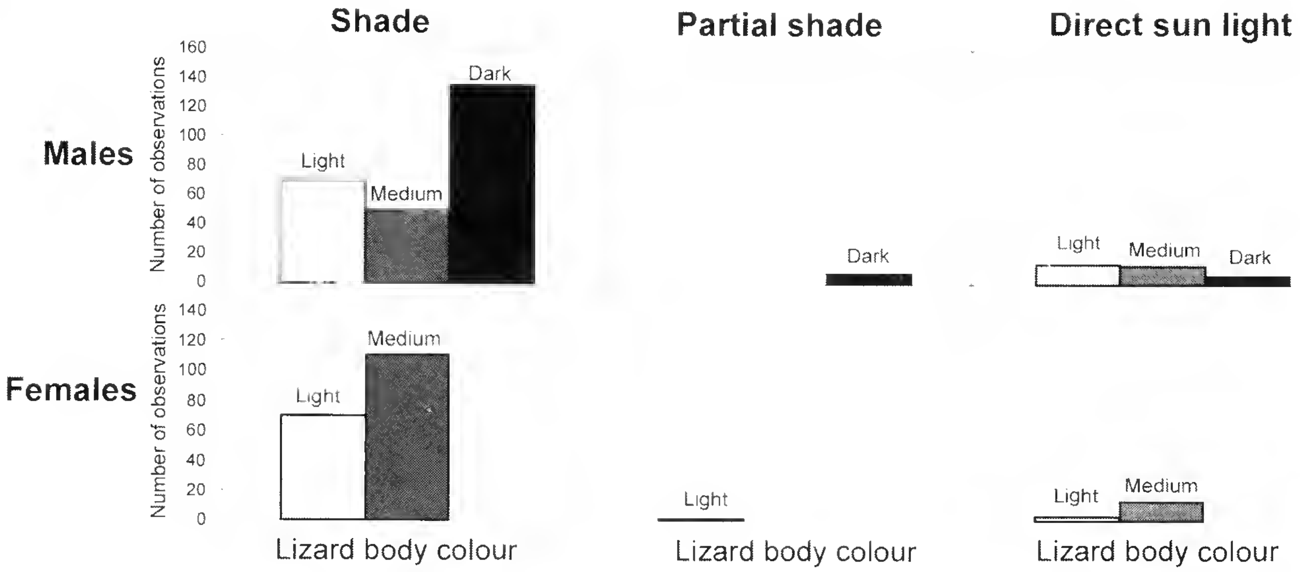

Figure 1. Body colour of male and female *L. gilberti* in shade, partial light and direct sun light.

- aggressive (males only) – arched (concave) back, forelimbs almost straight elevating the chest, head erect at about 45^0 to the horizontal;
- males courting – head bobs, body presses, body colour was mostly black and the tail often twitches.

We observed a number of *L. gilberti* with their tail arched over their back so that the tip was almost above the head. A female almost always waved her forelimb after sprinting a short distance, unless it was attempting to catch prey. Males also waved their forelimbs, but less often, and this action was often accompanied with a few quick head bobs. There was a slow and a fast head bob. The slow movement was most often accompanied by an arching at the neck. *Lophognathus gilberti* would sometimes head bob while stationary in the vigilant posture.

Movement patterns

Males moved a significantly greater distance per hour than females (*t*-test, two sample unequal variance, $P < 0.01$; we appreciate there is some replication of individuals in this comparison, but it was not possible to individually identify all lizards from day to day). We observed undisturbed females continuously for in excess of 25 min on 15 occasions and during that time they moved at a rate of 13.3 (± se 3.61, range 0–42.4) m h^{-1}. We observed undisturbed males continuously for in excess of 25 min on 27 occasions and during that time they moved at a rate of 37.8 (± se 5.67, range 1-127.3) m h^{-1}. Although it was not quantified, females appeared more timid, retreating to cover earlier than males when threatened.

Lophognathus gilberti rarely walked, and most movements were short sprints to catch a prey item, to chase another lizard, to avoid an attack by another lizard, or to avoid a person, vehicle or potential predator (*Varanus mertensi* and *V. mitchelli*). Most of the time *L. gilberti* sprinted bipedally, although they seemed unable to run bipedally on loose leaf litter. *Lophognathus gilberti* would rapidly climb a tree when threatened. On two occasions we saw a *V. mertensi* move through the study area and on one occasion we saw a *V. mitchelli* move through the area. On these three occasions, all *L. gilberti* observed these potential predators before we did and rapidly moved to the cover of dense vegetation. We observed *L. gilberti* on numerous occasions more than 2.5 m up a tree, mostly in their vigilant posture. To avoid detection they would often move around to the other side of the tree when approached. They were observed to jump from low branches or tree trunks over 0.5 m to the ground and jump over 0.3 m from the ground to tree trunks. These dragon lizards were rapid and agile movers along thick branches of trees. They appeared to avoid narrow branches, which they would only use if there was no other option and they were being pursued by a potential predator.

We never observed *L. gilberti* retreating to a burrow in the ground. We occasionally found them sleeping on trunks of large trees at night. We observed females occasionally digging shallow holes, often out in the open, which we presumed were 'test holes' for egg laying. We found no evidence that movement behaviour altered with the time of day (*e.g.* morning *vs* afternoon).

Use of space

On only 9.7% of occasions were *L. gilberti* observed more than five metres from a tree or other vegetation. Twenty six of 33 prey items were caught within 5 m of vegetation cover. On every occasion where we witnessed a confrontation between two lizards, the aggressor displaced the lizard being attacked suggesting that there was an established hierarchy, and that each lizard responded according to its place in that hierarchy. Large males with black colouration would generally not tolerate another similar-coloured male within its activity area; the activity area appeared to be defined as the space in which it was foraging at that time. In a male-male encounter, the aggressor would sprint straight at the other male. Most often the male being attacked would see the approaching male and would rapidly leave the area. We observed only one fight between males, and this was outside the study area. In this instance, a large male chased and caught another male. A brief battle followed; movements were very quick and specific actions were difficult to observe. It appeared that the attacker rapidly bit the other male on the neck, back and legs. The attacked male fled after a couple of seconds. We observed a second encounter between two similar-sized males that lasted for approximately 5 - 6 minutes. Both males had obviously seen each other from a distance of at least 10 m. They slowly approached to within 0.6 m of each other. Both lizards were in direct sun light (ambient temperature in the shade was 33 °C and surface soil temperature was 42.5 °C) and their colour was light brown, throat and chests were enlarged, and their crests were erect. One had its tail in the air and the other flicked its tail from side-to-side. Both lizards slowly raised and lowered their heads as they moved in a circle but maintained their distance apart (about 0.6 m). Eventually both males retreated to shade some 15 m apart, never getting closer than about 0.5 m. On one occasion we observed a large male lizard attack a bar-shouldered dove (*Geopelia humeralis*) on the ground; after a few bites the dove flew off. On other occasions *G. humeralis* were regularly seen on the ground within metres of *L. gilberti*.

Males regularly chased female *L. gilberti*. On most occasions the female quickly fled to the cover of vegetation. If the female moved into an open area the male often followed, and the female again moved away from the male. We observed a female *L. gilberti* to lie flat on the ground on three occasions when a male moved near, presumably to avoid detection. On only one occasion did we observe a male catch and mount a female. There was no obvious copulation as the female displaced the male and moved off within a couple of seconds. We observed one male *L. gilberti* chase a female into an open area, where the female remained in the sun for several minutes, eventually opening its mouth presumably to lose heat by evaporation.

We endeavoured to track individual lizards on sequential days but without clear markings to identify each lizard we could not be certain that we correctly identified all animals each day. However, we were able to positively identify a few of the *L. gilberti* based on their body size and obvious external markings (*e.g.* cut tail). These recognisable individuals moved their activity area on sequential days. From this we concluded that the daily activity area for most lizards changed from day-to-day. However, most of the recognisable lizards remained in the general area as we frequently saw a particular lizard using the same or adjacent area every couple of days.

When disturbed or fleeing from a predator, *L. gilberti* would, as a last choice, dive into the water. They swam rapidly to the bottom, and would swim through bottom vegetation until they stopped and remained motionless. On two occasions we watched specific sites where a *L. gilberti* were last seen in the vegetation on the bottom of a shallow clear waterway for in excess of 30 min and did not see these lizards move, nor were we able to find these lizards in a subsequent search.

Discussion

The rate of movement of males and females around their activity areas differed. Males moved more often and covered greater distances probably because they chased other males, females and prey items. Females, in contrast, only flee from males and chase prey items. *Lophognathus gilberti* is an accomplished arboreal lizard that uses tree trunks and low branches as observational perches. They appear reluctant to move around on narrow branches, possibly because their relatively long hindlimbs impede rapid movement along narrow branches. This conclusion concurs with those of Losos & Sinervo (1989) who report sprint speed of long-limbed *Anolis* on thin rods being slower than for species with shorter limbs.

Body colour appeared to be influenced by whether *L. gilberti* were in sun or shade. For males, their body colour was generally darker in shade than in sun, and lighter in sun than in shade. A lighter body colour would minimise solar heat absorbance, and lightening of body colour is a strategy used by other lizards to minimise the potential for heat stress in direct sunlight (Pianka *et al.* 1998). In contrast, more females were dark brown than light brown in sun and shade. The number of individuals that had a dark body colour in sun when ambient air and surface soil temperatures where high enough to lift the lizard's body temperature close to their thermal maximum (presumed to be 42–45 °C, see Curry-Lindahl 1979), suggests that body colour might also be used for camouflage or communicating with other conspecifics. Attacking males were usually dark grey or black in colour, but this was not always the case. Therefore we could not conclude that the dark colour of male *L. gilberti* was part of a threat display.

Lophognathus gilberti spent most of their active time close to vegetation cover. This could be for one of a number of reasons. Surface soil temperature in sun during periods when these dragon lizards were active was generally in the low 50s °C. Remaining in the sun on soil at this temperature even for relatively short periods would result in heat stress (Curry-Lindahl 1979). The dark body colour would presumably further reduce the maximum period of time these lizards could remain in the sun because of higher radiative absorbance. Secondly, most of the potential prey might be near vegetation. Seventy nine percent of prey were caught within 5 m of vegetation, which may either reflect where prey were, where lizards were or movement into open areas increased the risk of predation.

Within the study site, aggression by one male towards another invariably led to the attacked male leaving the area. There are at least two plausible explanations for this behaviour. Firstly, a strong hierarchy had been established among males, and subordinate males were generally not prepared to contest their rank in the hierarchy, or alternatively males are defending 'todays' territory. The only extended encounter observed between two similar-sized males did not result in physical contact, suggesting both adversaries were endeavouring to assert their dominance without fighting. This may have been because the body temperature of both males was near their critical thermal maximum. Males showed no aggression (*e.g.* charging, biting) toward females as might have been expected, given that males would normally want to attract females. Females regularly moved from their perch when males moved toward them. We observed no evidence of female–female aggression, although we observed smaller females moving away from larger females when they approached. These data suggest that females do not aggressively defend daily activity areas, but there may be a recognised hierarchy based on body size.

Activity area of male *L. gilberti* shifted on a daily basis. Daily activity areas of males at any given time did not overlap and a male often defended space that was occupied by other males on other days. Our data therefore indicate that home ranges (combined activity areas over many days) for male *L. gilberti* overlapped and daily activity areas shifted with little site fidelity from one day to the next. Shifting daily activity areas could reflect the search for prey or the search for receptive females (Pough *et al.* 1998).

Body colour, head and chest bobbing, and circumduction are all signs of lizard communication (Ferguson 1977; Gibbons 1979). What was not obvious from our observations was the purpose of some of these communications. Females waved their forelimb almost every time they moved (unless they captured prey) and this action occurred immediately upon ceasing to run. Males more often bobbed their heads at the conclusion of a short sprint, but they also waved their forelimbs. Blamires (1998) suggests that circumduction by *L. temporalis* is used to distract potential predators or to indicate to potential predators that their presence has been noted to discourage further pursuit. He also reported that juveniles waved their forelimbs more often than adults, and this is mainly done on the ground. There were no juveniles present in our study area and we observed circumduction independent of the apparent presence of predators and conspecifics. Therefore we do not agree with Blamires' (1998) interpretation of the purpose for this movement, although we are unable to suggest an alternative.

When a female was present males often rapidly bobbed their heads, did some quick 'body presses' and twitched the end of their tail. In this circumstance we presumed that this was part of the male courtship display. Males that can see each other were observed to arch their necks and slowly bob their heads. This often preceded an attack. We concluded that the arched neck and slow head bobbing was part of the display of dominance and defence of the activity area. Blamires (1998) reported the purpose of head bobbing was a threat display by large males, and was only used during the breeding season. Although James & Shine (1985) reported *L. gilberti* to be sexually active from September to February, we only saw one male mount a female and given the female displaced the male within a couple of seconds it is unlikely they copulated. All other advances by males were rejected by females, suggesting it was not the breeding season. Our view is that fast head-bobbing by males is used for courtship display and the slow head-bobbing with an arched neck and back is a threat display.

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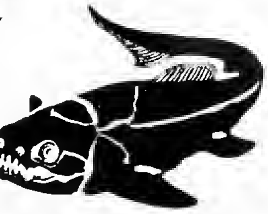

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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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The south-western Australian flora in autumn: 2001 Presidential Address

A S George

School of Biological Sciences, Murdoch University;
address for correspondence: 'Four Gables', 18 Barclay Road, Kardinya, WA 6163
email: ageorge@central.murdoch.edu.au

(Manuscript received November 2001)

Abstract

In the flora of south-western Australia, vegetative colour change in summer and autumn followed by regreening after rain is much more widespread than previously reported, though patchy in occurrence and variable within species. The term *diallagy* (adj. *diallagous*) is proposed to describe the strategy of reversible change between the green and coloured states. It is here recorded for 99 species in 59 genera of 24 families of flowering plants, both monocots and dicots. These species occur in a number of widely distributed habitats. In some species, extent of colour change increases as long as the dry weather continues. The change generally is reversed after 10-15 mm or more of rain falls over a short period (24 hours). Regreening takes from several days to several weeks. The mechanisms operating within the plants are yet to be investigated, but possibilities are discussed to point the way to further research; some are likely to be similar to that reported for *Borya*. In an extreme dry summer such as that of 2000-2001, death occurs in some species.

Paradoxically, other species flower at this season, in some cases close to diallagous species. It is suggested that these have retained a summer/autumn flowering period (from a tropical origin) to take advantage of pollinators at a season when few sources of nectar and pollen are available.

Keywords: summer/autumn drought, foliage colour change, diallagy, autumn flowering, monocots, dicots

Introduction

When we think of autumn colour we usually picture Northern Hemisphere trees in brilliant shades of yellow or red, followed by bare branches and perhaps snow on the ground. We don't associate autumn colours with the Australian bush. There is, as far as I am aware, just one cold-temperate Australian deciduous woody plant, the Tanglewood of Tasmania, *Nothofagus gunnii*. In northern Australia there are a number of winter-deciduous trees and shrubs, such as the Kapok Bush (*Cochlospermum* spp), Kapok Tree (*Bombax ceiba*), kurrajongs (*Brachychiton* spp), some *Terminalia*, Large-leaved Cabbage Gum (*Eucalyptus grandifolia*) and Boab (*Adansonia gregorii*). Oddly, some tropical species display autumn colours, such as the Boab. Strangest, perhaps, given its habitat, is the Cedar Mangrove (*Xylocarpus australasicus*) which, even with its roots in water, can turn colour and shed its leaves during the dry season. A number of these species flower when leafless, *e.g. Cochlospermum*, *Brachychiton* and *Bombax*. In this paper I show that, in the south-western Australian flora, we do have widespread autumn colour, albeit occurring intermittently and functioning differently from that of Northern Hemisphere deciduous trees and shrubs. Paradoxically, at the same season when soil moisture is at its lowest and temperatures are still high, other native plants are in full flower or even actively growing.

In south-western Australia, few people venture into the field during the autumn season. It is usually the end of a long, hot, dry summer, and there is still a widely-held view that little is happening in the bush at that time; spring is the wildflower season, though some flowering continues into summer. Consequently little has been written about the bush in autumn, or about the effect of drought. The words rarely appear in any paper or chapter title of works on the south-western flora, nor do they appear as index entries. Two exceptions are papers by Beard (1968) on drought in the Gibson Desert, and Hnatiuk & Hopkins (1980) on drought in the kwongan near Eneabba. Apart from work on *Borya* (Gaff 1981), only passing mention has been made of foliage colour change in the flora (*e.g.* Main 1967 pp 9, 11, 22, 33, 145; George 1984a p viii; Wilson 1997 p 278). Main (1967 p 145) did, however, refer to colour change of foliage and bark as indicators of autumn.

This paper is more in the line of natural history than science, being largely a compilation of observations made over many years and particularly in the autumn of 2001, but the Royal Society of Western Australia has its origins in that field so I may be forgiven a little indulgence. I believe that there is a great deal to learn about the summer-autumn drought in south-western Australia and its role in the biology of our biota and how they have evolved. From such initial observations, researchers often find topics for more in-depth studies.

I am concerned here with perennial 'evergreen' plants. Those in the south-western flora that survive or avoid dry periods by dying back to an undergound storage organ (bulb, rhizome, tuber) have been well described by Pate & Dixon (1981) and aestivating mechanisms in herbaceous stilt plants have been described by Pate *et al.* (1984). Nor shall I speak about annual or ephemeral plants that survive dry periods as seeds. Such plants are rather better documented than the others and their strategy is more readily understood. And I shall not deal with ferns, many of which are well-known drought avoiders by reducing water content but not changing chlorophyll, the fronds typically curling tightly to help avoid dessication.

Coloured (non-green) foliage is well-known in the flora in both new and senescing growth. New shoots of many species are characteristically various shades of red, some species of Proteaceae, for example, being quite spectacular. Colours such as yellow, brown and red are normal in some species as leaves senesce and die. During the recent summer and autumn, dying plants of several species turned an orange-brown as they died, *e.g. Nemcia reticulata* at Seabird north of Perth, *Dryandra sessilis* (both var *sessilis*, *e.g.* at Crystal Brook on the Darling Scarp, and var *cygnorum*, *e.g.* at Seabird) [see below for location of observation sites].

Previous work

The most significant work specifically on autumn dormancy in Australia is that of Don Gaff of Monash University (Gaff 1981 and references cited therein). Investigating 'resurrection plants', Gaff found the Western Australian *Borya nitida sensu lato* to be a prime example. Resurrection plants are also termed poikilohydrous, *i.e.* their water content follows closely fluctuations in the moisture of their environment. They have the capacity to reduce their water content and their metabolism to an extremely low level and remain thus for long periods until moisture increases, whereupon they revive and continue normal activity.

In *Borya*, the leaves turn yellow or orange as soil moisture declines with the onset of summer and the change in the cell structure is quite remarkable (Gaff 1981). In viable, yellow leaves, the chloroplasts, chlorophyll structure and cytoplasm appear to become disorganised, the vacuole frequently being fragmented or lobed, and the nucleus is the only organelle discernible. Chloroplasts lack grana and have few thylakoids. There are extensive gaps in the membranes bounding the plastid, and in extreme cases plastids may be recognised only because of their plastoglobuli. 'The disorganization of fine structure is not complete, an essential core of structure is retained as a base for reconstruction of the full cell system on reimbibition.' During drying, soluble protein increases but insoluble nitrogen decreases. A close, but not indivisible, association exists between tolerance induction and yellowing. Gaff noted that leaf senescence invariably negates the ability to tolerate desiccation. He also found that leaves of *Borya* collected dry in the field had recovered on rewetting after five years in storage.

Gaff's (1981) work covered several 'forms of *Borya nitida*' which now, following the revisionary work of Churchill (1985, 1987), can be referred to as species. Gaff's Mt Lindesay form is *Borya longiscapa*; his Shannon Mill form is a southern variant of *B. sphaerocephala*; his Kelmscott-Brookton form is typical *B. sphaerocephala*; and his Karalee form is *B. constricta*.

Gaff (1981) discussed the problem of seeking resurrection plants and reasoned that, in Australia, the south-western winter-rainfall zone should be a suitable region, where 'shallow soil pans on rock outcrops, particularly granite ones, usually provide the best opportunity for collecting plants in air-dry condition'. He wrote that they may be best recognised in the field, especially from a change in the colour of the foliage, for example 'an intense purple-black colouration of viable air-dry leaves in some species, *e.g. Tripogon loliiformis*, by a 'healthier' golden-straw colour in the viable leaf bases of grasses and sedges, and by retention of chlorophyll in ferns that have air-dried *in the field*' (Gaff's italics).

Gaff (1981) wrote that 'resurrection plants do not occur randomly throughout the plant taxa, but tend to be confined to relatively few families, some closely related, others distantly related. Within these families, the species tend to occur either in one genus or in a group of related genera.' He recorded some 16 species in Australia: one dicot (*Boea*, Gesneriaceae) and 15 monocots of 7 genera in 3 families (Poaceae, 'Liliaceae' [his records now in Boryaceae] and Cyperaceae). He predicted that certain other genera (all monocots) might include resurrection species since they did in other countries. He noted that some Stylidiaceae and *Drosera* might show this behaviour. He also recorded 15 species of fern and fern ally, representing 7 genera in 5 families, as resurrection plants in Australia.

Research in Darwin (Montagu & Woo 1999) has shown that, during the dry season, the wattle *Acacia auriculiformis* can reduce the chlorophyll and soluble protein content of its phyllodes by 73% and 52% respectively. After rain they recovered to almost the previous wet-season values. Some phyllodes were shed during the dry season but new growth did not begin until more than 11 weeks after rain fell, indicating that initial revival of activity depended on the surviving phyllodes.

Research by John Pate and colleagues at The University of Western Australia is also pertinent to this study. Although much of it has not been specifically directed at how plants survive the long summer, their findings reveal the mechanisms that may be operating. The following factors appear significant.

Many species have both shallow and deep (sinker) roots, the former taking up water from the upper soil layers during rainy spells, when nutrients are accumulated and stored, the latter increasingly from the watertable as the dry season approaches. Some plants such as *Banksia prionotes* continue growth and even flower during the dry season, using nutrients acquired during the winter and drawing soil moisture from deep in the profile (*e.g.* Pate *et al.* 1998).

All Proteaceae except *Persoonia* and some species in other families, especially in dry habitats, develop cluster or proteoid roots in autumn (Lamont 1984). These are specialised feeding roots that may assist plants to respond rapidly to rain events (Pate & Meney 1999).

Restionaceae have roots that penetrate no deeper than 2 metres, and in some *Alexgeorgea* spp no more than 50 cm (Meney & Pate 1999). Thus they are not reaching the watertable during summer.

Vesicular mycorrhizal fungi have been recorded in the roots of species of Restionaceae and Cyperaceae. They form a symbiosis with the host plants in autumn and early winter and may respond very rapidly to moisture at the end of summer, assisting the host to take up nutrients quickly (Meney *et al.* 1993; Pate & Meney 1999). Ectomycorrhizal fungi have been reported in several woody genera, especially in Epacridaceae, *Eucalyptus, Casuarina, Melaleuca, Leptospermum, Dillwynia* and *Gastrolobium* (Bowen 1981; Lamont 1984). They, too, may respond rapidly to increased moisture and so enable the host plant to react more quickly than one without such an association.

Hnatiuk & Hopkins (1980) described drought effects in kwongan south of Eneabba after two years of below-average rainfall. They recorded the response to water stress of 124 species but, because their observations were made in spring, change in foliage colour was not noted. Deaths occurred in 86 species. Seedlings were found of 49 of these, and 59 species with dead aerial parts resprouted from underground parts. For 31 species with dead individuals no regeneration was observed. The families most affected were Proteaceae and Epacridaceae. They noted a patchiness in the occurrence of water stress but believed that this was not due to topography, soil type or vegetation type.

A study of water stress due to drought in southern Queensland, New South Wales and Victoria recorded widespread wilting of native trees and shrinkage of bark, sometimes leading to death (Pook *et al.* 1966). Foliage of some eucalypts became dull, then yellowish and died. Variation was attributed to soil type and aspect of the site.

Methods

In south-western Australia the summer and autumn of 2000-2001 gave an extraordinary opportunity to observe the effects of drought on the flora. Through much of the South-West, roughly south and west of a line from Geraldton to Esperance, there was little effective rain from the end of September until late April or early May. Perth recorded its driest such period on record with 48.8 mm compared with the average of 144.5 mm. Of that 48.8 mm, 23.6 mm fell in November, and only 20.0 mm from then over the five months until 30 April. The first effective fall for 2001 (17.8 mm) occurred on 6 May. When describing floods, the terms '10-year' and '100-year' events are sometimes used for above-normal and extreme events that occur, on average, at those intervals. I suggest that the same might be applied to droughts, and that the summer of 2000-2001 was a 100-year event. In some localities its effect on the native vegetation was striking, and will be noticeable for some years.

From March to August 2001 I visited 20 sites to record any species whose foliage showed a change in colour. I visited most twice, before and after the first effective rain (10 mm or more within a 24 hour period). Some near Perth I visited more often. For each locality, a brief description is given below of the landform, soil and vegetation, dates visited, and first effective rain event for 2001. Rainfall is taken from the nearest official recording station (Table 1). As far as I can judge, similar rainfall occurred at my sites, except Charles Gardner Reserve where it was much less than that received in the town of Tammin some 17 kilometres to the north. I also include here some observations made in previous years at other localities. Geographically these range from near Eneabba to Perth, inland to Tammin and south-east to Corrigin. For most of these earlier observations no follow-up visits were made to assess regreening, although from my general field observations the leaves of the species recorded are normally green.

Species were identified, foliage colour described in simple terms, notes made on any change in position and texture, and colour slides taken using Fujichrome 100 film. Variation within and between populations was also noted.

My observations indicate that, in south-western Australia, plants presumed able to reduce their metabolic activity by internal processes shown by colour change are much more common than previously reported in terms of their taxonomic spread, geographical distribution, habitat, and appearance. Whether any of those newly reported here are true resurrection plants remains to be determined.

It must be emphasised that these observations are mostly from sites where colour change (either generally or in certain species) was particularly evident. They are by no means comprehensive but are intended to draw attention to survival strategies. Many areas showed little or none of the effects described here, confirming the observations of Hnatiuk and Hopkins on the patchiness of drought effects.

Dates given below are for 2001 unless stated otherwise.

Sites visited in previous years

Mt Lesueur (*ca.* 30°10' S, 115°15' E). Valleys and slopes north-east of Mt Lesueur, with varied kwongan. Visited 27 March 1977. Rainfall at Badgingarra for the period 1 October 1976 to 30 April 1977 totalled 55.6 mm, of which 48.0 mm fell in October-November, *i.e.* December to April rainfall was 7.6 mm. Populations of *Petrophile seminuda* and *Melaleuca radula* showed marked colour change.

Location 19769, *ca.* 15 km S of Corrigin (32°31' S, 117°56' E). Woodland, tall shrubland and kwongan on sand, clayey sand and laterite (George & Hnatiuk 1978). Visited 8 April 1977. Rainfall at Corrigin for the period 1 October 1976 to 30 April 1977 totalled 97.7 mm, of which 59.0 mm fell in October-November and 18.5 in April, *i.e.* December to March rainfall was 20.2 mm.

Hopkins Reserve, SE of Kulin, formerly reserve no. 13389, now 35134 (32°43' S, 118°17' E). A complex area of kwongan, mallee and woodland on sand, sandy loam and laterite. Visited 8 April 1977. For rainfall *cf.* previous site; Corrigin is *ca.* 55 km to the north-north-west of Hopkins Reserve.

Little Darkin Swamp area (*ca.* 32°04' S, 116°32' E). Visited 26 April 1994 at the end of a very dry summer/autumn. Varied landforms and vegetation, mainly lateritic gravel and clay-loam with woodland of *Eucalyptus wandoo, E. accedens, E. calophylla*, some sandy areas carrying *Banksia attenuata* woodland, and granite outcrops. Rainfall at Beverley for the period 1 October 1993 to 30 April 1994 was 30.8 mm, of which 24 mm fell in October and November.

Sites visited in 2001

'First effective rain' refers to the first fall above 10 mm after 1 January 2001 at the recording station closest to the site.

Naval Base, S of Fremantle (32°10' S, 115°46' E). This is a coastal site with low heath and tall shrubland, in sand over Tamala Limestone which outcrops frequently. Visited 7 April, 11 May, 5 June and 10 July. First effective rain 6 May (20 mm).

Cantonment Hill, Fremantle (32°02' S, 115°45' E). This is a low hill of Tamala Limestone near the centre of Fremantle with shrubland of *Acacia xanthina, Templetonia retusa, Spyridium globulosum*, and some open areas with *Desmocladus flexuosus*, exotic grasses *etc*. Visited 7 April and 20 May. First effective rain 6 May (20 mm).

Kings Park, Perth (31°57' S, 115°50' E). This is the Tamala Limestone escarpment facing the Swan River, just east of where the Crawley swimming baths were located. The vegetation is tall shrubland dominated by *Dryandra sessilis* var *cygnorum, Melaleuca huegelii, Templetonia retusa* and *Grevillea preissii*. Visited 26 April and 6 July. A number of plants of *Dryandra* and several *Templetonia* and *Dodonaea hackettiana* died. First effective rain 6 May (17.8 mm).

Rottnest Island (32°00' S, 115°31' E). Here, coastal dunes and low hills of Tamala Limestone carry low shrubland of *Acacia, Leucopogon, Acanthocarpus, Olearia, Rhagodia, Westringia etc*. Visited 6 April. First effective rain 6 May (24.0 mm).

Crystal Brook, Darling Scarp (32°01' S, 116°02' E). This site is on the Darling Scarp east of Perth. There are granitic outcrops on lateritic gravel slopes. Vegetation is mixed low shrubland with occasional *Eucalyptus wandoo* and thickets of mixed Proteaceae, Myrtaceae, Papilionaceae, *Acacia, Hibbertia etc*. Around the granite rocks is low herbfield with *Borya, Stylidium*, ephemerals and scattered small shrubs such as *Verticordia huegelii*. Visited 27 March 1997, 15 March 2001, 4 May, 17 May, 22 May, 5 July and 7 August. First effective rain 6 May (28 mm). In 2001, large areas assumed an orange aspect as shrubs went dormant or died. Some remained green, *e.g. Hakea incrassata*, many *Hakea trifurcata*. Deaths occurred in *Nemcia spathulata, Hakea incrassata, Hakea erinacea, Hakea trifurcata, Acacia pulchella, Dryandra lindleyana, Casuarina humilis, Gonocarpus, Jacksonia, Pimelea imbricata, Calytrix glutinosa, Petrophile biloba, Hovea pungens, Verticordia acerosa, Eucalyptus wandoo*. By 5 July regreening had occurred and a 'normal' aspect resumed apart from the many dead shrubs.

Lewis Rd, Forrestfield, Darling Scarp (32° 00' S, 116° 02' E). This site is similar to the preceding but with doloritic rocks; there are granitic outcrops higher on the Scarp. Visited 4 May, 5 July and 7 August. In 2001, deaths occurred in *Nemcia spathulata, Hakea trifurcata, Hakea lissocarpha, Acacia pulchella, Dryandra lindleyana, Daviesia divaricata*. By 5 July regreening had occurred and a 'normal' aspect was resumed apart from the many dead shrubs.

Hummerston Road, Piesse Brook, E of Kalamunda (31° 58' 30" S, 116° 04' 30" E). This is a gently sloping granitic outcrop surrounded by open woodland of *Eucalyptus wandoo* with a mixed understorey. Visited 27 March 1997, 22 May 2001 and 5 July. First effective rain 6 May (28 mm).

Seabird, S of Lancelin (31° 16' S, 115° 27' E). Coastal dunes immediately north of the caravan village; a low rise of Tamala Limestone just east of the road with low kwongan, and another rise with sand over limestone at the entrance to the rubbish tip about a kilometre further north, with kwongan and tall shrubland. Visited 22 April, 1 June and 11 July. First effective rain 6 May (25.8 mm).

near Minyolo Brook, Brand Highway (30° 42' S, 115° 30' E). A sandy flat on the east side of the highway with low kwongan dominated by *Gastrolobium oxylobioides, Daviesia angulata, Calothamnus sanguineus, Isopogon divergens, Hakea trifurcata, Hibbertia hypericoides, Ecdeiocolea monostachya* and *Caustis dioica*. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

corner Mullering Road & Brand Highway (30° 41' S, 115° 28' E). Deep sand with low open woodland of *Banksia attenuata, B. menziesii, Adenanthos cygnorum* and mixed understorey. Visited on 1 April and 27 May. First effective rain 6 May (22 mm).

***ca* 1 km S of Tiwest Mine turnoff**, Brand Highway (30° 39' S, 115° 28' E). A winter-wet clay depression on E side of road with open shrubland of *Melaleuca viminea* subsp *viminea, Casuarina microstachya* and *Hakea trifurcata*, interspersed with low herbfield of *Borya, Conostylis etc*. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

S of Badgingarra, Brand Hwy (30° 33' S, 115° 28' E). Shallow sand over laterite high on rise (near *Eucalyptus pendens*), with species-rich low kwongan. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

Hill River bridge, Brand Hwy (30° 20' 20" S, 115° 28' 30" E). This site, immediately south of the bridge, is a clay-loam flat with low kwongan. *Petrophile seminuda* is common here and has been recorded with red foliage in several years, *e.g.* autumn 1969. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

Boothendarra Creek, Brand Hwy (30° 17' S, 115° 29' E). Flat area with heath of *Thryptomene mucronulata, Melaleuca viminea* subsp *viminea* and *Ecdeiocolea monostachya*. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

S of Coomallo Creek, E side of Brand Hwy (30° 15' S, 115° 27' E). A clay-loam flat with heath of *Thryptomene mucronulata*, occasional *Calothamnus* (which remained green), and a thicket of *Casuarina campestris, Melaleuca platycalyx, Acacia multispicata* and *Petrophile seminuda*. Visited 1 April and 27 May.

N of Coomallo Creek, Brand Hwy (30° 12' 30" S, 115° 23' 30" E). A high lateritic rise with species-rich low kwongan. Visited 1 April and 27 May. First effective rain 6 May (22 mm).

Marchagee Track, between Coomallo and Gunyidi (30° 07-12' S, 115° 35-50' E). Several locations with kwongan and tall shrubland on sand or sandy loam. Visited 1 April and 27 May. First effective rain 6 May (22 mm at Badgingarra, 10 mm at Watheroo).

Pinjarrega Lake Nature Reserve (30° 07' S, 115° 59' E). On the Marchagee Track near the south-eastern corner of the reserve, clay-loam with open *Eucalyptus loxophleba* and *Melaleuca* sp, and an open ground layer of perennial monocots such as *Triodia danthonioides*, *Conostylis aculeata* subsp *bromelioides* and *Harperia lateriflora*. Visited 1 April and 27 May. First effective rain 6 May (10 mm at Watheroo).

N of Moora (30° 33' S, 116° 02' E). Western side of Cairne Hill, on a low quartzite ridge dominated by *Casuarina campestris*, with occasional *Acacia acuminata* open woodland on the adjacent flat. Visited 1 April and 27 May. First effective rain 6 May (10 mm).

Charles Gardner Flora Reserve, S of Tammin (31° 47' S, 117° 28' E). Visited 10 March, 7 June and 19 August. Effective rain at Tammin in 2001: 11 January (11 mm), 21 January (30 mm), 24 February (11 mm), 23 April (24 mm), 31 May (17 mm). During May, rain of 1-7 mm was also recorded on 12 other days between 6th and 30th. Summer rainfall over the reserve was probably much less, a farm adjacent on the southern side having received *ca.* 15 mm in January and February in contrast to just over 60 mm in the town (W Gardner, personal communication). Observations were made at three sites: 1, on a sandy rise towards the southern edge with scattered *Casuarina huegeliana*, *C. campestris*, Cyperaceae, *Santalum spicatum*, *Acacia merinthophora etc.*; 2, an area of tamma scrub on sandy loam along the western edge dominated by *Casuarina campestris* with *Verticordia eriocephala*; 3, a high lateritic ridge on the northern edge, with thick mixed scrub dominated by Proteaceae. On 7 June the reserve was still recovering from drought despite there having been some 78 mm of rain since 23 April (after no rain between 25 February and 23 April) and the soil being damp. Most *Schoenus calcatus* were still bright yellow, only a few (maybe 10%) showing clear regreening. Other Cyperaceae were at similar stages, except *Caustis dioica* which generally was green. *Astroloma serratuloides* was fully green and flowering. *Conostylis petrophiloides* had regreened, but many *Dryandra purdieana* still had yellowish or orange leaves. On 19 August the vegetation was generally fully green and in good condition, although flowering was just starting. *Dryandra speciosa*

Table 1.

Rainfall (mm) for localities nearest those where observations were made in 2001. An effective rain event is here taken as at least 10 mm within a 24-hour period. Note that for Swanbourne, Perth, Rottnest and Bickley, more than half of the rain for the period 1 October 2000 to 30 April 2001 fell during November. Tammin received effective falls in January, February and April. In the average annual rainfall column the second figure is the number of years for which there are recordings.

Locality	Average annual rainfall	Total rainfall in 2000	Average rainfall, 1 Oct to 30 April	Rainfall, 1 Oct 2000 to 30 April 2001	First effective rain event, 2001	Rainfall from then until 31 May 2001
Badgingarra Research Stn	572.8 39 years	274.4	134.4	21.0	6 May 22.0	108.2
Swanbourne	773.8 16 years	748.6	126.5	57.7	6 May 20.0	139.0
Perth	799.1 8 years	796.2	144.5	48.8	6 May 17.8	108.8
Lancelin	626.0 35 years	485.0	126.9	41.0	6 May 25.8	117.3
Bickley	1095.6 99 years	1192.2	241.5	63.8	6 May 28.0	146.2
Watheroo	423.5 99 years	352.2	111.6	26.0	6 May 10.0	47.8
Moora	464.1 99 years	376.6	118.7	19.6	1 Mar. 12.0 6 May 10.4	58.8
Rottnest	584.6 6 years	477.8	140.4	36.8	6 May 24.0	144.0
Tammin But see discussion in text	345.5 89 years	346.3	114.4	100.6	19 Jan. 11.0 21 Jan. 30.6 24 Feb. 11.0 23 Apr. 24.4	143.0

appeared to have had no flowers during its usual season (July-August), and *D. purdieana* had few flowers.

Results

Below are species in which I recorded the foliage changing colour, then regreening. Nomenclature follows Paczkowska & Chapman (2000) except that *Casuarina* is accepted instead of *Allocasuarina*. The list is alphabetical under families, with Dicotyledons followed by Monocotyledons. Dicots are shrubs unless noted otherwise. Monocots are all rhizomatous perennial herbs. Where known, species are described as seeders (*i.e.* killed by fire, regenerate from seed) or sprouters (having a lignotuber, rhizome or similar storage organ and sprouting from this after fire). Leaf orientation and texture remained normal except as indicated otherwise. The date when species were recorded as regreened is that when a sites was visited; plants may have been regreened before that date.

Dicotyledons

Casuarinaceae

Casuarina campestris Diels. Seeder, dioecious. A characteristic 'autumn' plant even in normal summers, commonly seen (both sexes) various shades of gold, brown or red-brown during late summer and autumn, *e.g.* Avon Location 19769 (S of Corrigin) 8 April 1977; Hopkins Reserve 35134, SE of Kulin, 8 April 1977; near Manmanning 8 February 1980; near Meenaar (W of Meckering) 27 February 1994. In 2001 brown at Charles Gardner Reserve on 10 March, regreened on 7 June; N of Moora, quite brown 1 April, partly regreened 27 May; S of Coomallo, brown or golden 1 April, regreened 27 May. Mentioned by Main (1967).

Casuarina huegeliana Miq. Seeder, dioecious. Foot of Crystal Brook hill: a number of trees (both sexes) brown 15 March, regreened 22 May.

Casuarina humilis Otto & F Dietr. Sprouter, dioecious. Crystal Brook: a number of plants (both sexes) turned pale purple or pink (27 March 1994, 15 March 2001) and regreened after rain 17 May 2001. Kings Park: stems pinkish brown 26 April.

Casuarina microstachya Miq. Seeder, dioecious. S of Tiwest Mine turnoff, Brand Hwy: branchlets (both sexes) yellow 1 April; regreened 27 May.

Dilleniaceae

Hibbertia hypericoides (DC) Benth. Sprouter. In 2001, plants at a number of localities (*e.g.* Seabird, Crystal Brook, Naval Base, Kings Park, Yanchep) generally turned golden or brown. Regreening took several weeks but generally was completed by 31 May. Plants had commenced flowering at Naval Base on 10 July and at Seabird on 11 July.

Hibbertia spicata subsp *leptotheca* J R Wheeler. Naval Base: leaves yellow 7 April; still mostly yellow 11 May; regreened 5 June; inflorescence growth started 10 July.

Epacridaceae

Astroloma serratifolium (DC) Druce. Seeder. Charles Gardner Reserve: leaves pale green 10 March; regreened and flowering 7 June.

Leucopogon conostephioides DC. Seeder. Boothendarra Creek: leaves yellowish 1 April.

Leucopogon insularis DC. Seeder. Seabird: leaves yellowish, occasionally red, and resting flower buds present, 22 April; green and plants flowering 1 June; flowering over, new vegetative growth 11 July. Rottnest Is: leaves yellow 6 April; not followed up.

Leucopogon parviflorus (Andrews) Lindley Sprouter. Naval Base: leaves yellow 7 April; regreened 5 June; flower buds developing 10 July.

Euphorbiaceae

Phyllanthus calycinus Labill. Sprouter. During summer this species typically loses many leaves and by autumn has few remaining. In 2001 at Crystal Brook, Naval Base and Seabird, the remaining leaves were yellowish. At Crystal Brook, these old leaves had regreened and new shoots were just beginning to develop on 17 May. The process was further advanced at Seabird on 1 June; by 11 July flowering had started there. At Naval Base, old leaves had regreened by 11 May, and by 5 June these had almost all fallen, the new shoots being then well advanced.

Stachystemon axillaris A S George. Seeder. Tathra National Park: leaves yellowish 15 February; not followed up.

Fabaceae

Bossiaea eriocarpa Benth. Sprouter. Seabird: leaves yellow 22 April; not noted on 1 June; regreened 11 July.

Gastrolobium calycinum Benth (York Road Poison). Seeder. Dale, near Little Darkin Swamp: leaves very pale 26 April 1994. Not followed up.

Gastrolobium oxylobioides Benth (Champion Bay Poison). Seeder. Near Minyolo Brook, Brand Hwy: leaves yellowish, 1 April; regreened 27 May.

Gastrolobium spinosum Benth (Prickly Poison). Seeder. Julimar Road, Chittering: leaves pale golden-brown, April 1994. Not followed up.

Gompholobium tomentosum Labill. Seeder. Leaves yellowish (Seabird 22 April, Naval Base 7 April); regreening 11 May (Naval Base), 1 June (Seabird) but some still yellowish.

Hovea pungens Benth. Seeder. Crystal Brook: leaves dull green to yellowish with resting flower buds, 27 March 1997; regreened and buds developing, 22 May 2001; flowering 6 July. Some plants died. One plant noted with one dead branch and one flowering 7 August.

Jacksonia alata Benth. A leafless perennial herb; seeder? Crystal Brook: stems turned yellow. Behaviour after rain varied, some plants regreening over several weeks (22 May), but many died.

Jacksonia sp. A leafless perennial herb; seeder? Charles Gardner Reserve: stems orange 10 March, still so 7 June; regreened 19 August.

Nemcia spathulata (Benth) Crisp. Seeder. Crystal Brook: yellowish, 27 March 1997 and in 2001; green 22 May, but many plants died.

Nemcia reticulata (Meisn) Domin. Seeder. Seabird: variable; leaves orange or green 22 April; regreened and with young buds 11 July; many plants died; one noted on

11 July with about half its branches dead, the others regreened.

Sphaerolobium macranthum Meisn. Seeder. A leafless perennial herb. N of Coomallo: stems golden 1 April; greening 27 May

Templetonia retusa (Vent) R Br. Sprouter. At Seabird, Fremantle and Kings Park: the leaves on most plants turned golden; some plants died. Most regreened after rain, the change becoming evident after 3-4 days and taking up to two weeks to become fully green. Some plants, however, were still yellowish at the end of May. Possibly these were on the verge of death and were slower to regreen. Beyond the dormant stage, the foliage becomes bleached as death sets in. Flowering had commenced at Seabird by 1 June; in full flower at Kings Park 6 July, and Naval Base 10 July. At Seabird there were still flowers on 11 July and the early flowers were already developing fruit; one plant was flowering even though the foliage was still yellowish.

Goodeniaceae

Dampiera sp. A clonal perennial herb; sprouter. Charles Gardner Reserve: many plants had deep reddish leaves and stems on 10 March and were similar on 7 June, but most had regreened by 19 August. Some reddish colouring may be normal, especially in ageing leaves.

Lamiaceae

Hemiandra glabra Benth subsp *glabra*. Seeder. Some plants at Seabird were yellowish on 22 April. On 1 June most were healthy green, but a few remained yellowish.

Hemigenia incana (Lindl) Benth. Seeder. Crystal Brook: most plants were dormant on 15 March, the leaves pale green and commonly slightly pink towards the margins which were a little more inrolled than usual. In some plants the leaves were brittle and brown with the appearance of death. On 22 May most were regreened and soft; most fully regreened 6 July. Some plants shed leaves but resprouted, others died.

Westringia dampieri R Br. Seeder. Rottnest Island: foliage golden 6 April. 2001.

Mimosaceae

Acacia acuminata Benth. Small tree; seeder; phyllodinous. N of Moora: mature trees with dull yellowish-green phyllodes 1 April; regreened 27 May.

Acacia lasiocarpa Benth var *lasiocarpa*. Seeder; bipinnate leaves. Seabird: leaflets quite yellow and inrolled 22 April; regreened and with bright green new growth 1 June; in bud 11 July. Plates 1, 2.

Acacia multispicata Benth. Seeder; flat-phyllode variant. Non-lignotuberous. Boothendarra Creek: phyllodes yellow 1 April; some fully green on 27 May, others still yellowish.

Acacia pulchella R Br var *pulchella*. Seeder; bipinnate leaves. Crystal Brook: leaflets yellow, closed together and rachis turned downwards 27 March 1997 and 15 April 2001; regreened and expanded 22 May 2001. Many plants died.

Acacia truncata (Burm f) Hoffmanns. Seeder; triangular phyllodes. Seabird: variable; on 22 April, some were green, others were yellowing; all green 1 June.

Myrtaceae

Baeckea crispiflora F Muell. Seeder. Charles Gardner Reserve: leaves reddish 10 March; regreened 7 June.

Baeckea aff *preissiana* (Schau) Domin. Seeder. Dale, near Little Darkin Swamp: leaves yellow to golden brown or orange 26 April 1994; not followed up.

Calothamnus torulosus Schauer. Sprouter. N of Coomallo: variable; a number of plants with pale purplish or pink foliage 1 April; regreened 27 May. Crystal Brook: some plants with pink or pale purple foliage 15 April; regreened 6 July.

Calytrix glutinosa Lindl. Seeder. Crystal Brook: leaves yellow, somewhat appressed 15 April; regreened 22 May but some plants were dead; surviving plants with new vegetative growth 5 July. A sticky white exudate appeared around the new shoots, apparently similar to that seen on species of *Eremaea*.

Darwinia citriodora (Endl) Benth. Seeder? Crystal Brook: leaves turned shades of red or pale purple March 1997 and 15 April 2001; regreening 22 May; fully regreened 6 July.

Darwinia speciosa (Meisn) Benth. Sprouter? N of Coomallo: foliage reddish 1 April; regreening but only a little on 27 May.

Darwinia aff *nieldiana* F Muell. Seeder. Marchagee Track: variable, but a number of plants quite yellow on 1 April; regreening 27 May.

Hypocalymma augustifolium (Endl) Schauer. Sprouter. Crystal Brook: leaves reddish 27 March 1997; dull green 18 April 2001; regreened and flower buds developing 6 July.

Melaleuca elliptica Labill. Seeder. Dragon Rocks Reserve, SSE of Hyden: leaves deep pink on upper surface but remained greenish below 18 April 2001 (M Pieroni, personal communication).

Melaleuca platycalyx Diels. Seeder. Boothendarra Creek: leaves pinkish grey with red-brown margins 1 April; regreening 27 May (margins remain brownish).

Melaleuca radula Lindl. Sprouter. NE of Mt Lesueur: leaves yellow 27 March 1977. Crystal Brook: leaves becoming grey 15 March; still so 22 May, and many leaves appearing dead; by 5 July, some leaves had regreened, and new shoots were developing at the lignotuber and along older stems on some plants with dead leaves. The new growth was farther advanced on 7 August, with some flower buds developing.

Melaleuca urceolaris F Muell ex Benth. Boothendarra Creek and S of Coomallo: leaves yellow and the oldest ones brown, with persistent dead flowers from previous year 1 April; regreening 27 May.

Melaleuca viminea Lindl subsp *viminea*. Seeder? S of Tiwest Mine turnoff, Brand Hwy, and S of Coomallo: leaves yellowish 1 April; fully regreened 27 May.

Thryptomene mucronulata Turcz. Seeder. Boothendarra Creek: leaves red-brown 1 April; regreened 27 May. Plates 3, 4.

Verticordia acerosa Lindl var *acerosa*. Seeder. Crystal Brook: stem and floral leaves yellow or brown 15 March; regreened 22 May but some plants dead.

Verticordia chrysanthella A S George. Sprouter. A group planted at the Western Australian Herbarium Kensington, regularly turns brown during the summer and regreens with the first autumn rain. Unseasonal summer rain, as occurred in January 2000, also causes regreening.

Verticordia eriocephala A S George. Seeder. Charles Gardner Reserve: leaves yellowish-green 10 March; regreened 7 June.

Verticordia huegelii Endl var *huegelii*. Seeder. Crystal Brook: leaves red 15 March; regreening 22 May; fully regreened 5 July; new growth 7 August. Some plants died.

Verticordia huegelii var *decumbens* A S George. Sprouter. Hummerston Rd, Piesse Brook: leaves reddish 27 March 1997; not observed again 1997. Regreening 22 May 2001, and a number of plants appearing dead; most surviving plants fully regreened 5 July, some with new leaves developing among dead ones.

Proteaceae

Conospermum huegelii Endl. Perennial herb; seeder. Crystal Brook and Hummerston Rd, Piesse Brook: this species normally has pale green foliage, but it appeared to be even paler during late summer (27 March 1997, 15 April 2001), regreening after the first rains (22 May 2001). Some plants died.

Dryandra purdieana Diels. Seeder. Charles Gardner Reserve: many plants with yellow and orange leaves 10 March; similar 7 June; mostly regreened 19 August.

Grevillea endlicheriana Meisn. Sprouter. Crystal Brook: leaves turning brown 15 March, 15 April; on 22 May many plants appeared dead, with grey leaves; on 10 July some plants appeared dead, on others leaves had regreened, and on some new shoots were developing either from stems or the lignotuber.

Isopogon scabriusculus Meisn subsp *scabriusculus*. Seeder? Charles Gardner Reserve: leaves dull to pale green, 10 March; regreened 7 June. The colour change was subtle.

Petrophile seminuda Lindl. Seeder. A characteristic 'autumn' plant, recorded red at various localities, *e.g.* Mt Lesueur 27 March 1977; near Meenaar (W of Meckering) 27 Feb 1994; West Dale area (near Little Darkin Samp) 26 April 1994; Hill River bridge, Brand Hwy 1 April 2001; Charles Gardner Reserve, 7 June. Regreened at Charles Gardner 19 August; regreened and flowering at Hill River bridge 5 September

Petrophile squamata R Br. Seeder. Tootbardi Road: leaves deep red, 27 March 1977.

Stirlingia abrotanoides Meisn. Seeder? N of Coomallo, Brand Hwy: in this small shrub the leaves became slightly paler than usual and the lobes closed together somewhat (1 April), 'regreened' and returned to normal 27 May.

Stirlingia simplex Lindl. Seeder? A small shrub with very soft, finely divided foliage that remains soft and turns pink or mauve as summer progresses, *e.g.* Dale (near Little Darkin Swamp) 26 April 1994; generally regreens with winter rain but in a few plants the pink tinge persists (Dale, 19 August 2001).

Synaphea spinulosa (Burm f) Merrill. Sprouter. Tootbardi Rd: leaves yellowish 27 March 1977; Charles Gardner Reserve: leaves yellowish 10 March; still so 7 June; regreened 19 August. In this genus the foliage of many species characteristically has a yellow tinge, but in some this becomes more pronounced during autumn.

Synaphea sp. Seeder. Reserve 19486: leaves yellowish 8 April 1977; not observed later.

Rhamnaceae

Spyridium globulosum (Labill) Benth. Seeder. Naval Base: leaves yellowish 7 April, regreened 11 May; in full flower 10 July. Cantonment Hill: leaves yellowish 7 April, regreened 20 May. Seabird: leaves of some plants yellowish 22 April; regreened 27 May, in full flower 11 July. In this species many leaves have damaged parts, of various brown or reddish shades. Some plants at Seabird died in autumn 2001.

Trymalium ledifolium var *rosmarinifolium* (Steud) Benth. Seeder. Crystal Brook: leaves pale, dull green or yellowish and somewhat appressed 15 March; still yellowish 17 May; regreened and flowering 5 July; Hummerston Rd, Piesse Brook: leaves pale green or slightly yellow 27 March 1997; not observed again in 1997, but green 22 May 2001.

Rutaceae

Boronia alata Sm. Seeder. On Rottnest Island the foliage turned red in autumn 2001 (G J Keighery, Wildlife Research Centre, personal communication).

Philotheca spicata (A Rich) Paul G Wilson Sprouter. Naval Base: leaves somewhat yellowish 7 April; regreened 10 July.

Santalaceae

Leptomeria empetriformis Miq. Like many of its family, both the stems and leaves of this semi-parasitic plant are usually yellowish green or somewhat reddish. At Seabird on 22 April they were quite an intense red, but changed to yellowish after rain (1 June); most were regreened by 11 July but the stems remained reddish.

Sapindaceae

Dodonaea aptera Miq. Seeder. Cantonment Hill: leaves dull, dormant flower buds present 7 April; leaves soft, fully green, and plants in flower 20 May.

Dodonaea hackettiana W Fitzg. Seeder. Kings Park: leaves dull, pale green or straw-colour with some plants appearing dead 26 April; most fully regreened 6 July but one plant dead.

Sterculiaceae

Thomasia cognata Steud. Seeder? Naval Base: leaves yellowish 7 April; regreening variably 11 May; fully regreened 5 June.

Thomasia macrocarpa Endl. Seeder. Crystal Brook: leaves yellow or pale green and hanging more steeply than usual 15 March; not noted in May; regreened and spreading, with new growth and buds 7 August.

Lasiopetalum drummondii Benth. Sprouter. N of Coomallo: leaves yellow-brown 1 April; some regreened and some still yellowish 27 May.

Plate 1. *Acacia lasiocarpa* at Seabird, 22 April 2001. Leaflets tightly rolled and closed together.

Plate 2. *Acacia lasiocarpa* at Seabird, 1 June 2001. Leaflets unrolled, spreading.

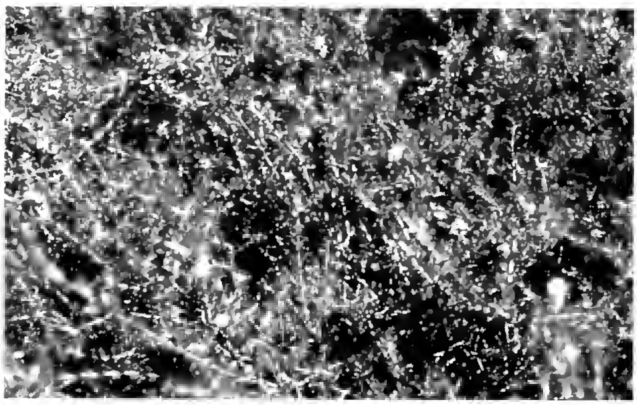

Plate 3. *Thryptomene mucronulata* at Boothendarra Creek, Brand Highway, 1 April 2001.

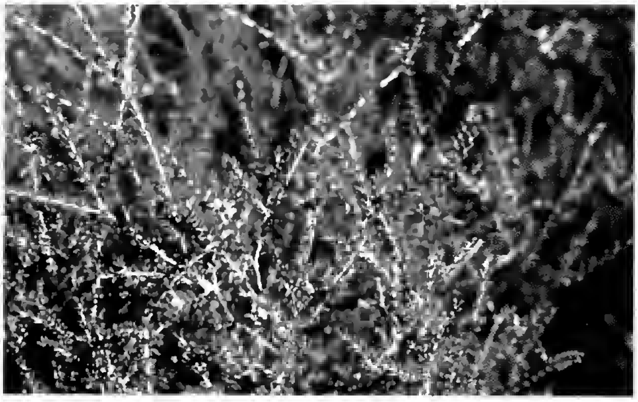

Plate 4. *Thryptomene mucronulata* at Boothendarra Creek, Brand Highway, 27 May 2001.

Plate 5. *Pimelea ferruginea* at Seabird, 22 April 2001. Leaf margins revolute; old flowers present.

Plate 6. *Pimelea ferruginea* at Seabird, 1 June 2001. Leaves almost flattened; flowers fallen; new shoots right.

Plate 7. *Schoenus calcatus* at Charles Gardner Reserve, south of Tammin, 10 March 2001.

Plate 8. *Schoenus calcatus* at Charles Gardner Reserve, south of Tammin, 7 June 2001.

Thymelaeaceae

Pimelea ferruginea Labill. Seeder. Seabird: leaves yellow with margins more revolute than usual 22 April; fully regreened and margins less revolute, some with vigorous new growth 1 June. Flowered well September-October 2001. Plates 5, 6.

Pimelea imbricata var *piligera* (Benth) Diels & E.Pritzel. Seeder. Crystal Brook and Hummerston Road. In this small shrub the leaves became grey and folded lengthwise. After rain some leaves regreened, with new shoots developing 22 May; new leaves further developed 5 July. During 2000-2001 some plants died.

Tremandraceae

Tetratheca confertifolia Steetz. Sprouter; perennial herb. N of Coomallo: leaves reddish 1 April; partly regreened 27 May.

Tetratheca sp. Seeder? A leafless perennial herb. Charles Gardner Reserve: stems orange 10 March.

Monocotyledons

Boryaceae

Borya sphaerocephala R Br. The classic resurrection plant of Western Australia. Leaves commonly turn orange from late spring until the first rains of autumn or winter. Abnormal summer rain causes regreening. Gaff (1981) recorded maintaining plants in the dormant state for 5 years [as *B. nitida* Labill]. Some populations turn straw-colour, *e.g.* at Charles Gardner Reserve 10 March 2001. A common species around granitic rocks in the Darling Range near Perth and farther inland.

Borya constricta Churchill. Occurs farther inland than *B. sphaerocephala* and generally turns a richer orange when stressed. Recorded *e.g.* at Mouroubra Station (S of Paynes Find) 19 April 1976; N of Merredin 10 March 2001.

Two south-western species of *Borya* (*B. laciniata*, *B. scirpoidea*) are drought avoiders, being deciduous or almost so during the summer, though the old inflorescences persist. Growth of new leaves begins immediately after the first rain falls in autumn.

Cyperaceae

Caustis dioica R Br. Sprouter. Dale, near Little Darkin Swamp: culms yellow 26 April 1994. Minyolo Brook, Brand Hwy: culms yellow 1 April 2001; regreened 27 May. Charles Gardner Reserve: culms yellow 10 March; regreened or yellow-green, 7 June; all regreened 19 August.

Lepidosperma sp. Sprouter? A robust plant with flattened culms. Hopkins Reserve, SE of Kulin: culms yellow 8 April 1977.

Lepidosperma sp. Sprouter? A robust plant with terete stems. Hummerston Rd, Piesse Brook: culms yellow-green, 27 March 1997.

Lepidosperma sp. Sprouter? A robust plant with slender flat stems. Crystal Brook: stems yellow 15 March; green 5 July.

Mesomelaena stygia (R Br) Nees. Sprouter? Charles Gardner Reserve: culms green or yellowish 10 March; still yellowish to green 7 June; regreened, some flowering 19 August.

Schoenus aff *brevisetis* (R Br) Roem & Schult. Seeder? Charles Gardner Reserve: culms pale yellowish-green 10 March; still somewhat yellow 7 June; regreened 19 August.

Schoenus calcatus K L Wilson. Seeder? Avon Location 19769: culms and leaves golden yellow 8 April 1977. Charles Gardner Reserve: bright yellow or yellow-orange 10 March; some plants half-green, others still yellow 7 June; all regreened 19 August. The mechanism in this species may be similar to that of *Borya*, *i.e.* a breakdown of the leaf cell structure, followed (after wetting) by regreening with reconstitution of the structure and resumption of normal functions. The time taken to regreen seems to be much longer. Plates 7, 8.

Schoenus aff *clandestinus* S T Blake. Seeder? S of Badgingarra: leaves golden 1 April; regreening 27 May.

Dasypogonaceae

Calectasia narragara R L Barrett & K W Dixon. Sprouter. N of Coomallo: leaves yellowish, 1 April; regreened 1 June.

Lomandra maritima T S Choo. Sprouter. Seabird: leaves orange 27 April; regreened 1 June.

Ecdeiocoleaceae

Ecdeiocolea monostachya F Muell. Sprouter. Near Minyolo Brook and Boothendarra Creek: culms orange or yellow 1 April; regreened 1 June. Mentioned by Main (1967).

Haemodoraceae

Conostylis aculeata subsp *breviflora* Hopper. Seeder. Boothendarra Creek: leaves yellowish 1 April.

Conostylis aculeata subsp *bromelioides* (Endl) J Green. Seeder? Pinjarrega Lake Reserve: leaves golden or brown 1 April; on 27 May some plants had green foliage, but others were brown and appeared dead.

Conostylis pauciflora subsp *euryrhipis* Hopper. Seeder? Seabird: leaves pale yellow 27 April; green 1 June.

Conostylis petrophiloides F Muell ex Benth. Seeder. Charles Gardner Reserve: leaves golden 10 March; green 7 June.

Poaceae

Triodia danthonioides (F Muell) Lazarides. Seeder. Pinjarrega Lakes Nature Reserve: leaves orange on 1 April; regreened 27 May (note: this plant has many old dead leaves in its 'normal' mature state).

Restionaceae (data on seeders/sprouters from Meney & Pate 1999)

Alexgeorgea subterranea Carlquist. Seeder. S of Badgingarra: many plants with yellow culms 1 April 27; those near road had regreened by 27 May, but those in undisturbed vegetation remained yellowish.

Catacolea enodis B G Briggs & L A S Johnson. Seeder. S of Badgingarra: culms yellow 1 April; regreened 27 May.

Desmocladus flexuosus (R Br) B G Briggs & L A S Johnson. Sprouter. Naval Base, Cantonment Hill: culms yellow 7 April; regreening 11 May (Naval Base); fully regreened 20 May (Cantonment Hill), 10 July (Naval Base).

Desmocladus parthenicus B G Briggs & L A S Johnson. Seeder. Marchagee Track: culms and branchlets yellow 1 April; regreened 27 May

Harperia lateriflora W Fitzg. Sprouter. Pinjarrega Lake Reserve: culms very pale green 10 March; fully green 7 June

Lepidobolus quadratus B G Briggs & L A S Johnson. Seeder. N of Coomallo: culms pale green or yellowish 1 April; regreened (with a blue tinge) 27 May.

Other drought strategies

Deciduousness and protection by dead leaves

Alyogyne huegelii (Endl) Fryxell (Malvaceae) . At Seabird in 2000-2001 this shrub had shed all or most leaves by 22 April, the stems generally turning deep red. A very few surviving leaves remained green. On 1 June new shoots were developing. The stems either remained red or turned somewhat green. In full leaf, with mature flower buds 27 September.

Opercularia spermacocea Juss (Rubiaceae). At Seabird, the leaves of this perennial herb were dead (dark grey, brittle) on 22 April but the stems remained green. On 1 June new shoots were developing; by 11 July flowering had started. The old leaves persist for at least a year, i.e. are not deciduous immediately.

Opercularia vaginata Juss (Rubiaceae). This suckering perennial herb is almost deciduous in summer. At Seabird, it was slower to develop new leaves than *S. spermacocea*. New shoots and early flowers, Charles Gardner Reserve, 19 August.

The semi-deciduous habit of *Phyllanthus calycinus* is described above.

Several perennial herbs were recorded in which the leaves die during summer but form a protective cover over the stems and/or rootstock. These include species of stilt plants, *e.g. Laxmannia squarrosa* Lindl (Anthericaceae) and *Stylidium bulbiferum* Benth and other species (Stylidiaceae) at Hummerston Road and Crystal Brook. The phenology of stilt plants was described by Pate *et al.* (1984), but they reported no death or colour change in the foliage, only slow growth or even a decrease in dry weight during summer and autumn. According to the rainfall figures that they cited, during the summer of 1980-81 when their study was made there was effective rain in January and March, hence the plants were not subject to a long summer drought.

In *Laxmannia squarrosa,* the leaves in a population at Hummerston Rd, Piesse Brook, turned yellow 27 March 1997 but were not observed again that year. In 2001, new leaves were present on 22 May, those of the previous year appearing dead. The dead leaves are not deciduous immediately but seem to persist for at least a year.

Schoenus aff *clandestinus* S T Blake (Cyperaceae) . At Charles Gardner Reserve the leaves of this very small cushion sedge died, turned white and curled up, providing a protective covering to the rhizome (10 March). On 19 August new leaves were well developed and most old leaf laminas had fallen.

Sacrificing parts

From observations made in autumn 2001 I suggest that another strategy for surviving drought is the sacrifice of foliage or whole branches. In several species, parts of plants died and the remainder survived. In *Eucalyptus wandoo* Blakely (Myrtaceae) at Crystal Brook and Forrestfield, most trees showed no or little drought effect, but the foliage died on a number of young plants (up to 4 m tall). In some of these a very few leaves remained green. On 7 August some of these plants had new epicormic shoots and appeared to have survived as they do after fire. These will be monitored to see whether they return to normal growth.

At Crystal Brook a plant of *Hovea pungens* lost one major stem but the other survived and flowered. Likewise, at Crystal Brook and Forrestfield, many plants of *Melaleuca radula, Grevillea endlicheriana* and *Hemigenia incana* showed this strategy. One plant of *Nemcia reticulata* was also noted at Seabird with half its branches dead, the remainder green.

In autumn 2001, many *Xanthorrhoea preissii* Endl (Xanthorrhoeaceae) at several localities (*e.g.* Forrestfield, Crystal Brook, Badgingarra) seemed stressed, the lower leaves and/or upper parts of leaves turning yellow. These parts did not regreen after rain.

Colour change in bark

Seasonal change in the colour of bark is well-known in some smooth-barked species of *Eucalyptus* (Brooker & Kleinig 1990). An outstanding example is *E. erythronema* Turcz in which the newly exposed bark is silver or white but gradually changes to deep red before peeling in autumn. The pastel pink or orange tones of *E. accedens* W Fitzg and *E. salmonophloia* F Muell also intensify during autumn, then become pale again during winter.

Discussion

One question that I have addressed is what term to adopt for the strategy of colour change and its reversal. Gaff (1981) and others have used 'resurrection plant' for *Borya* and other species but I believe that few of the species reported here have the ability to remain in the non-green state for several years, as is the case with resurrection plants, although *Schoenus calcatus* is an obvious candidate. Dormancy seems inappropriate, since it usually refers to a normal seasonal reduction in metabolism to a steady low state, *e.g.* as a seed or as a deciduous plant. Aestivation is used for animals that assume a low metabolic rate or torpor during summer (*cf.* hibernation), but in botany refers to the arrangements of floral parts and hence its use with another meaning would cause confusion. Ferns that can reduce their water content to a low level and recover have been described as desiccation-tolerant. The condition I am describing does not occur to the same degree every season, varying in response to current conditions. It may be reversed by abnormal rainfall, in contrast to typical dormancy that awaits a change in season (especially in day length or temperature). Quiescence also seems inappropriate, since a plant may be quiescent metabolically but not show outward symptoms as we have here. To describe the strategy of plants that show a reduction in metabolic rate indicate by change in colour of vegetative parts and then revert to the green state I am proposing the term *diallagy* (adj *diallagous*). This is derived from the Greek *diallage* (interchange).

Diallagy is generally indicated by a change in colour of the foliage. At first glance the plants may appear dead, but with experience one can usually distinguish between those still alive and those that have died (the latter commonly shown by a grey colour). A wide range of colours develops: brown, purple, red, yellow, orange. These are what I call our autumn colours. Most are more subtle than the brilliant colours of deciduous trees of the Northern Hemisphere, and of course they are not associated with leaf fall, but nonetheless they are quite evident. Once you become attuned to the condition you begin to see how widespread it is both taxonomically and geographically. I have, however, been tricked by plants that appeared dead but later regreened, *e.g.* several *Dodonaea hackettiana* in Kings Park, *Hemigenia incana* at Crystal Brook. A rule of studies in diallagy should be to always check after the rains come!

Table 2

Families in which diallagy is reported.

Dicotyledons	Monocotyledons
Casuarinaceae	Boryaceae
Dilleniaceae	Cyperaceae
Epacridaceae	Dasypogonaceae
Euphorbiaceae	Ecdeiocoleaceae
Fabaceae	Haemodoraceae
Goodeniaceae	Poaceae
Lamiaceae	Restionaceae
Myrtaceae	
Proteaceae	
Rhamnaceae	
Rutaceae	
Santalaceae	
Sapindaceae	
Thymelaeaceae	
Tremandraceae	

The texture of diallagous leaves tends to remain similar to that of the leaves in the green state. In some cases there is also an appearance of being slightly shrivelled but, given the sclerophyllous form of the leaves of most species in our flora, the latter is uncommon. In a few species leaf orientation changes, *e.g.* in *Acacia lasiocarpa* and *Acaica pulchella* where the rachis bends downwards, the pinnae close on the rachis and the leaflet margins become more tightly revolute. In *Hemigenia* and *Thomasia* the leaves may bend downwards slightly at the petiole.

The condition is highly variable in its expression. Sometimes it appears in whole populations, sometimes only in individual plants. A plant in the coloured state may occur close to one that appears normally green.

Diallagy is here reported in 99 species belonging to 59 genera and 24 families (Table 2) of the flora of south-west Western Australia. Because of its appearance in a wide taxonomic range, apparently with different mechanisms, the strategy has almost certainly arisen independently a number of times. Within one genus there can be both diallagous and non-diallagous taxa, *e.g.* *Verticordia*, *Petrophile*, *Leucopogon*. Passage into the diallagous state occurs gradually as summer progresses, presumably in response to dwindling soil moisture. Although my observations indicate that all or most plants of a species behave similarly, they are not necessarily the same in their appearance, individuals commonly differing in colour. This agrees with Gaff's (1981) statement that 'the degree of water stress survived without injury varies appreciably from one species to the next even within one genus'. I suggest that soil moisture is critical, and variable, since a coloured plant may occur close to a green one.

In most species the rate of change to the coloured state and back to rehydration is much slower than in *Borya*, in which regreening takes 3-5 days (Gaff 1981). I suggest that the slower change in diallagous plants is due to the soil moisture level, which would decline more gradually in the deeper soils where most of the newly recorded species occur, compared to the shallow soils on granitic outcrops where *Borya* species grow. Most species listed here, especially the dicots, change gradually during the summer, only reaching maximum 'autumn colour' in February/March/April. Any effective rainfall will halt or reverse the change. I suggest that an effective fall is at least 5 mm, and more likely 10-15 mm, within a short period, *e.g.* 24 hours. In this recent season, a fall of *ca.* 12 mm (measured in a domestic gauge) in Kardinya (a suburb of Perth) was sufficient to start *Templetonia retusa* turning green, whereas less than 5 mm elsewhere in the Perth metropolitan area was insufficient. This is in line with observations in the Wiluna area, Western Australia, by Arnold (1963) and in southern Africa by Gaff (1977), who reported full rehydration after 10 mm. In contrast to the African plants that Gaff (1977) reported (from a winter-dry region), the Western Australian examples are from a summer-dry region and hence withstand both drought and high temperatures (commonly over 35 °C in the shade, and many of them receive no or little shade except just after sunrise and before sunset).

The diallagous condition is to be seen through much of the south-west, from the coast to the wheatbelt. In the recent record long, dry summer, 'autumn' colours were evident on Rottnest Island, at Naval Base, Seabird near Lancelin, the Darling Scarp, and in the kwongan around Badgingarra and Tammin. In previous years I have recorded it near Mt Lesueur, Chittering, Manmanning, Meenaar, Corrigin, Kulin and Little Darkin Swamp. In 2001, others reported it at Dragon Rocks Nature Reserve and Ravensthorpe (M Pieroni, M Bennett, personal communication).

Both fire-tolerant (seeder) and fire-sensitive (sprouter) species are diallagous. Most arborescent plants remain green during the summer, but some species of *Casuarina* change in certain locations, and *Acacia acuminata* has also been seen with yellowish-green phyllodes north of Moora and north of Badgingarra.

Nor is habitat a deciding factor. At any one site one can see both diallagous and non-diallagous plants. I have seen the condition on a number of soil types, from deep sand to clay and loam. The heavier soils do, however, seem to become drier as summer proceeds and there are usually fewer or no species in those soils that flower during autumn. The exception may be species of *Eucalyptus*. Plants in low-lying areas subject to winter damp or inundation can also show diallagy once the soil moisture diminishes, *e.g.* north and south of Badgingarra on the Brand Highway.

In some years, a prolonged dry season can lead to death rather than diallagy. This happened last summer, when the 2000 wet season ended suddenly at the end of September. Along the Darling Scarp, considerable deaths occurred in March and April, *e.g. Hemigenia, Eucalyptus wandoo, Dryandra sessilis.* Likewise along the scarp above the Swan River in Kings Park, there were deaths in *Dryandra sessilis* var *cygnorum* and *Dodonaea hackettiana.*

Generally I have recorded species that change colour. It may be assumed that others at the localities sampled retained a normal green appearance. But this work is very preliminary; far more is needed to confirm these data and discover the extent of the strategy.

Autumn flowering, budding and fruiting

Flowering

In contrast to the strategies described above, quite a few species have their normal flowering during late summer and autumn. The following summary includes many of these. It excludes many more that may commonly be seen with a few summer flowers, usually as a result of late spring or unusual summer rains. The structure, anatomy and physiology of one widespread summer flowerer, *Banksia prionotes*, has been studied by Pate *et al.* (1998). It has adapted to do so when soil moisture is at its lowest and temperatures can be very high. It follows that if there are flowers and developing fruits in summer and autumn then there is an associated fauna pollinating and predating them. Have these, or at least some, retained a summer/autumn flowering pattern from their tropical origin? They will certainly attract pollinators, given the much lower number of species in flower. Some have scented flowers.

Summary of taxa that flower in late summer and autumn

Some 29 taxa of *Banksia* (Proteaceae), of 67 in the south-west, flower during March/April and 13 of these begin to flower then (George 1984b, 1996).

Strangea cynanchicarpa (Meisn) F Muell (Proteaceae) flowers in February, but its south-western congener *S. stenocarpoides* flowers in spring.

Dryandra vestita Meisn (Proteaceae) is widespread in the northern kwongan and central wheatbelt and flowers in mid-summer. *Dryandra aurantia* A S George, a rare species from Little Darkin Swamp, flowers in mid to late autumn. In 1994, after a particularly dry summer, it was in full flower on 26 April.

In *Verticordia* (Myrtaceae), seven taxa typically flower in summer and autumn: *V. harveyi* Benth (January-April), *V. tumida* subsp *therogana* A S George (November-March), *V. fastigiata* Turcz (February-July), *V. minutiflora* F Muell (January-June), *V. pityrhops* A S George (February-June), *V. sieberi* Diesing ex Schauer (all varieties) (January-April), *V. vicinella* A S George (January-April). Thus, the one genus may contain both diallagous and summer/autumn-flowering species.

Four species of *Beaufortia* (Myrtaceae) are summer/autumn flowering: *B. sparsa* R Br, *B. anisandra* Schauer, *B. squarrosa* Schauer, *B. aestiva* K Brooks. Other such Myrtaceae are *Calytrix fraseri* A Cunn (typically in full flower during February and March), and *Scholtzia involucrata* (Endl) Druce (Myrtaceae).

More than 93 south-western taxa of *Eucalyptus* (Myrtaceae) flower regularly in the autumn, and of these some 30 begin to flower during this season (Brooker & Kleinig 1990). Taxonomically those taxa are spread throughout the genus and through many vegetation formations. They include both trees and mallees. Examples include *Eucalyptus calophylla, E. erythrocorys, E. wandoo, E. patens, E. gomphocephala, E.gardneri, E. salubris, E. eudesmioides.*

A curiosity in the flora is the parasitic *Pilostyles*, the only genus of the family Rafflesiaceae in Australia. The family is pan-tropical and temperate, and some species have spectacularly large flowers. *Pilostyles* occurs in South America and south-western Western Australia, a clear example of Gondwanan distribution. In the two Australian species, the flowers have become reduced to insignificant size (1.5-3 mm wide) but have retained a flowering time similar to that of their tropical relatives. Like *Nuytsia* and other mistletoes, they draw nutrients and water from their hosts, hence low soil moisture is less likely to affect them.

Several south-western mistletoes (Loranthaceae) are summer-flowering, *e.g. Amyema miquelii* (Miq) Tieghem, *A preissii* (Miq) Tieghem. Summer-flowering species of *Acacia* (Mimosaceae) include *A. microbotrya* Benth and *A. huegelii* Benth. Autumn-flowering species of *Daviesia* (Papilionaceae) include *D. abnormis* F Muell, *D. angulata* Benth, *D. chapmanii* Crisp, *D. epiphyllum* Meisn and *D. speciosa* Crisp.

Pithocarpa (Asteraceae), a small genus of perennial daisies endemic in the south-west, flowers from late summer to autumn. It shows vegetative growth during winter and spring, is semi-deciduous, and then produces everlasting-type flower heads. Some species of *Olearia* (Asteraceae) are summer/autumn flowering. During field work for this paper in 2001, I recorded *O. paucidentata* (Steetz) Benth in full flower at Charles Gardner Flora Reserve, south of Tammin, on 10 March; interestingly it was still in flower on 7 June. *Olearia muricata* (Steetz) Benth was in late flower and fruit at Pinjarrega Nature Reserve, north-west of Watheroo, on 1 April.

The Sandalwood (*Santalum spicatum* (R Br) DC. (Santalaceae) flowers in summer. On 10 March 2001 it was in full flower at Charles Gardner Reserve. Several species of *Platysace* (Apiaceae) are summer-flowering, *e.g. P. cirrosa, P. juncea, P. effusa, P. sylvatica* and *P. peltigera.*

The yam *Dioscorea hastifolia* Endl (Dioscoreaceae), the only south-western representative of the family, flowers in autumn and early winter and appears independent of rain, drawing instead on reserves in its tuber. In 2001, it began flowering profusely on the Darling Scarp at Forrestfield in late April, before any rain fell.

The creeping, stilt-rooted triggerplant *Stylidium repens* R Br (Stylidiaceae) retains green leaves throughout the year. It has two flowering periods, in autumn and spring, but will respond to unseasonal rain as occurred in January 2000. Flowers develop within days. In 2001, at Piesse Brook, new stilt roots were also well developed 16 days after the first effective rain.

A number of species flower within days of the first effective rains, *e.g.* in Cyperaceae (*Lepidosperma, Schoenus*), Restionaceae (13 species, Meney & Pate 1999), Epacridaceae (*Astroloma*, *Leucopogon*), Mimosaceae (*Acacia*).

Budding

Many native plants initiate buds soon after flowering in winter or spring and hold them at an early stage until shortly before flowering the following season. There are two general strategies, referred to by Bell & Stephens (1984) as 'long continuous' and 'long arrested' bud development. The latter is especially common among Epacridaceae, Fabaceae and Proteaceae and Restionaceae (Meney & Pate 1999), a number of species of which initiate buds soon after flowering, then become dormant during summer (*e.g. Dodonaea aptera, Leucopogon insularis, Astroloma serratifolium, Hovea pungens, Templetonia retusa*). They appear to remain 'viable' even if the plant is diallagous. Growth recommences with the first rains, and some flower very quickly, others during winter. 'Long continuous' bud development occurs over summer with no resting period. Noteworthy among these is *Stirlingia latifolia* (Blueboy) which develops its flowering stems during the late summer, autumn and winter before flowering in early spring. It is especially floriferous the first year after fire.

Fruiting

The Western Australian Christmas Tree (*Nuytsia*) not only flowers as the weather is coming to its hottest and driest but then continues throughout the summer to develop and ripen its fruit. And this not protected within the foliage or by large bracts or woody follicles, but exposed over the crown of the tree. Obviously, *Nuytsia* has an advantage over most other plants in drawing both nutrients and water from its hosts. The fruit of many woody-fruited Proteaceae are also growing and maturing during summer, *e.g. Hakea, Xylomelum*, as do many capsular-fruited Myrtaceae.

Conclusion

In this paper I have tried to reveal some little-known aspects of our flora and pointed the way to further study. There must be more fascinating dormancy mechanisms to be revealed, reasons to be discovered why some plants flower and fruit at such an inhospitable season, and why others require this kind of dormancy before they will flower properly, or even survive. Over the coming years I hope to see research into our autumn colours in particular, with, perhaps, some spinoffs into the agricultural and horticultural industries. Following are suggestions for research topics in diallagy.

- How extensive is the strategy taxonomically?
- How extensive is the strategy geographically? Can satellite imagery be used to map it?
- What is the internal mechanism? What happens to the anatomy? What is happening to the physiology?
- What are the root systems?
- Is there an association with a sudden increase in toxicity of some species of *Gastrolobium*?
- How long can plants remain in the diallagous state?
- How long do they take to regreen?
- Is there a benefit, if any, besides survival?
- Can this be used in genetic engineering, *e.g.* to transfer drought-tolerance to crop plants?

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Palaeogeography and drainage evolution in the Gibson and Great Victoria Deserts, Western Australia

J S Beard

6 Fraser Road, Applecross, W A 6153
email: jsbeard@global.net.au

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Abstract

Data on the geography of the Gibson and Great Victoria Deserts were provided by vegetation and geological surveys published in the 1960-70's. Palaeodrainage maps were published by two different authors in 1973, but discrepancies between these could not be investigated until more altimetric data became available in the 1980's. Application of elevations to the palaeochannels and the general relief has revealed a number of anomalies attributed to epeirogenic movements thought to have been associated with repeated transgressions and regressions in the adjacent Eucla Basin. The Gibson and Great Victoria Deserts are situated on a Phanerozoic sedimentary basin, the Gunbarrel Basin, which overlies a much older Proterozoic structure, the Officer Basin. The Gunbarrel Basin contains a wide spread of Permian glacigene sediment capped with a lesser thickness of Early Cretaceous material. The adjacent Eucla Basin subsided later in the Cretaceous but the transgressions were not contiguous. Emergence of both basins followed and the Gunbarrel was substantially uplifted to form a plateau, the Gibson Plateau, of up to 400 m elevation sloping to the south. South-flowing drainages were initiated, forming the Keene, Carnegie, Throssel, Yowalga, Baker, Kadgo and Waigen Palaeorivers. In the north-west a single north-flowing drainage, the Disappointment Palaeoriver, was initiated flowing to the lake of that name. During the Eocene the Eucla Basin again subsided. Emergence which followed affected additional uplift of the Gunbarrel Basin by some 150 m, tilting the Gibson Plateau back towards the north. This resulted in the formation of basins of interior drainage in the Carnegie System and headwaters of the Throssell and Kadgo Systems, while other sections were rendered inactive by reduced grades. Decline of rainfall during and after the Eocene has since preserved this situation with all rivers inactive and subject only to siltation and salt-lake spreading. Downwarp of the Eucla Basin in the Miocene, and subsequent uplift which created the present Nullarbor Plain, seems not to have effected any modifications. There are no significant palaeochannels across the Nullarbor due to inactivity of the rivers further inland after the Miocene.

Keywords: Gibson Desert, Great Victoria Desert, palaeogeography, drainage

Introduction

The Gibson and Great Victoria Deserts (Figs 1 & 2) are situated in the remote, desertic eastern interior of Western Australia between latitudes 22° and 30° S. The Gibson Desert was named by the explorer Ernest Giles after his follower Gibson who was lost and perished there during Giles' unsuccessful attempt to cross the desert from east to west in 1873. After making a successful crossing further south in 1875, Giles named that area the Great Victoria Desert in honour of Queen Victoria, apologising for having discovered nothing better than a desert to name after her. Following the activities of the nineteenth century explorers, Forrest in 1874, Giles again in 1876, Lindsay 1891-92, Carnegie 1896-97, there was little further interest in the area for many years and it has remained largely uninhabited. The reason for this is not low rainfall - the average annual precipitation throughout the area is about 200 mm. The Gibson and Great Victoria are considered deserts as they are unsuitable for pastoral use. This is due to the underlying lithology of arenaceous rocks which produce sandy soils deficient in nutrients and a dominant plant cover of spiny grasses ("spinifex") unpalatable to stock. There is also a shortage of surface water and the topography is difficult, with most of the Great Victoria and part of the Gibson being covered with linear sand ridges.

To a large extent the two deserts cover the Officer Basin which originated by subsidence during the Proterozoic and became filled by up to 7 km thickness of sediments. Very little of these early deposits crop out, as the Basin continued to accumulate sediments sporadically during the Phanerozoic. During the Sakmarian stage of the Permian the highland areas were covered by an ice sheet and as the Officer Basin was still low-lying it was spread with glacigene sediments to a maximum known thickness of 450 m (Iasky 1990). These deposits are glacial or fluvio-glacial in origin, laid down in lacustrine and fluvial environments. They cover the whole Basin and form a large part of the outcrop. Later Permian, Triassic and Jurassic sediments are not found, but there is a widespread Early Cretaceous sequence, Valanginian to Aptian sediments up to 100 m thick,

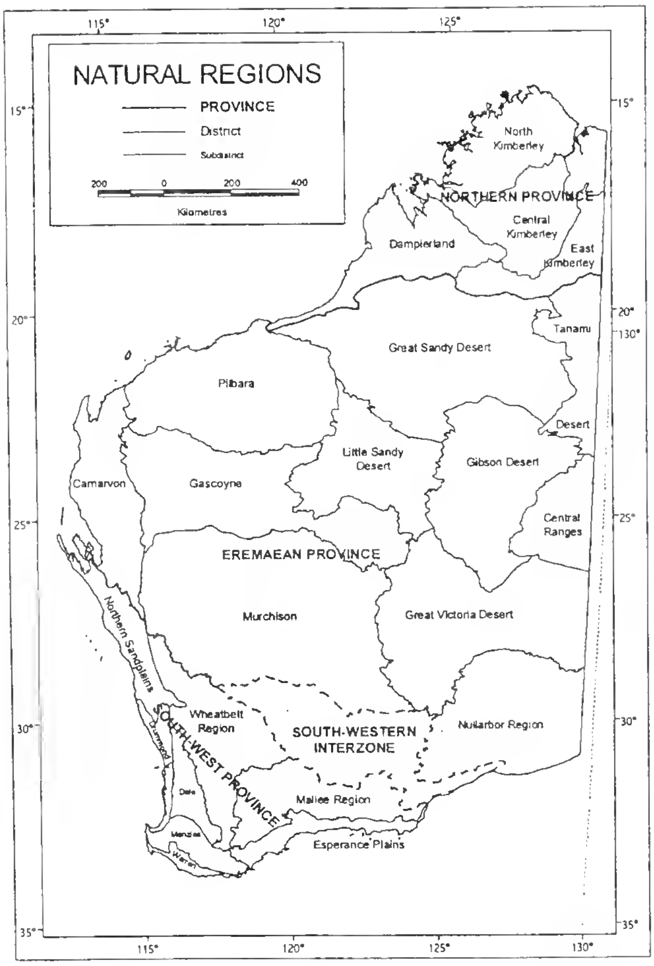


Figure 1. Natural Regions of Western Australia, after Beard & Sprenger (1984).

deposited in shallow sea conditions following a marine transgression. From the Late Cretaceous the Basin seems to have remained above sea level. An Eocene deposit, the Lampe Formation, is found only in channels in the Gibson Desert, and is not more than 5 m thick (Iasky 1990).

The Officer Basin, as a Proterozoic structure, has little bearing on modern topography and drainage. In recent work (Anon 1999) the area is called the "Gunbarrel Basin over Neoproterozoic Officer Basin". Its western boundary is taken as the line of continuous Permian outcrop but surface drainage is received from the Western Shield to the west of this. On the east the Basin is bounded by the outcrop of Proterozoic rocks forming part of the highland area of Central Australia, the Central Ranges region (Fig 1). The southern boundary is the northern limit of the Tertiary sequence in the Eucla Basin. These boundaries are shown in Fig 2A as accepted in 1973 (slightly modified since). On the north a basement ridge, the Warri Ridge, separates the Canning and Officer Basins, trending NW to SE. The approximate position is given by a line from the Warburton Mission to Lake Blanche on Fig 2A. This ridge has no present surface expression and does not coincide with the boundary between the surface drainage systems heading north-west through the Great Sandy Desert and south through the Gibson and Great Victoria.

The present topography of the Gibson Desert consists mainly of a plateau 400 to 550 m in height (the Gibson Plateau, a new name), which features extensive plains dissected at the edges and with occasional hill ranges, buttes and mesas. The plains have a laterite surface, apparently the remnant of a duricrusted soil profile from which surface sand has been removed by deflation and deposited in the valleys forming linear sand ridges. The laterite today is undergoing surface decomposition (Beard 1969). The Great Victoria Desert on the other hand is covered with east-west trending sand ridges occupying the southward slope from the interior plateaux of the Gibson and Warburton areas. The sandy desert ends at the boundary of the Nullarbor Plain at about 250 m above sea level. This boundary is accepted as that of the Eucla Basin. The Central Ranges region consists of two mountainous areas divided by a plain. In the north the Rawlinson group of ranges comprises mainly east-west strike ridges reaching 600 to 1000 m connecting with the Petermann Ranges of Central Australia. In the south the Warburton group consists of strike ridges in the west reaching 550-600 m and in the east of hills reaching 600-800 m. Between the two there is a sandy plain largely free of dunes and without organised drainage, standing at 500-600 m.

Figure 2 Legend

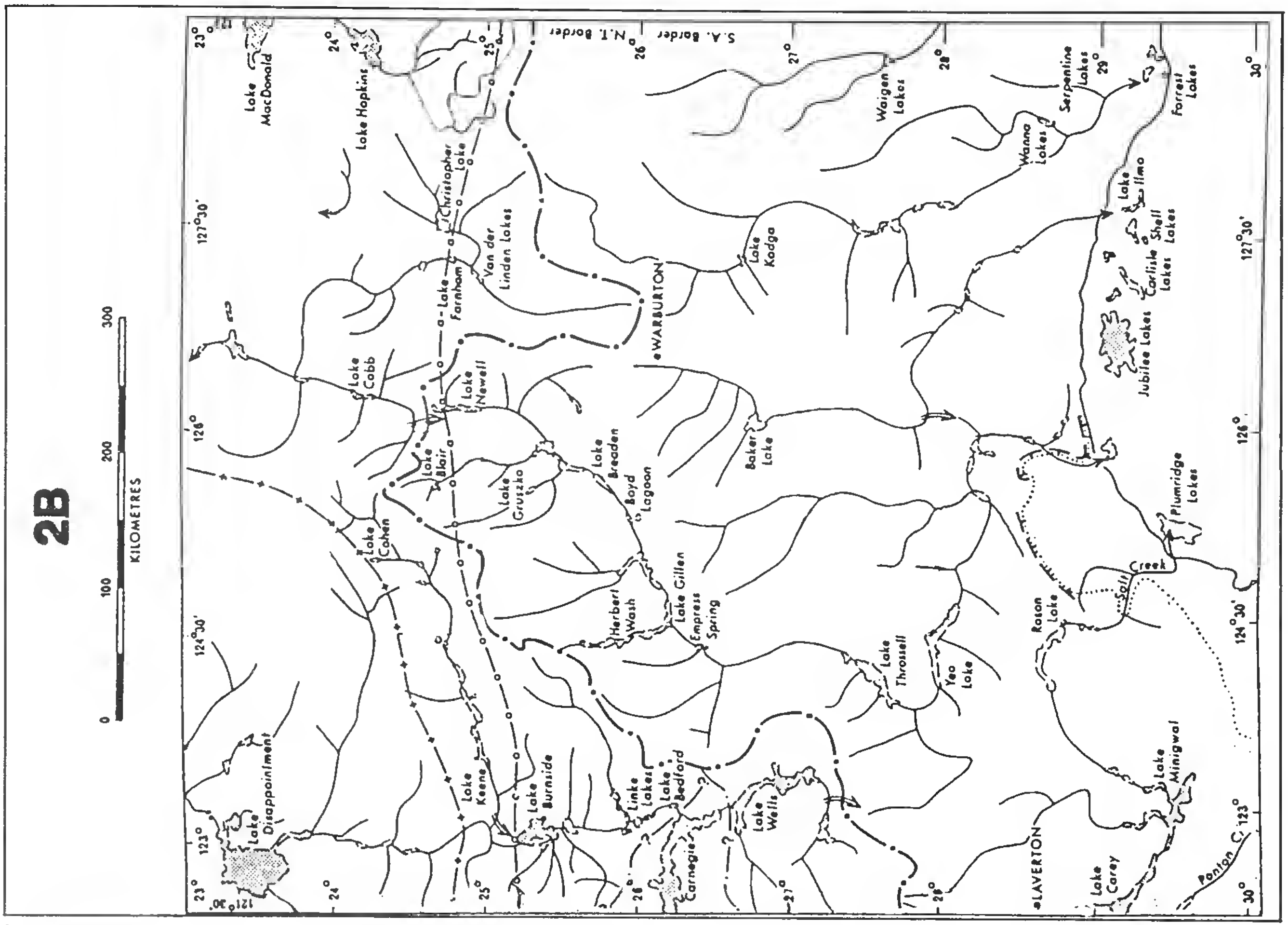
Figure 2A

▨	Boundary of sedimentary basins as accepted In 1973
— · — ·	Principal north-south watershed
—·—·—·	Boundary of Nullarbor Plain

Figure 2B

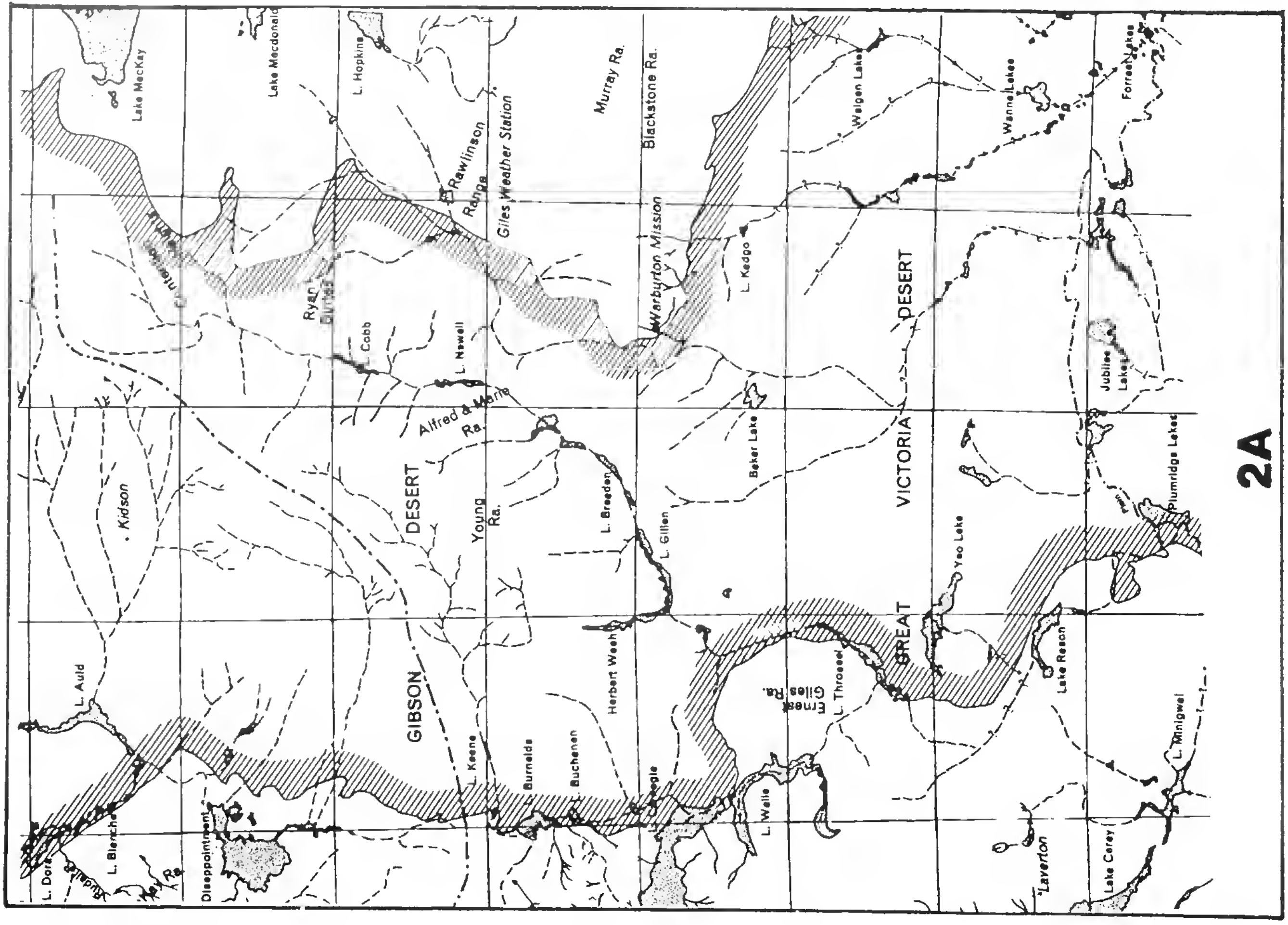
⊂⊃	Salt lake or claypan
——→	Palaeodrainage
– – →	Palaeodrainage Inferred
⇓	Direction of flow before river capture
↓?	Alternative Interpretation of course
....	Approximate position of Late Eocene shoreline
—·—	Main drainage divide
-?—· .	Alternative position of main drainage divide
—o—	Position of main drainage divide after Mulcahy & Bettenay 1972
—+—	Position of main drainage divide after Beard 1973
┬ ┬ ┬	Prominent scarp

Figure 2. Previous treatments of palaeodrainage in the Gibson and Great Victoria Desert area brought to the same scale of 1: 5 000 000. **A**: Part of State map by Beard (1973); **B**: Slightly modified from Bunting *et al.* (1973).



2B

KILOMETRES
0
100
200
300
Lake MacDonald
Lake Hopkins
Lake Christopher
Van der Linden Lakes
Lake Farnham
Lake Cobb
Lake Newell
Lake Blair
Lake Gruszka
Lake Breaden
Boyd Lagoon
Lake Cohen
Herbert Wash
Lake Gillen
Empress Spring
WARBURTON
Lake Kadgo
Baker Lake
Waigen Lakes
Wanna Lakes
Serpentine Lakes
Forrest Lakes
Lake Ilmo
Carlisle Lakes
Shell Lakes
Jubilee Lakes
Plumridge Lakes
Salt Creek
Rason Lake
Lake Throssell
Yeo Lake
Lake Minigwal
Lake Disappointment
Lake Keene
Lake Burnside
Linke Lakes
Lake Bedford
Carnegie
Lake Wells
LAVERTON
Lake Carey
Ponton C.
N.T. Border
S.A. Border
23°
24°
25°
26°
27°
28°
29°
30°
121°30'
123°
124°30'
126°
127°30'



2A

Lake MacKay
Lake Macdonald
L. Hopkins
Rawlinson Range
Giles Weather Station
Murray Ra.
Blackstone Ra.
Ryan Dunes
L. Cobb
L. Newell
Alfred & Marie Ra.
Warburton Mission
L. Kadgo
Waigen Lakes
Wanna Lakes
Forrest Lakes
Kidson
DESERT
Young Ra.
L. Breaden
L. Gillen
Baker Lake
VICTORIA
DESERT
Jubilee Lakes
Plumridge Lakes
L. Auld
GIBSON
Herbert Wash
Ernest Giles Ra.
L. Throssell
GREAT
Yeo Lake
Lake Rason
L. Dora
L. Blanche
Disappointment
L. Keene
Burnside
Buchanan
Carnegie
L. Wells
Laverton
Lake Carey
L. Minigwal

A new era of exploration of these deserts began in the 1950s when geological and geodetic surveys began. The Commonwealth Government constructed a graded road from South Australia to Carnegie Station in Western Australia in 1956-58, and numerous other tracks were opened in the 1960s by government agencies and mining companies. A full coverage of aerial photographs became available from 1953. Publication of topographic and geological maps on a scale of 1:250 000 commenced in the 1960s. At the same time the present writer carried out sporadic field work and began vegetation mapping from aerial photography. Vegetation maps at a scale of 1:1 000 000 were published (Beard 1974, 1975) after some preliminary papers (Beard 1968, 1969, 1970). The 1969 paper drew for the first time actual boundaries for the desert areas derived from vegetation mapping, treating them as natural ecological regions (Fig 1). Since this mapping showed salt lakes, salt flats and other bottom land vegetation it was found that drainage patterns showed clearly although there are no currently active streams and rivers in the area. Streamflow today may be intermittent after exceptional rains or has become inactive, but it was clear that extensive valley systems existed which had been developed in the distant past. A palaeodrainage map of the whole State incorporating these data, scale 1:2 500 000, was published by Beard (1973), and the relevant portion for the Gibson and Great Victoria Deserts is reproduced as Fig 2A. At the same time geologists working in the area were able to use their mapping of alluvial deposits and knowledge of the topography to produce a palaeodrainage map (Bunting *et al.* 1973) which appears here as Fig 2B. These two maps have been reduced at the same scale for contrast in the Figure. Van de Graaff *et al.* (1977) later incorporated the geologists' map in a small scale palaeodrainage treatment for the whole State. The two treatments in Figs 2A and 2B are broadly similar. The principal and central drainage feature is the Throssell Palaeoriver, and to the east of it the Baker Palaeoriver. Both were named as rivers by Beard (1973) and revised to palaeorivers by van de Graaff *et al.* (1977). Further east are the Kadgo and Waigen Palaeorivers (new names). On the west side there is a drainage line running north-south along or close to the boundary of the Gunbarrel Basin and named the Disappointment Palaeoriver by van de Graaff *et al.* (1977). The northern part is directed north to the lake of that name but it was not clear whether the southern part which includes Lakes Carnegie and Wells originally drained north or south. Ground photographs of the landscapes in this area are available in Beard (1990). This paper follows other studies of geomorphology and drainage evolution in Western Australia (Beard 1998, 1999, 2000).

Methods

The purpose of this paper was to resolve, by using more recent data, several major discrepancies between the two previous treatments of the palaeodrainage, which were:

1. Bunting *et al.* (1973) cut off the headwaters of the Throssell Palaeoriver between Lakes Newell and Cobb, attributing this to river capture. Later when it became clear that there was no outlet to the north, van de Graff *et al.* (1977) attributed it to tectonic movement along the Warri Gravity Ridge, forming "the only true internal drainage system in Western Australia". The south-eastern tributaries which they included in this system were shown by Beard (1973) as flowing to the south to the Baker Palaeoriver.
2. Van de Graaff *et al.* (1977) cut off part of the headwaters of the Baker Palaeoriver, shown as deflected into the Throssell Palaeoriver at Lake Breaden.
3. Beard (1973) showed a relatively short unnamed drainage line leading north into Lake Disappointment. Drainages further south beginning with the Keene Palaeoriver and including Lakes Burnside, Buchanan, Carnegie and Wells were shown as heading south and connecting with the Throssell system. Bunting *et al.* (1973) on the other hand incorporated all these into a north-trending Disappointment Palaeoriver, while admitting that there were indications of a former southerly flow which had become diverted.
4. The outlet from Lake Throssell to the south was conjecturally shown by Beard (1973) as connecting with Lake Rason, but treated with more confidence by van de Graaff *et al.* (1977) with a different course passing through Lake Yeo.

Some other problems have called for clarification. Fig 2B shows that all the south-flowing palaeodrainages have substantial deviations to the east before reaching the Eucla Basin. Southward from Lake Wells the palaeochannel trends south for 100 km until suddenly taking a three-quarter turn northwards towards Lake Throssell. From the directions of flow the Throssell Palaeoriver can be inferred to have flowed south along this stretch until making a junction with the Lake Wells outflow at the sharp bend, the combined stream then flowing south and east. Instead, the combined stream is deflected east into Lake Yeo and then another 125 km to the east before turning south to the Eucla Basin. Where this river course parallels the scarp of the Eocene shoreline (Fig 2B) it is at about the same height but there is a ridge some 50 m higher between the two. Further east palaeorivers descending from Lakes Baker, Kadgo and Waigen show less strongly developed easterly deflections. To accord with modern practice, the forms Lake Yeo and Lake Baker are used instead of Yeo Lake and Baker Lake on older maps, *e.g.* Fig 2B.

The early work was hampered by lack of figures for heights. In the 1960-70s there were no contoured maps published, and spot heights were relatively rare. Beard (1968-75) operated without heights, relying on his mapping of the vegetation to show playa lakes, bottom-land vegetation of different kinds, and other indications of the topography. Van de Graaff *et al.* (1977) described the use of a grid of spot heights with a spacing of 11 km which had recently become available from gravity surveys. From these, 25 m form lines were drawn by hand on 1:250 000 scale maps, taking into account topographic and geological information available at the time. It was not possible to make any close check on the discrepancies in interpretation until more reliable altimetric data became available. This began in the 1980s when the Commonwealth began publication of a new series of 1:250 000 topographic maps which were contoured at 50 m intervals and had more abundant spot heights. The grid of Fig 2A represents the national grid used for 1:250 000 topographic, geological and vegetation maps. Issue of the new series of contoured maps was completed for this area between 1984 and 1989. A decade earlier the Geological Survey of Western Australia was working to produce geological maps at the same scale which were issued for this area between 1975 and 1979 and are very valuable in the present context for their mapping of surface deposits. In most cases the memoir accompanying each map includes a 'physiographic diagram' which shows form lines and a classification of physiographic units.

In the present study the contoured series of topographic maps was examined one by one, and relevant data on valley form, watersheds and heights were extracted on a reduction to 1:1 000 000. Each sheet was then compared with its corresponding geological map and the information in its attendant explanatory memoir. To assist interpretation, profiles of the principal palaeochannels were drawn, compared in the case of the Throssell palaeoriver with a profile of the western watershed of the Throssell catchment.

Results

To assist in clarifying the geography, a simplified map is given in Fig 3 showing the palaeorivers and their catchments outlined by the watersheds as ascertained in the present study.

In the course of studying the available data, it soon became clear that the situation was more complex than initially realised. Instead of a simple assessment of the discrepancies between the previous treatments, a thorough reappraisal of the geological history of the area would be required. This is detailed in the following sections, catchment by catchment.

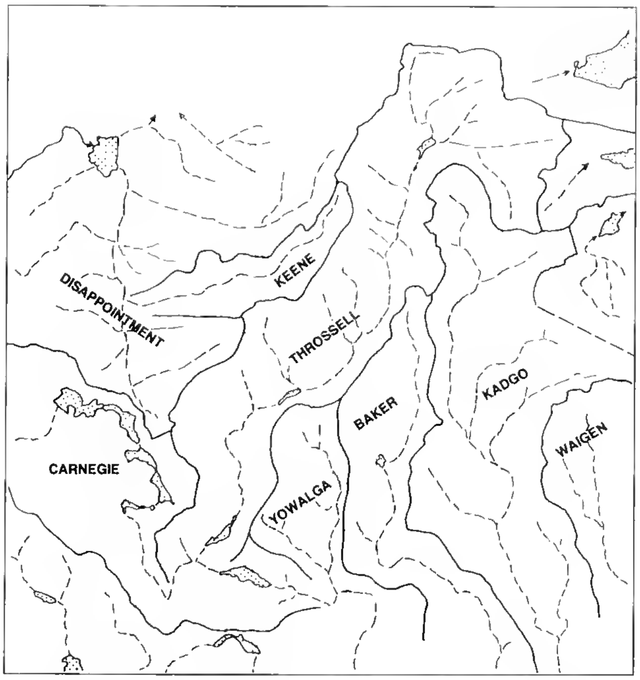


Figure 3. Palaeorivers of the study area (broken lines) with their catchments outlined by the watersheds (continuous lines).

Throssell Palaeoriver

The principal palaeoriver of the area is the Throssell, taking a south and south-westerly course through the Gibson Desert. Over 1000 km long, it is the longest river or palaeoriver in the State. Fig 4A shows a profile from the source of the main branch as far as Lake Yeo, a distance of 900 km. The lowest point on the profile is at a dry lake bed 170 km from the source at a height of 310 m, lower than Lake Yeo at 342 m. The uppermost part of the catchment appears to have subsided into an interior basin, as detected by earlier workers, although the alignments show clearly that it originally formed part of the Throssell system. At first sight on the topographic map the severance of the upper part of the Throssell palaeoriver appears due to an obstruction between Lakes Cobb and Newell associated with the Clutterbuck Hills, an outcrop of hard resistant sandstone of Proterozoic age up to 506 m in height on the east side of the valley. A similar hill is present on the opposite side of the valley but the outcrop is Permian (van de Graaff 1975). These hills cause a constriction and the valley between them is filled with sand dunes forming a col with a contoured height between 400 and 450 m *cf* Lake Cobb 342 m, Lake Newell 381 m. The col is probably due to no more than sand accumulation between the hills, and the profile in Fig 4A shows that this is not responsible for blocking off the upper part of the valley. There has been subsidence in the north or alternatively uplift in the south. South of Lake Newell as far as Lake Throssell the present surface of the palaeochannel is virtually level with heights varying only between 380 and 410 m over a distance of 410 km. The channel is probably substantially silted but depths are not known except for 101 m recorded at Lake Throssell (Bunting *et al.* 1978). South of Lake Throssell the palaeochannel falls 35 m in 80 km to Lake Yeo. It would appear that it is not only the uppermost section of the river course that has been affected by epeirogenic movement, as the course cannot originally have been level for 410 km.

To confirm this, a profile (Fig 4B) was constructed for the watershed which bounds the Throssell valley on the west side. This shows substantially the same outline. For the first 225 km from the north end it remains more or less level, on average 415 m from 12 spot heights, while the river bed deepens alongside. After the river reaches its lowest point the watershed also trends uphill rising from 410 m to 552 m in the Young Range over 140 km. South of this point it maintains a fairly even height again, averaging 518 m from 23 spot heights, as far as the Ernest Giles Range, a distance of 280 km. Here there is a further small increase in height, averaging 543 m from 14 heights over 180 km to reach the Truscott Hills. The watershed ends abruptly at Mt Venn, 500 m. South of this the palaeochannel from Lake Wells takes a sharp turn to the north-east in the direction of Lake Yeo. The watershed is continuous over a length of 920 km, mostly across gently undulating laterite plains with occasional hills, buttes and mesas. Apart from these it is often difficult to distinguish on the ground but can be positioned from mapping. This watershed is an effective indicator of the modern topography of the Gibson Desert and also of past epeirogenic movements. It is at its highest in the south, dropping in the north accompanying the basin formation of the upper Throssell palaeoriver. Van de Graaff *et al.*

(1977) attributed the latter to tectonic movement associated with the Warri Gravity Ridge, a subterranean feature formed in the Proterozoic, but since it is clear that wider movements have to be considered, it seems more probable that these were related to movements in the Eucla Basin.

Disappointment Palaeoriver

The channel running north into Lake Disappointment was so named by van de Graaff *et al.* (1977) who connected Lakes Carnegie and Wells to its upper reaches. Beard's (1973) map had shown this drainage, south of the confluence with the Keene Palaeoriver which comes in from the north-east, as flowing originally to the south and finding an outlet to Lake Throssell. Van de Graaff *et al.* (1977) agreed with this as the original alignment but considered that the system north of Lake Wells had been reversed to the north at a later stage. It is suggested here that this drainage line was originally formed after the end of the Early Cretaceous transgression by rivers which continued to discharge eastward off the Western Shield and were ponded at the break of slope at the former shore line. It is probable that flow took place partly to the north and partly to the south.

Examination of the latest maps shows a valley floored here and there by salt lakes and pans extending south from Lake Disappointment. Fig 2 shows this alignment, and a profile has been drawn in Fig 5A. The Lake itself stands at 325-330 m elevation. From it the valley trends fairly steeply uphill to the 400 m contour in 100 km (0.75 m km^{-1}) and then at a lower grade to Lake Burnside at 425 m in another 90 km (0.28 m km^{-1}). South of Lake Burnside the alignment continues uphill to Lake Bedford at 443 m and beyond to a source on high ground at about 480 m. There is no question therefore that this section represents the Disappointment Palaeoriver and that the tributary Keene River now belongs to it as it comes in north of Lake Burnside at about 395 m. Mapping however shows that there is not and has never been any outflow to Lake Disappointment from Lake Carnegie. This enormous salt lake, 120 km long and the largest in Western Australia, 441-444 m above sea level, is aligned slightly south of east turning to south-east at the eastern end. Between the latter portion and Lake Bedford there is a range of low hills of Precambrian rocks (Jackson 1978) about 470 m high with high points at Red Hill 474 m and Pt Katherine 513 m. There are gaps but none suggesting a connecting channel between Lake Bedford and Lake

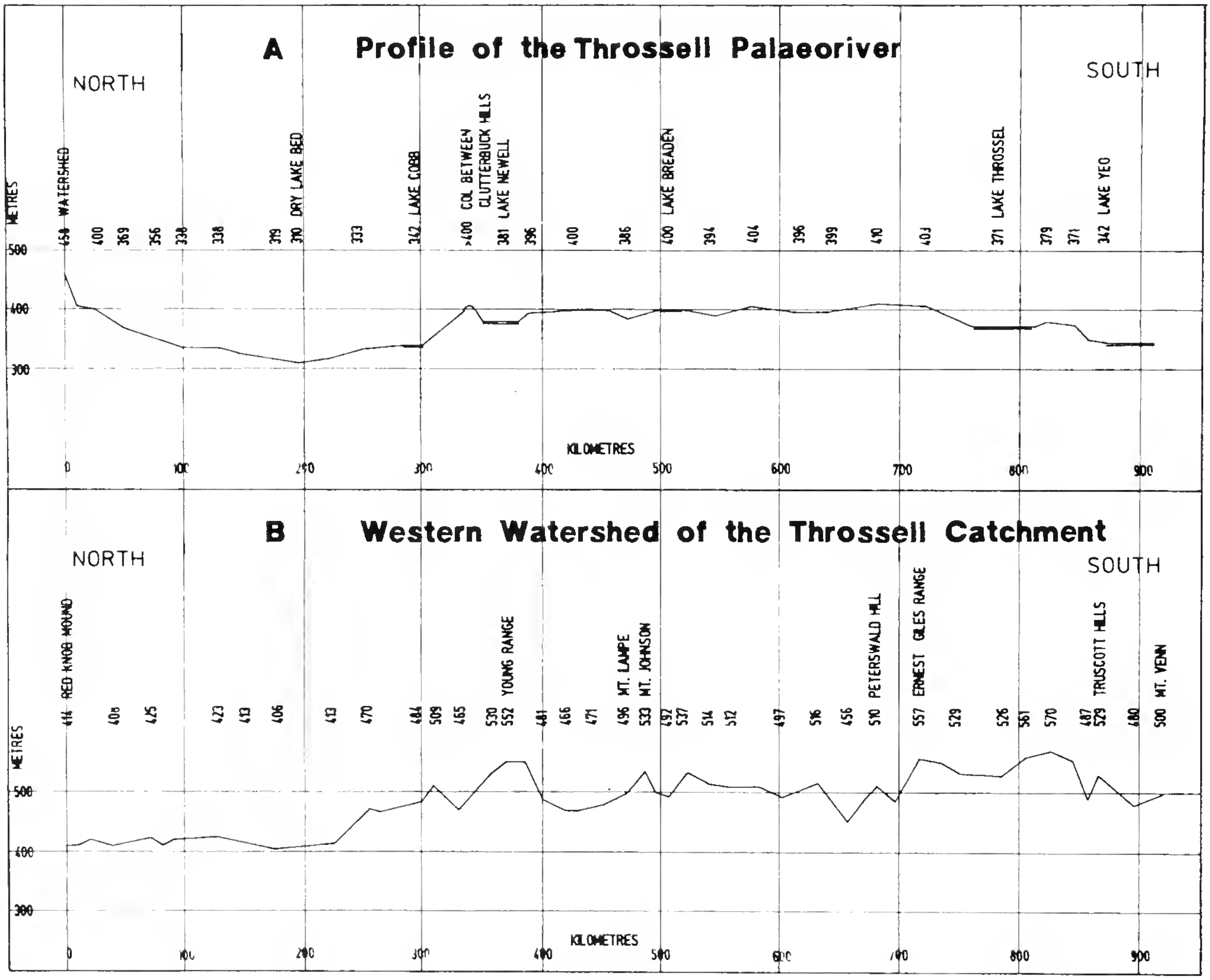


Figure 4. Throssell Palaeoriver. A: Profile of the palaeochannel; B. Profile of the western watershed of the Throssell catchment .

Carnegie, although the two are at much the same elevation. Further west, Lake Carnegie is cut off on the north by the Timperley Range and associated hills. It is much more likely that Lake Carnegie was connected to Lake Wells (441 m) on the south. There is an isthmus 5 km wide between the two due to another Precambrian ridge, but there are two gaps only 2 m higher than the lakes. Lake Wells trends southward for 80 km. The contoured map shows that there is no outlet further southward to Lake Throssell as suggested by Beard (1973) since a main watershed is interposed with heights exceeding 526 m. Instead, the alignment of Lake Wells swings to the west through an unnamed lake 35 km long and slightly higher, 451 m. At the western end of this lake there is again a well-marked drainage channel to the south, initially with greater spot heights of 464, 459 and 455 m. It takes 70 km to return to the same height as Lake Wells. The alignments however show that Lakes Carnegie and Wells must originally have flowed south this way and been affected by the same epeirogenic movements as the Throssell catchment, resulting in a similar profile to the Throssell (Fig 4B).

The drop at the north end of the palaeoriver into Lake Disappointment is more pronounced than that in the headwaters of the Throssell Palaeoriver, so much so as to suggest a downwarp at the site of the lake, although the descent may only represent the northern end of the Gibson Plateau. Lake Disappointment has been shown by previous authors with an outlet to the Percival Palaeoriver in the Canning Basin, connecting at Lake Winifred south of Lake Auld, which has spot heights of 261-263 m. This is about 65 m lower than Lake Disappointment but there is no obvious palaeochannel between the two. A line of lakes and pans leads to the east from the north-east corner of Lake Disappointment but without any indication of an outlet to the north to Lake Winifred. There are anomalies in the course of the Savory Creek before it joins Lake Disappointment at its north-west corner and it is possible that there has been diversion of drainage originally through the Rudall River by uplift of the hills. This however is beyond the scope of the present paper and should await a similar study of the Canning Basin.

Carnegie Palaeoriver

The Carnegie-Wells system (Fig 5B) is separate and may be named the Carnegie Palaeoriver. In its northern section, as with the middle course of the Throssell (Fig 4A) the alignment is level on the surface at the present

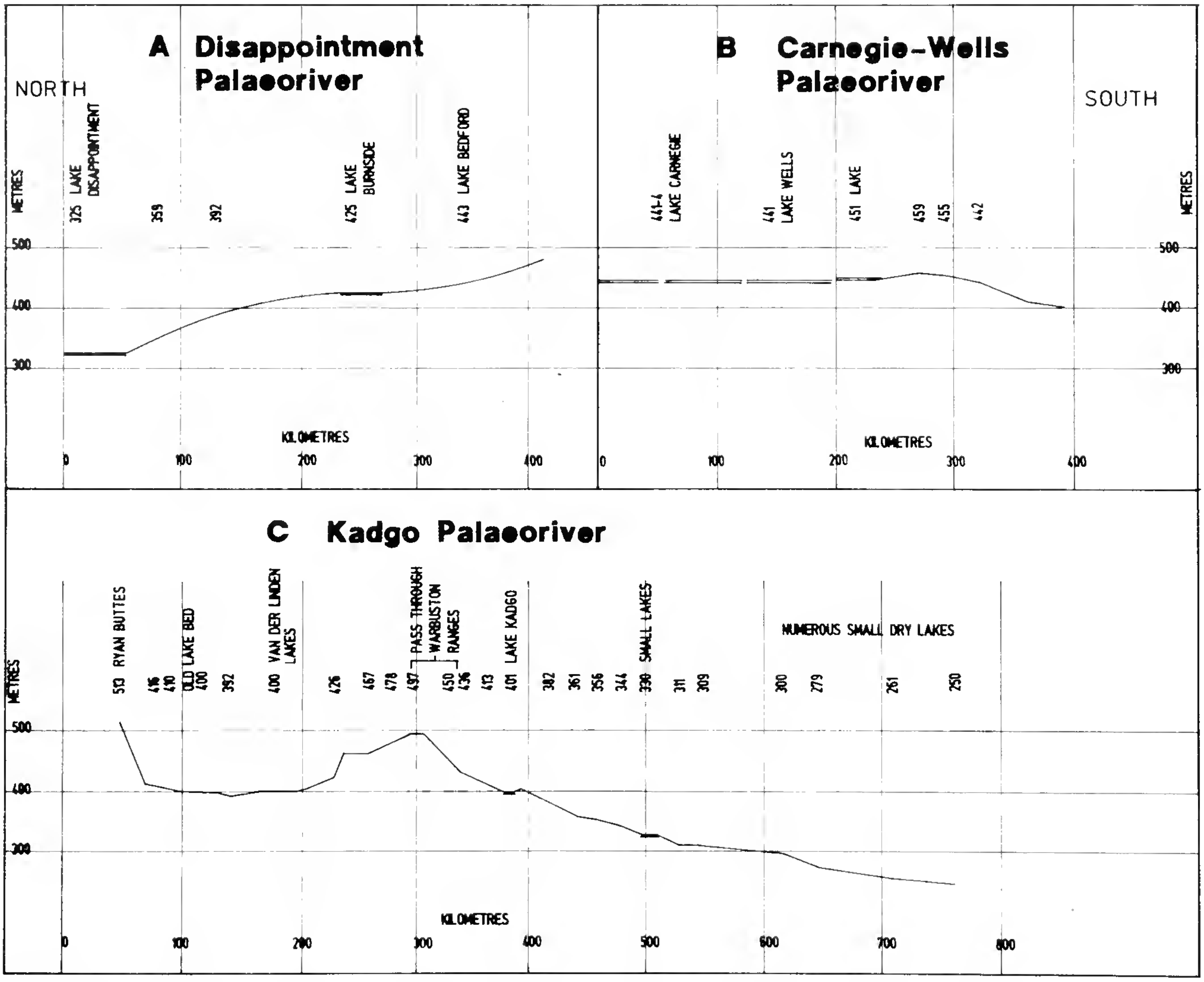


Figure 5. A: Profile of the Disappointment Palaeoriver; **B**: Profile of the Carnegie-Wells Palaeoriver; **C**: Profile of the Kadgo Palaeoriver.

day but there is a rise at the southern end in keeping with the watershed shown in Fig 4B. It is evident that the same epeirogenic uplifts have affected this palaeoriver equally and extended to the adjoining slope of the Western Shield. In particular while drainage was initiated following the first uplift forming the first rivers, these were ponded by the second uplift which had caused an obstruction at the south, and the lakes accumulated sediment and spread widely. North-west of Lake Carnegie there is a curious feature also related to this, a very large area of flat swampy ground at a height of 470 to 500 m and measuring 60 km south-west to north-east. It is a huge flat similar to Lake Carnegie but not so salted as to become a playa. The Oolgahroo Creek enters this from the north-west. No creeks can be distinguished on the flat, but it is drained by numerous creeks from its southern edge into Lake Carnegie. At the eastern end at Lake Augusta (456 m) flow starts to the east and becomes the Lalaline Creek, further down called the Coomborn Creek, leading into Lake Burnside and therefore part of the Disappointment Palaeoriver. However this cannot be construed as joining Lake Carnegie to the Disappointment system, rather the opposite. It appears to be a case of river capture and reversal. The alignment of the Keene Palaeoriver is to the south and south-west, taking a sharp turn to the north on joining the Disappointment Palaeoriver. The relatively steep slope of the latter north of this point suggests the likelihood of some river capture and it is suggested that the Keene did flow initially to the south and via Lakes Burnside and Augusta into the Carnegie-Wells system.

Kadgo Palaeoriver

The Kadgo Palaeoriver was shown by all previous authors as rising in the highlands of the Warburton area (Fig 2A,B) and finding its way southward via the Wanna Lakes to the Forrest lakes at the edge of the Nullarbor Plain. However the present study shows (Fig 5C) that it originally rose very much further north at the Ryan Buttes and came down through Lake Farnham and the van der Linden Lakes. Bunting *et al.* (1973) and van de Graaff *et al.* (1977) showed this northern section as reversed to the north by the same apparent downwarp affecting the upper Throssell palaeoriver and connecting with the latter some way north of Lake Cobb (Fig 2B) while Beard (1973) showed southerly flow as far as the van der Linden Lakes, escaping to the west from there to become the headwaters of the Baker palaeoriver. Map contours now show that both these solutions were incorrect. Actually the system rises in the Ryan Buttes (maximum altitude 480 m) and flows south to a spot height at 410 m, passes through a dry lake flat at 394 m, then a long distance level at about 410 m, an unnamed playa lake at 392 m, Lake Farnham <400 m and into the van der Linden Lakes at 400 m. Most of this stretch is level like the Throssell palaeoriver.

There is an east branch centred on Lake Christopher, about 400 m, which joins to the van der Linden Lakes. Drainage into it is derived from north and south of the Rawlinson Range. In addition a valley much obscured by sand ridges extends 50 km to the north to the foot of the Gillespie Hills and to the north-east for about 75 km between the Crocker and Carnegie Ranges. A valley leading south-east from Lake Anec terminates at a col of 450 m at 20 km from the lake. There is no possibility of a former connection between Lake Christopher and Lake Anec leading through to Lake MacDonald.

The south branch is a well-marked valley running south from the van der Linden Lakes to the Warburton Ranges. However, the present heights along this valley increase steadily towards the south from 411 to 497 m. At first sight therefore drainage cannot have escaped by this route and the van der Linden system must be another basin of interior drainage. It has been shown above, however, that the Gibson Plateau and the Carnegie-Wells Palaeoriver were both uplifted in the south, in the latter case disrupting drainage, and this movement may be assumed to have affected the adjoining Shield rocks to the east. As the above valley approaches the Warburton Ranges it begins to slope to the south. An active creek, the Lilian Creek, appears and passes through the Warburton Ranges at Snake Well between Miller Hill 570 m and Cassidy Hill 557 m in a gap 5 km wide. It passes 12 km further down, heading now south-east at Beal Outstation, through the Townsend Ridges in a gorge fronted on the north by the Lennard Bastion and on the south by a hill of 614 m. It cuts through these ridges at their highest point. The Lilian Creek here is clearly an antecedent stream and has functioned since the remote past. The creek soon dies out in the sandy desert but a palaeochannel is traceable for 50 km to Lake Kadgo (401 m) and beyond. In a further 50 km it falls to 360 m. In this 100 km stretch the grade is 1.4 m km^{-1}. After this the channel slopes at a lower grade, falling 60 m in 100 km. This is followed by a level stretch for 60 km perhaps representing the slight uplift further west which obstructs access to the south. Beyond this it again falls at 0.6 m km^{-1} to reach the Nullarbor Plain. The steeper slope south of the Townsend Ridges is in accord with a concept of uplift of the Warburton area, and the internal system further north becomes the headwaters of the palaeoriver to the south. A profile of the above alignment of the Kadgo Palaeoriver is given in Fig 5C, but it should be noted that it has also two palaeo-tributaries to the east which drained the plateau country between the Rawlinson and Warburton groups of ranges.

Yowalga, Baker and Waigen Palaeorivers

These southward flowing palaeodrainages have the same characteristics as the lower portion of the Kadgo Palaeoriver and call for no special description.

The Eucla Basin

The Eucla Basin subsided three times to receive accumulations of sediment, in the Early Cretaceous, Middle Eocene and Miocene, with intermediate uplifts (Hocking 1990). These are shown diagrammatically in relation to the Gunbarrel Basin in Fig 6. This figure shows a north-south profile of the two Basins at longitude 126° at six different stages;

A. Early Cretaceous transgression (Neocomian).

B. Cretaceous emergence (post-Cenomanian).

C. Middle Eocene transgression.

D. Post-Eocene emergence.

E. Miocene transgression.

F. Present day.

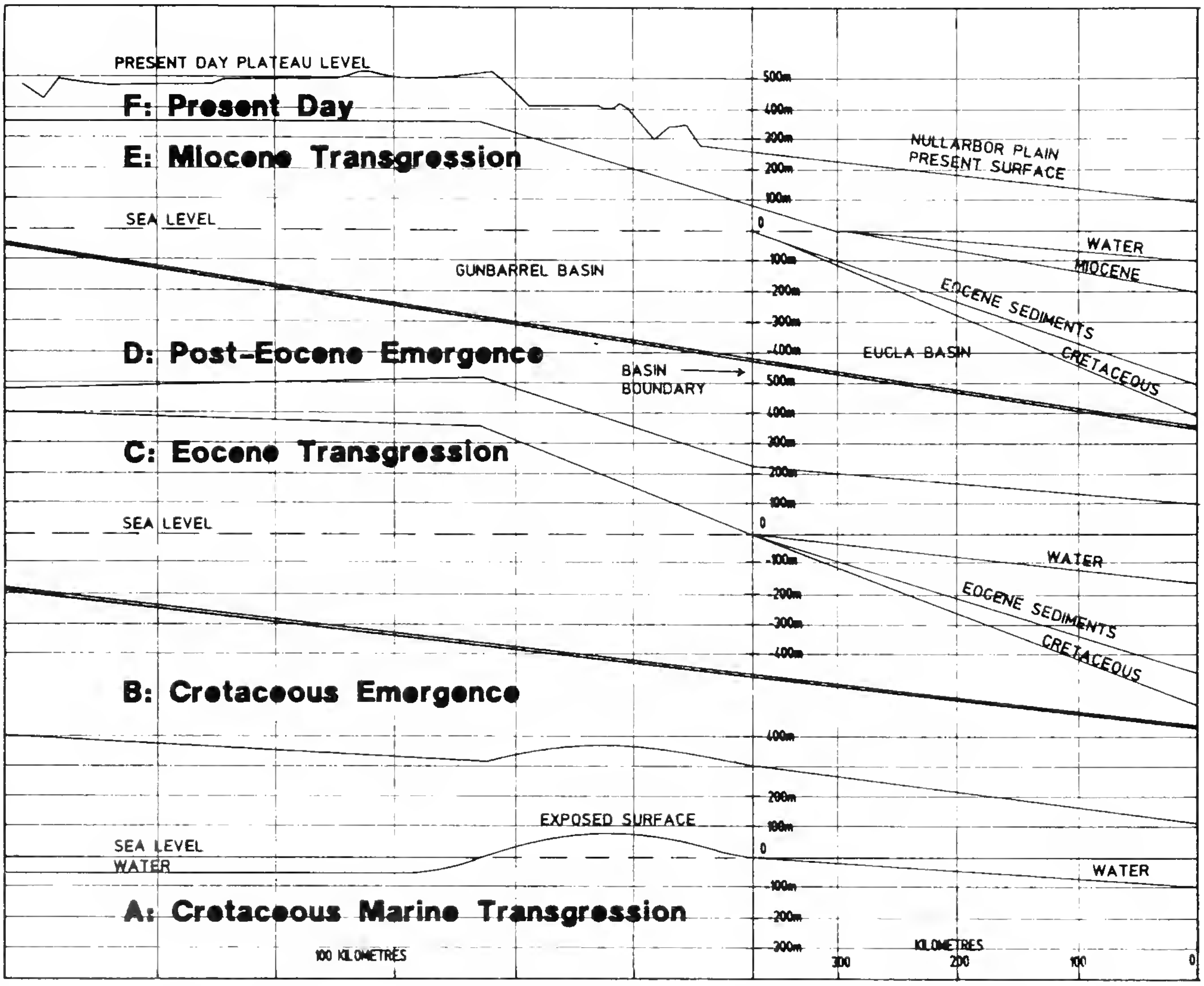
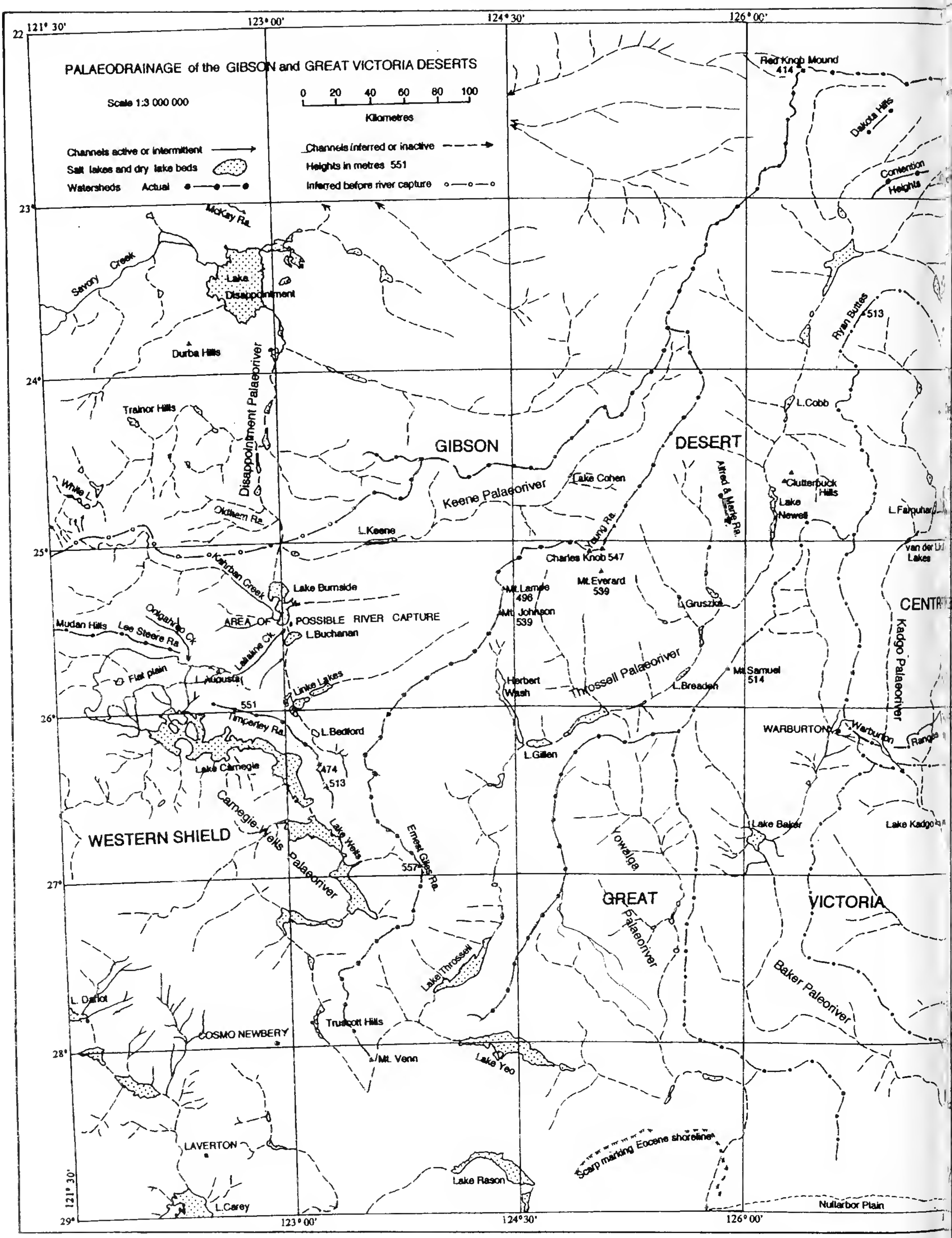


Figure 6. North-south profile of the Gunbarrel and Eucla Basins at different stages. A: Early Cretaceous Transgression; B: Cretaceous Emergence; C: Middle Eocene transgression; D: Post-Eocene Emergence; E: Miocene Transgression; F: Present Day.

Fig 6F, the Present Day, terminates the cycle with an actual measured profile along the watershed marking the eastern side of the Throssell Palaeoriver catchment from the Ryan Buttes at 23° 30′ S, 126° 30′ E for 550 km to 28°, thence in a straight line due south for 100 km to the edge of the Nullarbor Plain and on to the edge of the Great Australian Bight. The profiles of the other stages conform to this same line. The northernmost section of the profile stands at 530 m at its highest point and shows a slight fall from there to the north.

The tectonic movements involving transgression and regression are interpreted in terms of the Eucla Basin as a virtually unfaulted, southward-dipping sheet of sediment (Hocking 1990). No block-faulting was involved and we must assume gentle up and down warping of the Basin and its surrounding country. Attempts have been made to correlate high sea levels globally during the Cretaceous (*e.g.* Haq *et al.* 1988) but Western Australian examples show that tectonism must also be considered. In the Perth Basin on the western side of the Western Shield, a marine transgression took place in the Neocomian synchronously with the Canning and Gunbarrel Basins, until a regression in the Aptian. The Eucla Basin however only experienced a transgression later from the Barremian to the Cenomanian while along the south coast of Western Australia there is no evidence for Cretaceous transgression. In the Perth Basin the Aptian regression was brief and transgression returned until the Maastrichtian, but this did not apply elsewhere. The Eucla Basin together with the south coast of Western Australia experienced transgression in the Middle Eocene.

Effective history begins with the glaciation of the Early Permian when the Gunbarrel Basin was low-lying between areas of basement rocks on either side. Ice caps formed on these from which detritus was distributed generally over the surface of the Basin (Iasky 1990). During the Valanginian stage of the Early Cretaceous a widespread marine transgression covered the Canning and Gunbarrel basins with general deposition of sediments. At first, the seaway extended only from the Indian Ocean. The Eucla Basin began to subside later during the Barremian. The latest geological map of the State (Myers & Hocking 1998) shows Cretaceous sediments of this age extending generally as far south as 26° S (about equal to a line from Lake Carnegie to the


PALAEODRAINAGE of the GIBSON and GREAT VICTORIA DESERTS
Scale 1:3 000 000
0 20 40 60 80 100
Kilometres
Channels active or intermittent
Channels inferred or inactive
Salt lakes and dry lake beds
Heights in metres 551
Watersheds Actual
Inferred before river capture
121° 30'
123° 00'
124° 30'
126° 00'
22
23°
24°
25°
26°
27°
28°
29°
121° 30'
Red Knob Mound
414
Dakota Hills
Contention Heights
McKay Ra.
Savory Creek
Lake Disappointment
Ryan Buttes
513
Durba Hills
Disappointment Palaeoriver
L.Cobb
Trainor Hills
GIBSON
DESERT
Alfred & Marie Ra.
Clutterbuck Hills
Lake Newell
L.Farquhar
White L.
Lake Cohen
Keene Palaeoriver
Oldham Ra.
L.Keene
Young Ra.
van der Linden Lakes
Charles Knob 547
Mt.Everard 539
Kahrban Creek
Lake Burnside
Mt.Lamble 496
Mt. Johnson 539
L.Gruszka
CENTR
Kadgo Palaeoriver
Mudan Hills
Lee Steere Ra.
Onigahrdo Ck
AREA OF POSSIBLE RIVER CAPTURE
L.Buchanan
Lakaline Ck.
Flat plain
L.Augusta
Linke Lakes
Herbert Wash
Throssell Palaeoriver
L.Breaden
Mt.Samuel 514
551
Timperley Ra.
L.Bedford
WARBURTON
Warburton Ranges
L.Gillen
Lake Carnegie
474
513
Carnegie-Wells Palaeoriver
Lake Wells
Ernest Giles Ra.
557
Yowalga
Lake Baker
Lake Kadgo
WESTERN SHIELD
GREAT
Palaeoriver
VICTORIA
Lake Throssell
Baker Palaeoriver
L. Darlot
Truscott Hills
COSMO NEWBERY
Mt. Venn
Lake Yeo
LAVERTON
Scarp marking Eocene shoreline
Lake Rason
L.Carey
Nullarbor Plain
123° 00'
124°30'
126° 00'

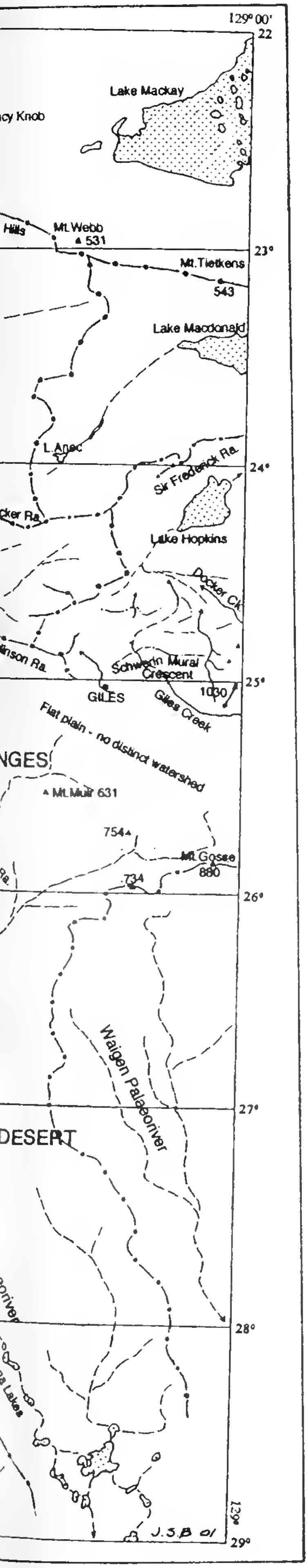


Figure 7. Corrected palaeodrainage map incorporating the results of this paper.

Warburton Range) with a tongue extending to 27° 30′ S. The rest of the western Gunbarrel Basin is shown with the outcrop as Permian.

Fig 6A shows a marine transgression covering both the Basins except for an emergent ridge between the two. After the Cenomanian, uplift of both Basins took place, a suggested movement of about 400 m, forming a plateau level in the Gibson Desert area, the Gibson Plateau, while the Eucla took on a slope to the south. The dividing ridge between the two remained. Formation of drainage and incision of rivers began. Those draining the Gunbarrel were obstructed by the dividing ridge and deflected to the east, probably due to a greater uplift on the west associated with an upward tilt of the adjacent Western Shield. The basic uplift of 400 m affected the whole region, the eastern margin of the Western Shield being raised by this amount. Beard (1998) showed that the Central Watershed of the Shield originates in the south at a height of 400 m, rising slightly northward. The Gunbarrel Basin must have experienced a similar tilt up to the north as initial drainage of the plateau was principally south. Drainage and erosion must have affected the Eucla Basin also but the landscape has been covered by later deposits. The Eucla Basin is shown in Fig 6 as not uniformly uplifted but taking on a slope to the south (Hocking 1990). In the Cretaceous, Australia and Antarctica had not separated fully. The basin deepened southwards and sediments thickened in that direction (Hocking 1990).

The next significant event was sinking of the Eucla basin during and after the Palaeocene, steepening the slope of the tributary rivers and causing renewed erosion so that an initial sequence of clastic sediments was deposited such as the Hampton Sandstone. As the tectonic movement stabilised, the deposits changed to limestone. "In the Eocene the Eucla Basin was a broad, arcuate, northward shallowing ramp, the margins of which approximated the present day basin margins" (Hocking 1990). The geological survey of the map Neale (van de Graaff & Bunting 1975) shows a feature interpreted as a modified wave-cut marine scarp at a present altitude of about 325 m which appears to represent the maximum extent of the Eocene transgression (Fig 6C). The Eucla Basin must have sunk as a whole, without block faulting, either uniformly or by tilting down to the north. In Fig 6B the Gibson Plateau is shown sloping slightly to the south with the original obstructing ridge in place. Both Cretaceous surface and basement take on a steeper slope because of the uplift. The former shoreline is assumed to be raised 325 m. With the Eocene transgression (Fig 6C) this returns to sea level but there is not a subsidence of the whole Gunbarrel Basin which remains uplifted and takes on a steeper slope to the south. The top of the slope on these diagrams agrees with the highest point in the modern profile (Fig 6F).

The next stage is the Post-Eocene emergence (Fig 6C). It is assumed that the Gibson Plateau did not sink again with the Eocene transgression. However, we also have to account for a further uplift of the southern part of the plateau by about 150 m as demonstrated in Figs 4A and 4B. It is suggested that this occurred with the Post-Eocene emergence and that the Eucla Basin rose by some 250 m to its present height. The surface of the Eocene deposits in the Basin is then shown sloping down to 100 m above sea level. The Post-Eocene emergence evidently involved a substantial uplift, shared with the whole southern coast of the State. The limited deposit of the Eocene Lampe Formation on the Gibson Plateau can be associated with disturbance caused by this uplift.

In the Miocene transgression (Fig 6E) the Eucla Basin did not subside as deeply as before and Miocene deposits are only 100 m thick. Following the transgression, the Basin rose to its present level (Fig 6F). As noted above, the profile in this figure is the actual one of the present day. It is possible that the additional uplift of the southern Gibson Plateau took place at this time instead of earlier, or alternatively that it rose at the end of the Eocene, subsided again wholly or partly and rose again after the Miocene.

It has been shown above that it is necessary to interpret the tectonic movements in the Eucla Basin as extending to the Gunbarrel Basin behind it. The uplift causing regression in the mid to late Cretaceous must also have uplifted the Gibson Plateau and the country on either side of it on the Western Shield and Central Ranges Region, and caused initiation of the palaeodrainage at that time. The second regression at the end of the Eocene further uplifted the inland country, essentially creating the modern topography as we see it. These events correlate with major movements elsewhere in Western Australia. Uplift of the whole Western Shield by 200-400 m appears to have taken place in the later Cretaceous (Beard 1998, 1999). Transgression occurred along the south coast during the Eocene (Middleton 1991) but not on the west coast. Late or Post-Eocene uplift was expressed in the formation of a marginal swell along the west coast with uplift of the continental margin by 150-200 m in a belt 80 km wide (Beard 1999, 2000).

Conclusions

Conclusions reached above are summarised as follows:

1. The two previous treatments of palaeodrainage in Figs 2A and 2B are in general agreement, with minor discrepancies.
2. Application of altimetric data recently available shows cases where palaeochannels are level over long distances or even have reverse slopes, indicating that tectonic movements have disturbed the original courses.
3. The palaeogeography of the area needs to be interpreted in terms of such movements in the Eucla Basin where marine transgressions implying downwarp occurred in the Early Cretaceous, Middle Eocene and Miocene, to be followed by uplift and regression (Fig 6).
4. The Gunbarrel Basin was invaded by the sea from the north in the Early Cretaceous from the Valanginian to the Cenomanian as far as 27° 30′ S (modern latitude). A transgression from the south affected the Eucla Basin slightly later from the Barremian. The two transgressions did not meet but were separated by an east-west ridge between 28° and 29°.
5. Uplift later took place. Initial development of the palaeodrainage patterns visible today must have taken place during the remainder of the Cretaceous since evidence elsewhere indicates that rainfall was high at that time whereas it declined markedly during the Tertiary. Considerable uplift of the Gibson Plateau is therefore postulated, perhaps as high as 400 m and with a slope to the south.
6. South-trending drainages were obstructed from direct access to the Eucla Basin by the east-west ridge referred to in paragraph 4 above, and were diverted to the east.
7. Silt carried by these drainages was transported to the south across the on-shore Eucla Basin.
8. The downwarp effecting the Eocene transgression may not have lowered the Gibson Plateau as a whole, merely steepened the south slope.
9. Following this transgression the Eocene uplift did affect the Gibson Plateau, mainly in the south, with an additional uplift of about 150 m, raising the plateau and its summits to heights similar of those of today. Decline of rainfall in the Tertiary reduced modification of the landscape.
10. This uplift disrupted the previous drainages but decline of run off meant that new outlets were not found. The Carnegie system was cut off in the south and formed into a basin of interior drainage, likewise the headwaters of the Kadgo and Throssell systems.
11. As the channels became inactive, siltation and salt-lake spreading became general.
12. No further modifications have been directly attributed to the Miocene transgression and subsequent uplift.

A corrected paleodrainage map for the area incorporating the above conclusions appears as Fig 7, compiled from topographic and geological maps. Principal palaeochannels are shown by broken lines and watersheds are indicated outlining the catchments. Hardly any of the palaeochannels carry drainage at the present day and most of them are choked with sand ridges. Active and intermittent channels are shown by continuous lines, chiefly in the northwest where the Savory Creek is the only active river on the map. Numerous small watercourses can be distinguished in aerial photography rising in the hills and ranges and quickly lost on the plain. These are mostly too small to appear in Fig 7. It is only in the more mountainous country of the Central Ranges Region that some longer watercourses of this nature can be distinguished, leading into Lake Hopkins which drains to the east into the Northern Territory. Otherwise palaeochannels have to be inferred from contours, from salt lakes, sand-free dry lake beds and calcrete deposits. These channels are in fact quite well marked although they have been extinct for most of the Tertiary, essentially since the Eocene with temporary renewals during pluvial periods.

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Low temperature and low moisture storage of seed of the endemic Australian genus *Eremophila* R Br (Myoporaceae)

A Cochrane[1], K Brown[2] & A Kelly[3]

[1]Department of Conservation and Land Management, Locked Bag 104, Bentley Delivery Centre WA 6983
[2]Environmental Weeds Action Network, 108 Adelaide Terrace, East Perth WA 6000
[3]24 Carnarvon Street, Victoria Park East WA 6101

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Abstract

Many species of the Australian endemic genus *Eremophila* (Myoporaceae) have the potential for minesite rehabilitation, revegetation and horticulture due to their demonstrated tolerance of fire, drought, salinity, frost and grazing. Fresh seed is not always available and so the ability to store seed, off site and under optimal conditions, without loss of viability, is an important land management option. Long term seed storage is an important *ex situ* conservation strategy for rare and threatened species. This study investigated the ability of *Eremophila* seed to survive desiccation to 5 ± 1% moisture content and storage at low temperature (–20 °C) for one year. Seed set in 14 species ranged from 1 to 91% and germination in 12 species ranged from 29 to 87% for fresh seed and 50 to 100% after storage for one year. Germination was lower in five collections after storage, although in three cases another cohort of the same species exhibited greater percent germination after storage. *Eremophila* seed has the potential for storage without loss of viability. Existing seed viability equations provide a framework for extrapolation of these short-term results to the long term that should offer predictions compatible with results after 125 years of storage.

Keywords: seed storage, *Eremophila*, low temperature, low moisture

Introduction

Eremophila are hardy perennial, prostrate to tall shrubs or small trees occurring throughout the arid- and semi-arid zones of mainland Australia. Their main centre of diversity is the Austin phytogeographic region of Western Australia (Beard 1980). They are an extremely versatile group of plants growing in a variety of soils including deep sands and gravelly clay loams, in both neutral and alkaline soils (Richmond 1993). *Eremophila* species are highly adapted to effective germination and growth under harsh conditions and in nutritionally impoverished soils if environmental conditions are favourable (Richmond 1993). Tolerance of these species to inhospitable environments such as dry, nutrient poor and saline sites (Elliott & Jones 1984) suggest that many species should be incorporated into minesite rehabilitation and rangeland revegetation programs (Richmond 1993). A number of species are highly ornamental, displaying large colourful flowers over an extended period of time, and have an outstanding potential for cultivation (Bond 1982; Richmond & Ghisalberti 1994a). *Eremophila* fruits are indehiscent and drupe-like, sometimes fleshy, with 2 to 4 locules per fruit (Chinnock 1981). One to three seeds may form per locule. Fruits may remain on plants for several months after ripening until dispersal by natural means or by animal or bird movement. In many species of *Eremophila* the woody endocarp structure of the fruit provides a physical (Richmond 1993) and possibly chemical (Warnes 1982; Richmond & Ghisalberti 1994b) barrier to germination. Plants are generally propagated vegetatively as germination from seed is unreliable (Elliot & Jones 1984; Richmond & Ghisalberti 1994b).

A number of studies have investigated various aspects of the taxonomy, biology, ecology and demography of the genus (*e.g.* Beard 1968; Barlow 1971; Smith 1975; Chinnock 1982; Richmond & Ghisalberti 1994a, 1996) and propagation of plants from seed (Richmond 1993; Richmond & Osborne 1993; Richmond & Chinnock 1994; Richmond & Ghisalberti 1994b). Natural regeneration of plants occurs after disturbance or heavy rains (Richmond & Ghisalberti 1996). No studies have been made on the storage potential of *Eremophila* seed, although Richmond & Ghisalberti (1994b) conducted research into the viability of *Eremophila* seed of different ages. There is some evidence to suggest loss of *Eremophila* seed viability with age (Elliott & Jones 1984; Richmond 1993).

It is widely accepted that viability of seed of many species may be lengthened under low temperature and low moisture conditions (Roberts 1973; Ellis *et al.* 1985; Dickie *et al.* 1990). International standards for long term storage of orthodox seed for genetic conservation recommend storage at moisture contents of 5 ± 1% (4% for oily seeds, 6% for starchy seeds), in hermetic containers at –18 °C or lower (Cromarty *et al.* 1990). Under these conditions, seed should remain viable for many hundreds of years.

Although species in the genus *Eremophila* have not previously been tested for response to low temperature and low moisture storage, a range of other Western Australian species have responded well to storage under

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these conditions (Cochrane & Kelly 1996). The potential importance of members of the genus for rangeland revegetation, minesite rehabilitation and horticulture may rest on the ability of seed of those species remaining viable for long periods of time between collection and use in planting.

This study tests the hypothesis that seed of *Eremophila* species endemic to Western Australia are capable of desiccation and low temperature storage (–20 °C) without significant loss of viability. To test this hypothesis, an assessment of seed set and germinability was made for each species.

Methods

Fresh mature indehiscent fruits of 14 species of *Eremophila* were collected from 20 natural populations throughout south-western Western Australia between 1994 and 1999.

Seed Set

Seed set, defined in this study as the proportion of locules in a fruit containing at least one healthy seed, was determined by cutting woody fruits with a sharp scalpel under a dissecting microscope to establish the number of locules that contained whole seed. Fruit may be parthenocarpic and lacking evidence of seed initiation, or seed within fruits may be aborted, insect predated or dead (Richmond 1993). Fully developed seed are healthy, plump, firm and white.

Seed Germination and Storage

To overcome both the physical restraint and inhibitory nature of the fruit wall, and thus ensure successful germination, all seeds were excised from fruits prior to the establishment of germination trials. Extracted whole seeds were germinated on a 0.75% (w/v) agar solution in 90 mm glass Petri dishes in temperature and light controlled incubation cabinets, using a 12-hour photoperiod, at a constant 15 °C. The growth hormone gibberellic acid was added, as GA_3, to the agar solution at a concentration of 25 mg L^{-1} to assist with dormancy breaking. Previous trials on this genus have established that the addition of GA_3 offered higher percentage germination than seed germinated without treatment (A Cochrane, unpublished data).

Germination trials were undertaken on fresh seeds and on seeds after moisture content reduction and storage at –20 °C for a period of one year. All fruits were prepared for initial germination trials and storage within two months of collection. Seeds were stored within the woody fruits and whole fruits were dried for up to 8 weeks in a dehumidifying room at 15 °C and 15% relative humidity until moisture contents had reduced to 5 ± 1%. Seed moisture content was determined by the low constant temperature oven dry method (ISTA 1996). Fruits were hermetically sealed in laminated foil bags and frozen at –20 °C for storage.

After one year in storage a sample of fruits were unfrozen, allowed to re-hydrate for 24 hours to prevent imbibition damage, seed extracted and germination tests conducted. Pre- and post-storage germination treatments were identical. Petri dishes were checked twice weekly and germination was determined by radicle emergence.

Statistical Analysis

Cumulative germination percentages have been calculated on the basis of total seed numbers. Germination time has been expressed as the time in days from sowing to first germination and last germination. Arcsine transformed percentage values were analysed by one-way analysis of variance and Fisher's least significant differences. The probability level chosen for significant difference was $P < 0.05$. One-way analyses of variance were conducted on time to first and last germination.

Results

Seed Set

There was considerable spatial and temporal disparity in seed set in the genus, with demonstrated variation between species and between populations of the same species (Table 1). Reproductive success ranged from a low of 1% in one collection of *E. caerulea* subsp *merrallii* to

Table 1

Number of locules per fruit and mean seed set (percent of fruit with at least one locule containing seed) for 14 species of rare and threatened *Eremophila* from south-western Western Australia (n = number of fruit sectioned).

Species	Locules per fruit	% seed set Mean ± SE (range)	n	Collections tested
E. caerulea subsp *merrallii*	4	15 ± 5.8 (1-29)	154	4
E. chamaephila	3	37	65	1
E. lactea	2	48 ± 6.8 (33-65)	75	4
E. denticulata subsp *denticulata*	5+	80.5 ± 10.5 (70-91)	32	2
E. microtheca	4	53	100	1
E. nivea	4	57 ± 6.5 (32-75)	304	6
E. pinnatifida	2	27 ± 5.2 (14-41)	603	6
E. resinosa	4	31.5 ± 4.7 (24-45)	956	4
E. rostrata	4	32	110	1
E. scaberula	3	44 ± 15.6 (26-75)	300	3
E. subteretifolia	2	52.5 ± 22.5 (30-75)	30	2
E. veneta	4	60 ± 15.3 (30-80)	60	3
E. verticillata	2	18.75 ± 1.2 (17-22)	660	4
E. viscida	4	45.25 ± 9.2 (25-75)	80	4

Table 2

Percent germination for fresh and one year old stored seed for 12 species of *Eremophila* from 18 natural populations from south-western Western Australia.

Species	Population	Fresh Seed Germination (%)	Stored Seed Germination (%)
E. caerulea subsp *merrallii*	1	75	67
E. caerulea subsp *merrallii*	2	50	61
E. chamaephila	1	57	94
E. denticulata subsp *denticulata*	1	50	71
E. lactea	1	70	86
E. microtheca	1	73	76
E. nivea	1	67	50
E. nivea	2	80	100
E. nivea	3	63	83
E. pinnatifida	1	29	50
E. resinosa	1	77	67
E. scaberula	1	70	60
E. scaberula	2	39	67
E. scaberula	3	48	61
E. subteretifolia	1	83	62
E. veneta	1	38	60
E. veneta	2	38	100
E. viscida	1	87	90

91% in a collection of *E. denticulata* subsp *denticulata*. In many cases individual fruits contained no seed.

Seed Germination and Storage

The initial germination test results on fresh seed were variable, ranging from 29 to 87% (Table 2). Subsequent tests on stored seed showed less variability and ranged from 50 to 100%. The mean percent germination for fresh seed and for one year old stored seed was 61 ± 4% and 73 ± 3.7%.

Five collections (*E. caerulea* ssp *merrallii*, *E. nivea*, *E. resinosa*, *E. scaberula* and *E. subteretifolia*) failed to achieve the same or greater percent germination after storage. Three of these collections (*E. caerulea* ssp *merrallii*, *E. nivea* and *E. scaberula*) were represented by at least one other cohort of the same species from a different population that exhibited greater percent germination after storage indicating variation in germinability within the species. There was a significance difference between percent germination for fresh seed and for stored seed (df=1, $F = 4.45$, $P < 0.05$). The rate of germination differed between fresh and stored seeds (Table 3). There was a significant difference between overall time to first germination (10 ± 0.5 days for fresh seed *vs* 13 ± 1 days for stored seed) (df = 1, $F = 7.19$, $P < 0.01$) and last germination (24 ± 4 days for fresh seed *vs* 32 ± 4 days for stored seed) (df = 1, $F = 2.26$, $P < 0.01$).

Discussion

Bell *et al.* (1993) considered that low seed set in the genus *Eremophila* may be attributed to the ability of many species to resprout from protected buds after fire. All species investigated in this study are thought to regenerate from soil-stored seed reserve after fire yet fruits rarely contained the full complement of seed, with many empty. Resource limitations, in particular in populations that are located in fragmented landscapes, may contribute to this low reproductive success. Habitat fragmentation has the ability to change patterns of plant reproduction by affecting pollinators and predators, and the availability of potential mates, resources and microclimate. Cunningham (2000) attributed differences in fruit and seed production between different populations of *Eremophila glabra* to changes in important reproductive functions due to habitat fragment shape and size. In rare species that are restricted to small populations, the effects of inbreeding depression may impact on the reproductive success of outcrossing plants. The considerable inter- and intra-specific variation in seed set demonstrated in this study suggests the need for further investigation into both resource and genetic constraints in the genus *Eremophila*.

Despite low seed set for the species investigated in this study, germination was higher than previously noted for many species in *Eremophila*. The primary factor for poor germination from fruits of *Eremophila* is due to seed abortion (Richmond 1993) and the incubation of only healthy extracted seed in this study, rather than whole fruits, has no doubt led to these higher results.

These data suggest that seed of *Eremophila* have the ability to remain viable after drying and storage at sub-zero temperatures for periods of up to one year without a compromise in viability over the short term. The effects of moisture and temperature during storage are critical to the maintenance of seed viability. Extrapolation of results is required if data from short-term research is to provide advice on *ex situ* conservation of the species for the long term. A seed viability equation that provides a framework for extrapolation of these short term results to the long term should offer predictions compatible with results after 125 years of storage (Ellis & Roberts 1980).

Kullman (1981) reported the average time to germination of 28 species of *Eremophila* was 32.5 days under natural conditions, but did not provide seed age or quantities germinated or explain natural conditions. This present study has demonstrated a faster rate of

Table 3.

Germination times in days for fresh and one year old stored seed of 12 species of *Eremophila* from 18 natural populations from south-western Western Australia.

Species	Population	Fresh Seed		Stored Seed	
		Time to first germination	Time to last germination	Time to first germination	Time to last germination
E. caerulea subsp *merrallii*	BR	10	20	24	24
E. caerulea subsp *merrallii*	HR	12	54	14	39
E. chamaephila	GP	14	44	14	17
E. denticulata subsp *denticulata*	PR	8	8	9	24
E. lactea	GPW	12	12	11	39
E. microtheca	LI	11	15	9	45
E. nivea	BR	7	12	24	35
E. nivea	DR	7	21	8	11
E. nivea	KS	7	12	7	32
E. pinnatifida	D	11	19	14	74
E. resinosa	WR	10	74	14	35
E. scaberula	M20	9	16	9	48
E. scaberula	M5	10	17	14	21
E. scaberula	M9	8	18	14	38
E. subteretifolia	BL	9	33	14	28
E. veneta	HNR1	10	10	10	14
E. veneta	HNR2	10	14	10	14
E. viscida	ER	9	33	13	43

germination for a range of species under laboratory conditions than that reported by Richmond & Ghisalberti (1994b) for excised seed. This may be attributed to the additions of the growth hormone gibberellic acid, (as GA_3), which can promote germination in a range of species from Western Australia (Bell *et al.* 1993). The speed of germination in the field may be of importance for survival and successful establishment of plants. Whilst this research has demonstrated a slower rate of germination of seed post-storage, viability of that seed was not compromised. It is possible that the rate of germination of seed of these arid and semi-arid zone plants is inhibited by low temperature storage. Further investigations may be required to establish whether the success of field germination of stored seed is affected by low temperature and low moisture storage conditions.

For many species there will be years when seed set fails, and other years when seed yields are above average. Improving the potential for storage of seed means that collections of material can be made several years prior to their requirement in rehabilitation or revegetation programs, maximising the benefit of heavy yields that are usually a response to favourable environmental conditions. With so many species having tolerance to fire, drought, frost, grazing and salinity, the demand for seed material is unlikely to abate with future increases predicted.

Seed storage by conventional means (low moisture and low temperature) offers a cheap and effective method of preserving a broad range of genetic material for short term rehabilitation and revegetation needs, and goes a long way to meeting the long term challenge of *ex situ* conservation of endangered flora in Western Australia. In addition to the requirements for minesite rehabilitation for widespread species, there are some 71 rare, threatened and poorly known species of *Eremophila* endemic to Western Australia that will benefit from the advances made in the identification of appropriate storage conditions for maximising long term viability in the genus.

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Same day plantation establishment of the root hemiparasite sandalwood (*Santalum spicatum* (R Br) A DC: Santalaceae) and hosts

G S Woodall & C J Robinson

Department of Agriculture, 444 Albany Highway, Albany WA 6330
email: gwoodall@agric.wa.gov.au

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Abstract

Interest and investment in a plantation sandalwood (*Santalum spicatum* (R Br) A DC) industry in southern Western Australia has been steadily growing over the last few years. Current plantation establishment involves planting host seedlings in year one and then direct sowing of untreated seeds of the parasitic sandalwood in year two or three. An innovative establishment technique in which host seedlings of *Acacia acuminata* Benth and partially germinated sandalwood seeds are planted on the same day was compared to the current establishment methods. The study showed that sandalwood and host establishment in one season is achievable and that it was three times more successful than the most widely used and promoted technique at present. Results also indicated that water availability influenced the germination, summer survival and growth of sandalwood. The use of small seedling hosts on well-watered, cleared land results in a higher rate of sandalwood establishment and growth.

Keywords: sandalwood, *Santalum spicatum*, establishment, host, hemiparasite.

Introduction

The heartwood of the hemiparasitic Western Australian sandalwood (*Santalum spicatum*) contains valuable fragrant oils. The sale of 1 814 tonnes of *Santalum spicatum* in the 1999-2000 financial year generated a revenue of $11 642 000 for the State of Western Australia (Anon 2000). Most wood is sourced from natural populations in the Goldfields, and some is salvaged from dead remnants in the Midwest. Sandalwood was once extensively harvested from the medium rainfall "wheatbelt" areas of the State, but this resource has been exhausted due to over exploitation and clearing for agriculture.

There has been growing interest from the farming community and other investors in the development of a plantation *Santalum spicatum* industry in the wheatbelt. Extensive trials have shown that *Santalum* species show improved growth and vigour when cultivated with leguminous hosts (Radomiljac & McComb 1998; Brand *et al.* 2000; Loveys *et al.* 2001). Current recommendations for *Santalum spicatum* plantation establishment (Brand & Jones 2001) involves the planting of host seedlings (usually *Acacia acuminata* as the sole host species) during winter of the first year. In the second or third year, four untreated sandalwood seeds are sown around each *Acacia* host tree during April or May. While this method can be successful in years with favorable conditions, it requires 3300 (up to 15 kg) sandalwood seeds per hectare and there is a lag phase of up to several years between host and sandalwood establishment, which requires two separate operations. The high seeding rate is required because field germination is generally low, less than 20%, even when seed viability is consistently high at 80-90% (Loneragan 1990).

Although the establishment of sandalwood and hosts in one season may have previously been considered desirable, it was not thought practical as host seedlings are generally planted in July and August whereas the optimum time to sow sandalwood seeds has been shown to be during April and May (Loneragan 1990; Brand & Jones 2001). Also, the field survival of pot-raised sandalwood seedlings (either alone or with a pot host) has not been successful when planted in unirrigated low rainfall (< 600 mm) areas (Loneragan 1990). Loneragan (1990) reported that only 2% of sandalwood seedlings pot grown with *Acacia acuminata* then planted in the field survived their first summer. The aim of this research was to determine whether hosts and sandalwood could be established in the same year and at the same time.

Methods

Site descriptions

Sandalwood germination and survival was monitored at three sites. Sites 1 and 2 were 50 m apart and located 10 km south-west of Borden, Western Australia. Site 3 was located 29 km south of Borden. The soil at sites 1 and 2 was duplex with grey sandy topsoil, 0.3-0.8 m deep, underlain with clay. Site 3 was a red deep loamy duplex, with clay at 0.8 m. Prior to 2000 site 1 had been used for grain production (cereals, lupins and canola). Site 2 was in remnant vegetation that had been partially cleared (> 20 years ago) and had been grazed until 1997. Recruitment of *Acacia acuminata* and *Allocasuarina huegeliana* (Miq) LAS Johnson had occurred at this site after the removal of stock. Site 3 was also used for grain production until 1998, when rows of *Acacia acuminata* were direct seeded (4 m apart) and the site fenced to exclude stock.

Sandalwood establishment

Remnant trees growing within a 20 km radius of Wagin, Western Australia provided the 120 sandalwood seeds that were sown at site 1. Seeds sown at the other two sites were collected from remnant trees growing within a 20 km radius of Borden. The epicarp was removed from all seeds prior to treatment. Glasshouse testing showed that Borden and Wagin seed had similar viability (95%). Seedling emergence of untreated Borden and Wagin seed, sown at other sites in 2000, were not significantly different (data not shown).

All seeds sown at site 1 were cracked using a wetting and drying procedure where seeds were moistened for 6 hours then placed on activated desiccant (silica gel) for 6 hours. This procedure was repeated three times. Cracked seeds were vacuum infiltrated (see Loveys & Jusaitis 1994) with a gibberellic acid solution (500 mM GA_3: Sigma Chemical Co, USA). The solution also contained two fungicides, Fungarid™ and copper oxychloride, used at concentrations recommended by the manufacturers. Seeds were sown (late June 2000) in trays containing a mixture of coarse sand, perlite and peat (2:1:0.5). Trays were watered sparingly and after twenty days when the cracked endocarp had opened 2-3 mm (see Fig 1D,E), they were removed and sown at site 1. Given ideal conditions, the radicle emerged 5-10 days later through the cracked endocarp from the swollen bud (Fig 1E). Site 1 was scalped, ripped and mounded (rows 4 m apart) and sown with a host seed mix (predominantly *Acacia* species at 500 g ha^{-1}) in a one pass operation using a Chatfields tree planter. Immediately, a small *A. acuminata* (< 150 mm tall) seedling was planted by hand on the mounds every 5 m together with a partially germinated sandalwood seed. The top of the seedling roots and the sandalwood seed were both planted 5 cm below the soil surface, and as close to each other as practically possible.

At site 2, untreated seeds (1000) were sown in May 2000 at a depth of 5 cm in rip lines adjacent to regenerating hosts in the remnant bush. At site 3, untreated seeds (120) were sown at a depth of 5 cm during May 2000, as recommended by Brand & Jones (2001).

Emergence, summer survival and growth

Emerged sandalwood seedlings were counted at each site in October 2000. In April 2001, sandalwood seedlings that had survived summer were counted. At site 1, girth measurement at the soil surface was used to assess host and sandalwood growth in May 2001, approximately 10 months after planting the partially germinated sandalwood seeds and *Acacia acuminata* seedlings. Sandalwood girth was also measured at 150 mm above the soil surface, as this is the industry standard (Loneragan 1990).

Plant water status

To determine level of moisture stress at site 1, a pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, USA) was used to measure midday water status of small branches of *Acacia acuminata* and *Santalum spicatum* in May 2001 (prior to any significant autumn rainfall) as described by Turner (1998).

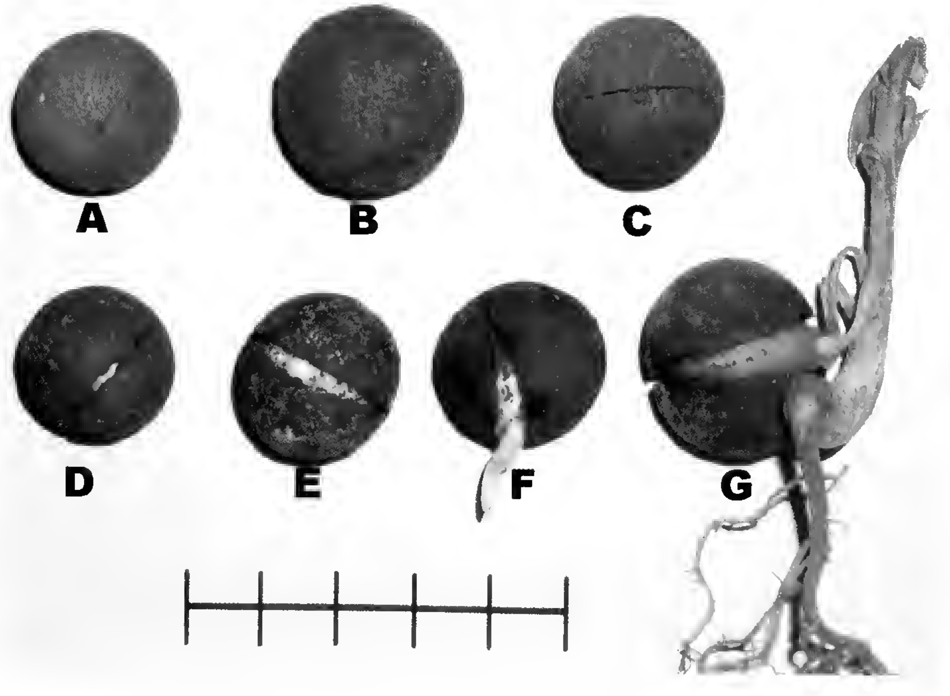

Figure 1. Sandalwood germination sequence. **A**: Dry seed with fine crack at seed apex. **B**: Moistened seed, note fine crack is no longer visible. **C**: Opening of crack after sowing. **D**: Swollen kernel visible as endocarp crack widens. **E**: Kernel between the crack is swollen and raised forming a bud from which, the radicle emerges 5-10 days later given ideal conditions. **F**: Germinated seed with emerged radicle. **G**: Seedling with developing shoot and root system. Seeds similar to those shown in **D** and **E**, were sown at site 1. Scale bar increments are 10 mm, 50 mm total. Note that the time taken to reach each developmental stage varies according to the growing conditions.

Statistical analyses

Genstat™ 5 release 4.1 program (Rothamsted, UK) was used for all statistical analyses.

Rainfall data

Rainfall data for Borden were obtained from the Western Australian Bureau of Meteorology, Perth.

Results

Rainfall

Rainfall at Borden for the year 2000 was 86 mm below the long term average of 381 mm. Rainfall received during the crop growing season (April-October) was 113 mm below the long term average. Drought conditions persisted during the summer and autumn of 2000-2001 (Fig 2).

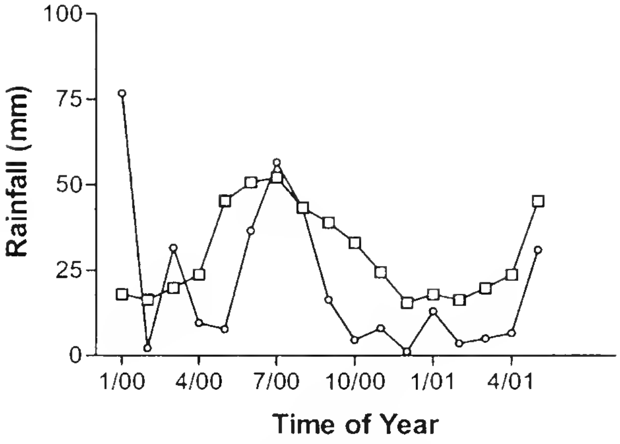

Figure 2. Total monthly rainfall at Borden during 2000-2001 (o) compared to long term averages (□).

Emergence and summer survival

Seventy per cent of all partially germinated sandalwood seeds sown at site 1 produced a seedling that emerged from the soil surface (Fig 3A). This percentage emergence was approximately three times higher than that observed for untreated seeds at the other sites (Fig 3A). At numerous other locations, in the southern Western Australia, field emergence of untreated seeds was generally less than 25% (J Brand, Department of Conservation and Land Management, personal communication). At site 1, 90 % of seedlings survived their first summer (Fig 3B), thus over 60 % percent of the partially germinated seeds produced a seedling that was alive at the end of the summer period (Fig 3C). Similar summer survival was observed at the other sites, consequently only 15-20 % of seeds sown produced a seedling that was alive at the end of the summer period (Fig 3C). These results show that establishing sandalwood and hosts in a "same day" operation is achievable and is more successful, under the dry conditions experienced during 2000-2001, than the technique currently used to establish sandalwood (*ie.* hosts established one to several years prior to sandalwood establishment *e.g.* Site 3).

Growth and water relations

Sandalwood growth at site 1 (10 months after sown in the field) was related to the growth of the *Acacia acuminata* host (adjusted $r^2 = 0.62$; $P < 0.001$; Fig 4A). The biomass of host and sandalwood at this time appeared similar (Fig 5). Sandalwood growth during the first year in remnant vegetation (site 2) was significantly less (sandalwood mean diameter at the soil surface of 2.5 mm, least significant difference (LSD) 1.7 mm) than that measured at the other sites, 7.8 (site 1) and 7.1 mm (site 3). Mean diameter at 150 mm above the soil surface (industry standard) at sites 1 and 3 was 5.2 and 4.2 mm respectively. Most sandalwood seedlings at site 2 were less than 150 mm tall.

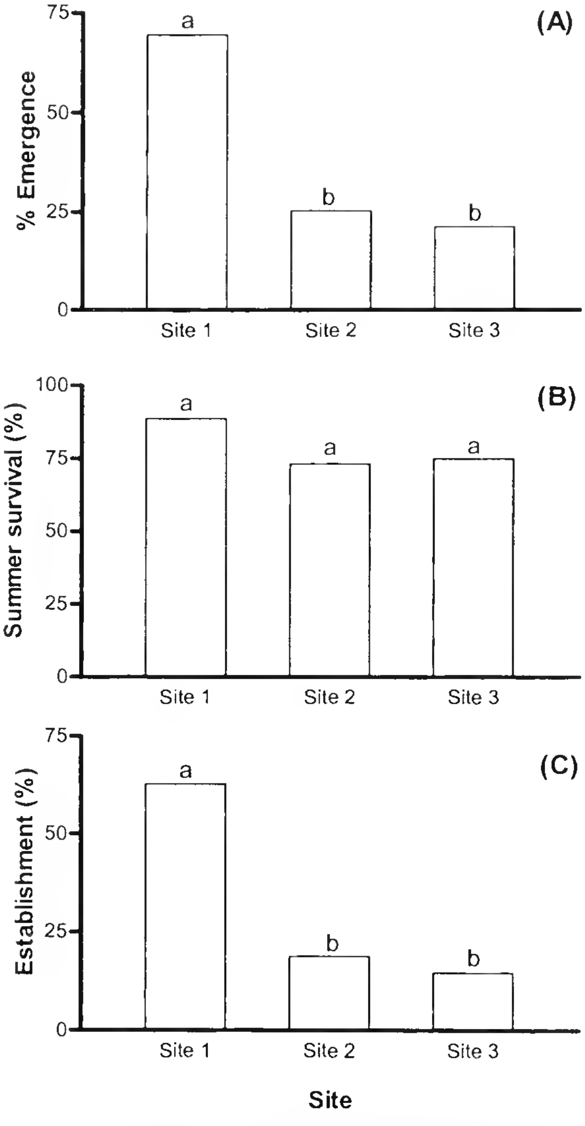

Figure 3. A: Percentage of sandalwood seeds that produced an emergent seedling at the three sites. B: Summer survival of sandalwood seedlings at the three sites (%). C: Percentage establishment at the three sites (ie. percentage of sandalwood seeds that produced an emergent seedling which survived over summer). Within each graph, bars with different letters are significantly different at the 0.05 level of significance (least significant difference determined from a generalised analysis of variance).

The relationship between growth and water status was investigated in May 2001 at site 1. Plant water status influenced the growth of both the sandalwood and the host at this site. Water status accounted for 52 % and 42 % of the observed variation in host and sandalwood growth

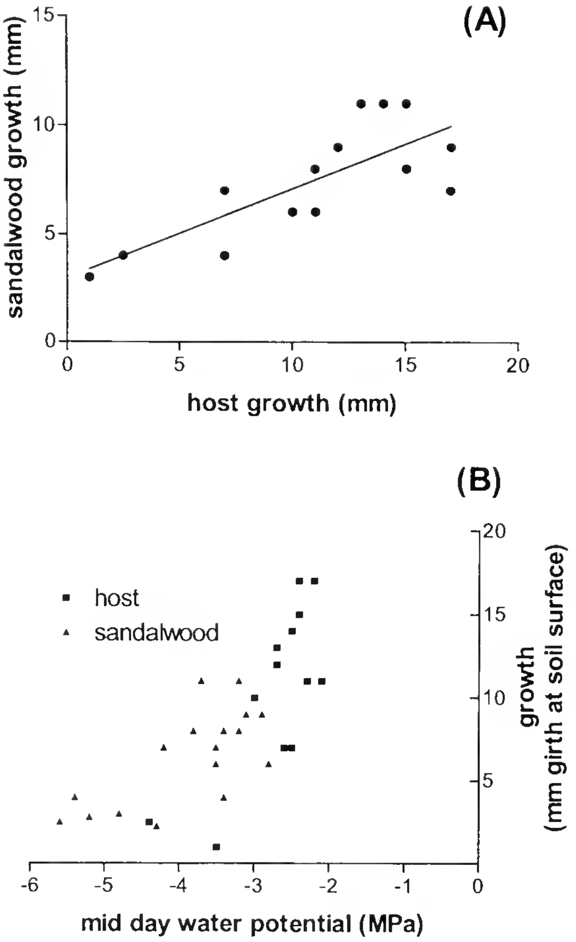

Figure 4. Sandalwood growth as related to (**A**) host growth (adjusted $r^2 = 0.62$ $P < 0.001$) and sandalwood and host growth as related to (**B**) plant water status (adjusted $r^2 = 0.54$, $P < 0.001$).

respectively (Fig 4B). Host and sandalwood growth increased with increasing water potential in a linear relationship (adjusted $r^2 = 0.54$, $P < 0.001$; Fig 4B). Mean midday water potential of sandalwood was significantly lower (-3.9 MPa) than that of their adjacent host (-3.2 MPa). It was observed that some sandalwood seedlings which had not survived summer were beside host seedlings (*Acacia acuminata*) that had died; others were beside host seedlings of low water potential (data not shown), suggesting that these sandalwood seedlings may have died from moisture stress.

Discussion

This study has clearly shown that sandalwood and host establishment in the same season is achievable with a 70 % establishment rate and that it was more successful than current techniques under the dry conditions experienced during 2000-2001. Establishment of host and sandalwood in the same year reduces the length of time to harvest by one to two years and would provide cost savings (labour and machinery time) relative to separate introduction of sandalwood in subsequent years. The process of partially germinating seeds would be more expensive than using untreated seeds, but the quantity of partially germinated seeds required per hectare would be approximately a third of that required by the standard technique. A limiting factor to the sandalwood plantation industry may be a seed shortage of local or better provenances in coming years. Brand *et al.* (1999) showed that local provenances are likely to perform best in terms of plantation growth. Sandalwood seed from wheatbelt provenances is limited because most of the original populations have been removed. Therefore, it is important that as little seed as possible is used to establish plantations in the immediate future.

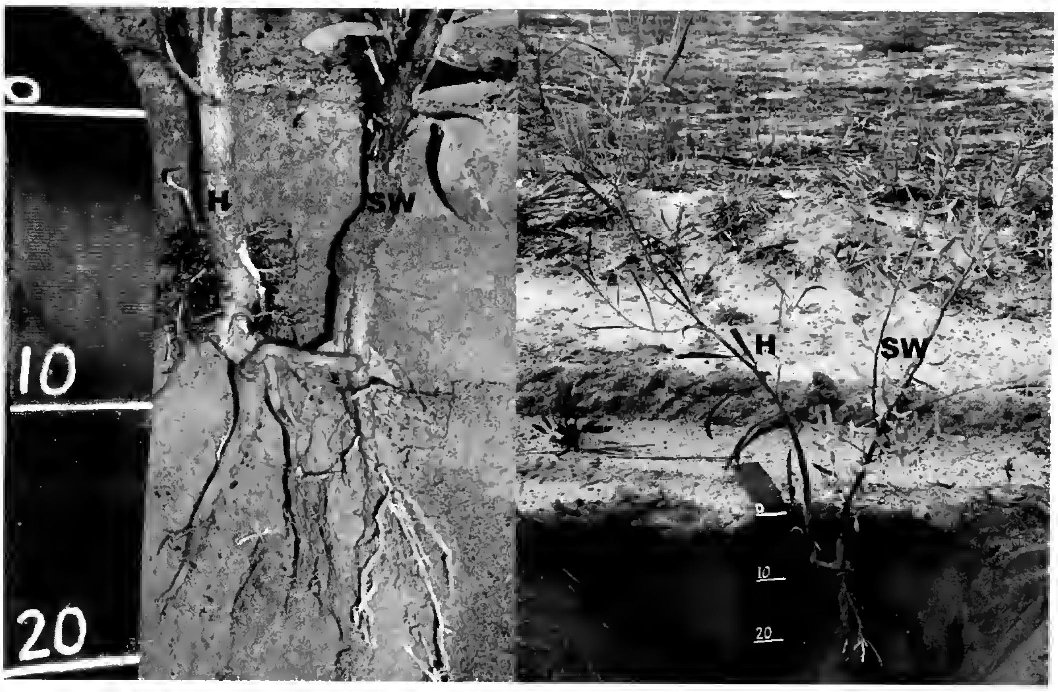

Figure 5. Sandalwood and host growth at site 1. **Left:** rooting morphology of host (H) and sandalwood (SW); note the thickened sandalwood root and haustorial attachment into the main taproot of the host. **Right:** Shoot and root growth of host, planted as a small seedling, and sandalwood, planted as a partially germinated seed; note the other hosts that have germinated in the rip line. Scale bar increments are 0.1 m.

The roots of young sandalwood seedlings are brittle (Herbert 1925; Barrett 1987) and growers who have tried to plant young sandalwood seedlings, either planted alone or with a pot host, have noted that many of the seedlings are damaged even when handled carefully. Haustorial connections that may have formed between the pot host and the sandalwood are also brittle and are easily broken during transplantation into the field. The radicle and plumule of the partially germinated seeds used in this study had not emerged when planted in the field (see Fig 1). These partially germinated seeds were easy to handle and were not damaged during the transplantation process. This avoidance of damage to the germinating sandalwood seed may have led to improved germination and survival.

Replacement of annual crops and pastures with perennial plants results in a drying of the soil profile (Harper *et al.* 2000). The principal hosts of sandalwood are perennial and the current establishment technique recommends that the hosts be planted one or two years prior to the sandalwood (Brand & Jones 2001). The extent to which perennials, in this case acacias, reduce soil moisture would be dependent on their transpiration. The transpiration of a plantation is dependent on the energy balance and leaf area index of the canopy, on the physiological control by the stomata of water loss from the leaves, on the humidity of the air adjacent to the leaves in the canopy, on the availability of water in the soil and on the supply of water by the conducting tissue (Barrett *et al.* 1996). It is apparent therefore that the relatively low sandalwood establishment at sites 2 and 3 during a dry year in the presence of older hosts (> 2 years old) could be due to reduced soil moisture (compared to site 1), and that these lower levels of soil moisture were in part due to the presence of the larger hosts themselves. At site 1, which was cleared land with good weed control, there was adequate moisture available over a sufficient time period, enabling complete germination of the sandalwood seeds and successful attachment to a host root before the soil topsoil dried out during spring through to summer.

Plant water status measured at midday reflects the level of moisture stress experienced at that time (Ritchie & Hinckley 1975). In this study there was considerable variation in the level of water stress experienced by young seedlings at site 1 and this is the first study to show that increasing levels of water stress reduced sandalwood and host growth. In some parts of site 1 the small host seedlings were presumably able to access soil moisture derived from the current years' rainfall and moisture stored in soil profile that had not been removed by previous annual crops and pastures.

Although other potential hosts were direct seeded on the day of sandalwood/*Acacia acuminata* planting, many of these germinated later in 2000 and were not considered capable of supporting the sandalwood over the dry summer-autumn period. Recent excavation (Fig 5) revealed that it was the *Acacia acuminata* seedling that supported the parasite over the dry summer period. It is likely that as the direct seeded hosts develop adjacent to the original *Acacia acuminata* seedling that they too will be eventually parasitised by the sandalwood.

This current study has shown that sandalwood and host can be established on the same day. It was not the intention of the study to determine which parts of the "same day establishment" methodology were most critical, but to demonstrate that "same day establishment" was achievable and to show the benefits relative to other current techniques. From the results we were not able to determine whether the partial germination of the sandalwood nuts was or was not critical for same day sandalwood establishment. However, success was most likely due to the young hosts and attached sandalwood being able to access adequate water in the absence of mature hosts, and the selection and use of sandalwood seeds that have already begun the process of germination. The technique of partially germinating sandalwood seeds in controlled conditions takes only 15-20 days to achieve a state that may take 8 weeks in the field. This process ensures that all seeds sown at least begin germination, which cannot be guaranteed when untreated seeds are sown directly into the field. Once planted into moist soil, the partially germinated seeds will continue to grow and are considered more likely to make haustorial contact with the host planted along side them than an untreated field sown seed that is endeavouring to grow through soil with lower water availability under mature hosts. The value of the process is even greater in dry years like 2000.

Parasitism of hosts by sandalwood can weaken and cause the death of the host, particularly when young (Herbert & Gardner 1921). Brand *et al.* (1999) concluded that differences in host survival between *S. spicatum* planting years might have been related to the initial period of growth without a root parasite. In a subsequent study (Brand *et al.* 2000) the sandalwood was not sown until the *Acacia acuminata* were 5 years of age and over the following three years the sandalwood did not adversely affect host survival. Thus, it was recommended that *Acacia acuminata* seedlings need to be at least 1 m tall before introducing sandalwood (Brand & Jones 2001). The current study has shown that small *Acacia acuminata* hosts (< 1 m tall) can survive and support a young sandalwood seedling of similar size. Indeed sandalwood growth on such small hosts during a very dry year was impressive, with a mean diameter of 5.2 mm at 150 mm above the soil surface at 9 months of age. Similar sandalwood growth rates, 5-8 mm per year, have been observed on larger hosts (Brand *et al.* 1999, 2000). In this study, even if the primary *Acacia acuminata* hosts that were planted as seedlings next to each partially germinated sandalwood seed die in the future, there are numerous other *Acacia* hosts available (including *A. acuminata*) that have germinated and grown as a result of the direct seeding. These additional hosts should provide water and nutrients to the sandalwood and ensure that sandalwood survival and vigor is maintained.

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Notes on ....

A whale shark feeding in association with a school of giant herring at Ningaloo Reef, Western Australia

S G Wilson

Department of Zoology, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009
Present address: Edgerton Research Laboratory, New England Aquarium, Central Wharf, Boston, MA 02110, USA
email: swilson@neaq.org

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Abstract. A whale shark was observed feeding among a school of giant herring at Ningaloo Reef. It is suggested that both the whale shark and the herring school were targeting the same planktonic prey.

Key words: whale shark, *Rhincodon typus*, giant herring, *Elops hawaiensis*

Introduction

The whale shark, *Rhincodon typus*, is a suction filter-feeder that targets dense concentrations of planktonic and nektonic prey, including aggregating crustaceans such as euphausiids and copepods, and schooling baitfishes such as sardines and anchovies (Compagno 1984). Fishermen often use its presence as an indicator of waters rich in plankton and plankton-feeding fish that may, in turn, attract more valuable predatory species (Colman 1997). There are a number of reports of feeding associations occurring between whale sharks and schools of predatory fishes, such as mackerel, jacks and tuna (*e.g.* Gudger 1941; Springer 1957; Hoffman *et al.* 1981). In each of these cases, the whale sharks appeared to be targeting the same prey as the predatory fishes rather than the predatory fishes themselves.

Similar feeding associations have not been reported in whale sharks seasonally aggregating in coastal waters off Ningaloo Reef, Western Australia, where they are thought to feed predominantly on the neritic euphausiid *Pseudeuphausia latifrons*. On a number of occasions whale sharks have been observed feeding in these waters on surface schools of this species (Taylor & Grigg 1991; Clark 1992; Taylor 1994). Additionally, two whale shark faecal samples collected off Ningaloo Reef were found to contain crustacean remains resembling *P. latifrons* (Wilson & Newbound 2001). Other potential prey includes the large schools of baitfishes frequently sighted at this location at the time of the whale shark aggregation (Taylor 1994).

Materials and Methods

The author accompanied pilots of fixed-wing aircraft flown along the northern section of Ningaloo Reef from 4-11 May 2001.

Results

On 7 May 2001 at 1100 hrs, a whale shark was observed from the aircraft swimming northwards along the reef front ~1 km south of South Passage (see Fig 1 in Wilson *et al.* 2001). A school of giant herring (*Elops hawaiensis*), recognisable by their distinctive body shape, was visible feeding at the surface ~300 m to the northeast of the whale shark. Although not initially swimming on an intercept course, the shark made a 45-degree turn towards the school at a distance of ~100 m. Fig 1 shows the whale shark approaching the herring school. The shark stopped swimming when in the middle of the school (Fig 2), then adopted a stationary feeding posture (Fig 3) similar to that described by Springer (1957), Hoffman *et al.* (1981), Taylor *et al.* (1983) and Silas (1986), with its head just below the surface and its tail pointing downwards at a 45-degree angle. It remained in this

Figure 1. Whale shark approaches the herring school.

Figure 2. Whale shark stops swimming in the centre of the herring school.

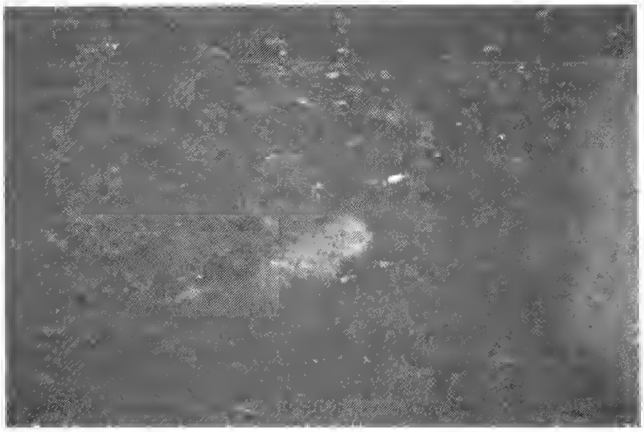

Figure 3. Whale shark adopts a stationary feeding posture.

posture for a period of 3-4 minutes, after which time the herring school dispersed and the shark continued swimming northwards.

Discussion

It seems likely that the whale shark described here was targeting the same prey as the herring, rather than attempting to feed on the herring themselves. A whale shark tour operator reported a similar observation that took place in shallow water directly off the front of Ningaloo Reef (P O'Halloran, personal communication): the whale shark was hanging vertically in the water, with its head just the below the surface and its tail sweeping along the sandy bottom, in the middle of a herring school; small, planktonic prey were being consumed by both the whale shark and the herring. This suggests that occurrences of whale sharks feeding among schools of giant herring may not be uncommon in these waters.

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Note from the Honorary Editor:

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Morphological and physiological adaptations to waterlogging by *Eucalyptus* seedlings from the semi-arid Pilbara, Western Australia

S K Florentine* & J E D Fox

School of Environmental Biology, Curtin University of Technology, GPO Box U 1987, Perth WA 6845
*current address: School of Science, University of Ballarat, PO Box 663, Ballarat VIC 3350
email: s.florentine@ballarat.edu.au

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Abstract

This study was undertaken to investigate the adaptation to long term waterlogging of semi-arid eucalyptus species. Long-term waterlogging of *Eucalyptus victrix* seedlings significantly increases seedling stem diameter. Flooding reduces photosynthesis, transpiration and stomatal conductance. Flooding does not increase shoot fresh or dry weight of 4-, 8- or 17- week old seedlings. Leaf emergence may be stimulated for flooded seedlings compared with unflooded seedlings. Root dry weight is not significantly greater for 17- week old flooded plants than 13- week old seedlings. We suggest that maintenance of a high root/shoot ratio is a drought adaptation. Furthermore, a comparative study of flood tolerance in semi-arid eucalypt species suggests that those species intolerant of flooding seldom express morphological adaptations and fail to recover from physiological damage. Flooding significantly reduced the transpiration rate and stomatal conduct of all three species. Diurnal transpiration, stomatal conductance and leaf water potential of *E. terminalis* and *E. leucophloia* were significantly different between treatment (flooding) and control seedlings.

Keywords: *Eucalyptus*, flooding, floodplain, semi-arid, *E. victrix*, *E. terminalis*, *E. leucophloia*

Introduction

The large Australian genus *Eucalyptus* has species adapted to a wide range of climatic and edaphic conditions (Goor & Barney 1968). Vernacular names often indicate tolerance of environments subject to flooding; *e.g.* flooded gum *E. grandis*, swamp gums *E. camphora* and *E. ovata*, and swamp mahogany *E. robusta*. These are all species that can withstand some degree of inundation (Ladiges & Kelso 1977; Clemens & Pearson 1977; Kozlowski *et al.* 1991). Some species (*e.g. E. camaldulensis*) are dependant on periodic flooding with seed germinating on flooded areas following flood recession (Parsons *et al.* 1991). We examine and compare here the flood tolerance of three *Eucalyptus* species found in the semi-arid Pilbara region, one of which grows in flood prone areas and two which grow in non-flood prone areas.

Within the large genus *Eucalyptus*, species of the sub-genus *Monocalyptus* are less water and frost tolerant than are *Symphyomyrtus* species (Noble 1989; Davidson & Reid 1987). No *Monocalyptus* species have been shown to tolerate waterlogged conditions (McComb *et al.* 1989; van der Moezel & Bell 1990; Bell *et al.* 1994), although of two south-west Western Australian *Monocalyptus*, *E. marginata* (jarrah) is very intolerant to waterlogging (Davison & Tay 1985) whereas *E. patens* is often found in low-lying areas (Bell & Williams 1997). Species intolerant of waterlogging generally show no morphological changes and no recovery of gas exchange during exposure to the waterlogged condition (Tang & Kozlowski 1982). Species tolerant of waterlogging often show reduced stomatal conductance and transpiration but tend to recover immediately after adventitious roots are formed (Gomes & Kozlowski 1980a,b).

Symphyomyrtus species that occur on or adjacent to the Fortescue floodplain, in the semi-arid Pilbara region include *E. victrix*, *E. camaldulensis* var *obtusa* Blakely and *E. leucophloia* Brooker. Trees that occur in flood plain environments experience exposure to flooding that may be regular or irregular and of varied duration and frequency. *E. victrix* L Johnson & K Hill forms open, grassy woodlands in the flood plain of the Fortescue River valley (Xin *et al.* 1996). This area is subject to summer flooding from cyclones or heavy thunder storm activity between January and March. Depending on the topography of the woodland, flood water may remain for a month or more.

The present study was undertaken to examine aspects of tolerance to flooding by *E. victrix* seedlings using plants of different ages from germination. This paper compares three Pilbara eucalypts (*E. victrix*, *E. terminalis* and *E. leucophloia*) that differ in ecological habitat. *E. victrix* is confined to typical floodplain sites, *E. terminalis* occurs on river banks but is also scattered on hillsides, whereas *E. leucophloia* occurs mostly on stony hills. Based on their ecological distribution, it is hypothesised that seedlings of the non-floodplain *Eucalyptus* species *E. leucophloia* and *E. terminalis* are less tolerant in terms of ecophysiology and seedling growth to flooding than the typical flood plain species *E. victrix*. We test the

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hypothesis that *E. victrix* seedlings will not show growth-related changes in CO_2 assimilation rates when exposed to prolonged flooding.

Methods

Effects of flooding

Seedlings of *E. victrix* were germinated and grown under similar conditions until imposition of flooding treatment on some seedlings at 4, 8, 13 and 17 weeks after planting. Seed was extracted from mature fruit capsules of *E. victrix* collected in February 1995, from the coolibah woodland of the Fortescue near Ethel Creek (l22° 54'S, 120° 10'E), and were stored in a sealed jar at laboratory temperature (about 21° C). Aliquots of seed were sown onto sterilised coarse sand on Aug–Sept 1995. Uniform size (5-6 cm height) seedlings were transplanted into cylindrical pots (150 mm height and 80 mm wide), containing clay soil collected from the coolibah woodland. All the pots were kept in a glass house and watered 3 to 4 times a week. Two weeks after, to simulate the natural condition, seedlings were moved to an open area.

Cylindrical pots of 13 cm diameter were filled with coolibah woodland soil (red clay loam, pH 7) and the bottom openings sealed with plastic draining tapes. Seedlings were transplanted into pots at the 2-4 leaf stage, approximately three weeks after sowing. Plants were maintained in a shade house until Dec 1995 when they were placed in full sunlight. After five days acclimatisation, flooding treatment commenced. The plants were then 13- or 17-weeks old at the start of flooding, with mean heights of 14.1 and 19.0 cm respectively. Fibreglass tanks of 2.5x0.5x0.5 m were filled with rainwater to a depth of 1 cm above the pot soil level (12 plants of 13-week old; 8 plants of 17-week old). Rainwater was added daily to maintain the level. Control plants were placed adjacent to the tanks and these were maintained in a freely drained condition and were watered to excess three times a week. All plants were in full sun. Further seed was sown and seedlings prepared as before, to give 4- and 8-week old seedlings. Measurements were made on seedling height, leaf number, and leaf dimensions (length and width). New leaf emergence and leaf death were also noted. Any changes in seedling morphology, particularly stem swelling, leaf colour changes and development of adventitious roots were recorded at weekly interval. All plants were harvested 32 weeks after flooding of the 13- and 17- week sets and carefully removed from pots. Fresh weights of root and shoot were obtained. Plants were then put in separately labelled paper bags and dry weights obtained after 24 hr at 105 °C.

Leaf gas exchange

Leaf gas exchange measurements (net photosynthesis, stomatal conductance, transpiration) were made on the 13- and 17-week old seedlings on fully expanded individual leaves from each plant. Measurements commenced 8 days after the start of flooding and continued for 6 weeks using a portable gas exchange system (model LCA-3, Analytical Development, UK) with leaf chamber attachment (Parkinson PLC-031 3B). Data were collected under ambient conditions with photosynthetic active radiation (PAR; 400–700 nm) >500 µmol $m^{-2} s^{-1}$, consistently between 1200 and 1300 hrs.

Comparison of flooding tolerance

Seeds of *E. victrix*, *E. terminalis* (desert blood wood) and *E. leucophloia* (migum/snappygum) were collected from sites near Newman (23° 21' S, 119° 44' E), Western Australia on 27 March 1997. Air-dried, but uncleaned seeds were stored in air-tight bottles and kept at room temperature until use. On 25 July 1997, seeds were sown in sterilised coarse sand in seedling trays at the Field Trial Area of Curtin University. On 15 August, 50 uniform sized (5-6 cm high) seedlings from each species, were transplanted into cylindrical pots containing clay soil collected from a coolibah woodland. All pots were kept in a glass house and water was added 3 to 4 times a week. On 21 January 1998 (to simulate the natural condition) uniform size seedlings (29 seedlings of *E. victrix* and *E. leucophloia* and 35 seedlings of *E. terminalis*) were selected. Roots of all three of the species had penetrated through the basal holes. For uniformity all plants were removed carefully from pots and roots were trimmed. The seedlings were then placed in the middle of plastic pots (13 cm dia) and any gaps were filled with coolibah woodland soil. Pots were watered and left in the glass house for one week. Plants were then taken outside and randomly divided into two groups (control and treatment). The flooding treatment involved by placing seedlings randomly inside three fibre-glass tanks (2x2 m) filled with rain water. The water level was maintained at 15 to 20 mm above the soil surface. Control seedlings were kept on a table beside the tanks. Daily maxi and min ambient temperatures were recorded throughout the experiment.

Gas exchange measurements were made at irregular intervals, commencing from two weeks after the start of waterlogging. In addition, diurnal ecophysiological and environmental measurements were made on 10 April 1998. Gas exchange measurements (net photosynthesis, transpiration, stomatal conductance and internal CO_2 concentration) were recorded for five seedlings of each of the three *Eucalyptus* species from both control and waterlogged treatment. Recordings were made every 3 hours between 0600 hours and 1800 hours local time using an open portable gas exchange system. Diurnal leaf water potentials (Ψ) of excised leaves were determined using a pressure chamber (Model Mk 3005, Soil Moisture Equipment, CA; Scholander *et al.* 1965) at 3 hourly intervals, on the same seedlings as gas exchange measurements were taken. All the leaves used for the water potential study were kept in labelled bags and added to respective seedlings at the end of the experiment for dry weight measurements.

All plants were harvested on 11 April 1998, 65 days after the waterlogging treatment commenced. Each plant was carefully removed from its pot, washed, surface dried between paper towels, and placed in separately labelled bags. At this time observations were made of any morphological adaptations to waterlogging: roots (mainly adventitious root), shoots (hypertrophy), leaf (colour changes; Royal Horticulture Society Colour Chart) and soil surrounding root parts. Samples were stored at 6 °C and the following day projected leaf area, length and width were determined using a digital image analyser (DIAS, Delta-T Devices). Plants were then oven-dried at 105 °C for 24 hr and dry weights were measured separately for shoots and roots.

Statistical analyses

Data were analysed by one-way ANOVA using SuperANOVA software program (Abacus Concepts, CA). Residual plots of each ANOVA were obtained to examine homogeneity of variance. Based on residual plots, data were transformed to log or square root as appropriate and reanalysed. The data presented here are of uniform means.

Results

Flooding of *E. victrix* seedlings

The net photosynthetic rate of 13-week control plants fluctuates between 7 and 15 μmol m^{-2} s^{-1} over the 50 day experimental period, whereas net photosynthetic rate of flooded plants declining to less than 5 μmol m^{-2} s^{-1} after two weeks flooding and remains below 7 μmol m^{-2} s^{-1} thereafter (Fig 1). The net photosynthetic rate of flooded and controlled 13-week old seedlings was significantly different from the first measurements. After waterlogging, the 17-week old plants showed no significant difference in net photosynthetic rate but the effect was highly significant during the subsequent measurements.

Changes in stomatal conductance were generally similar to those for photosynthesis, with a highly significant difference for 13-week old flooded plants but no significance difference for 17-week old ones (Fig 1). Control plant gas exchange values also gradually decreased during the study period, apart from a fluctuation at 40 days for the 13-week old seedlings. Fifteen days after the flooding treatment began, most values for flooded plants were below those of the corresponding control, and remained less.

Transpiration rates of both 13- and 17- week sets were similar for control and flooded plants up to 21 days (Fig 2). However, this changed in both 13 and 17-week old seedlings. There was a clear significant difference after 13-weeks, with higher rates for controls.

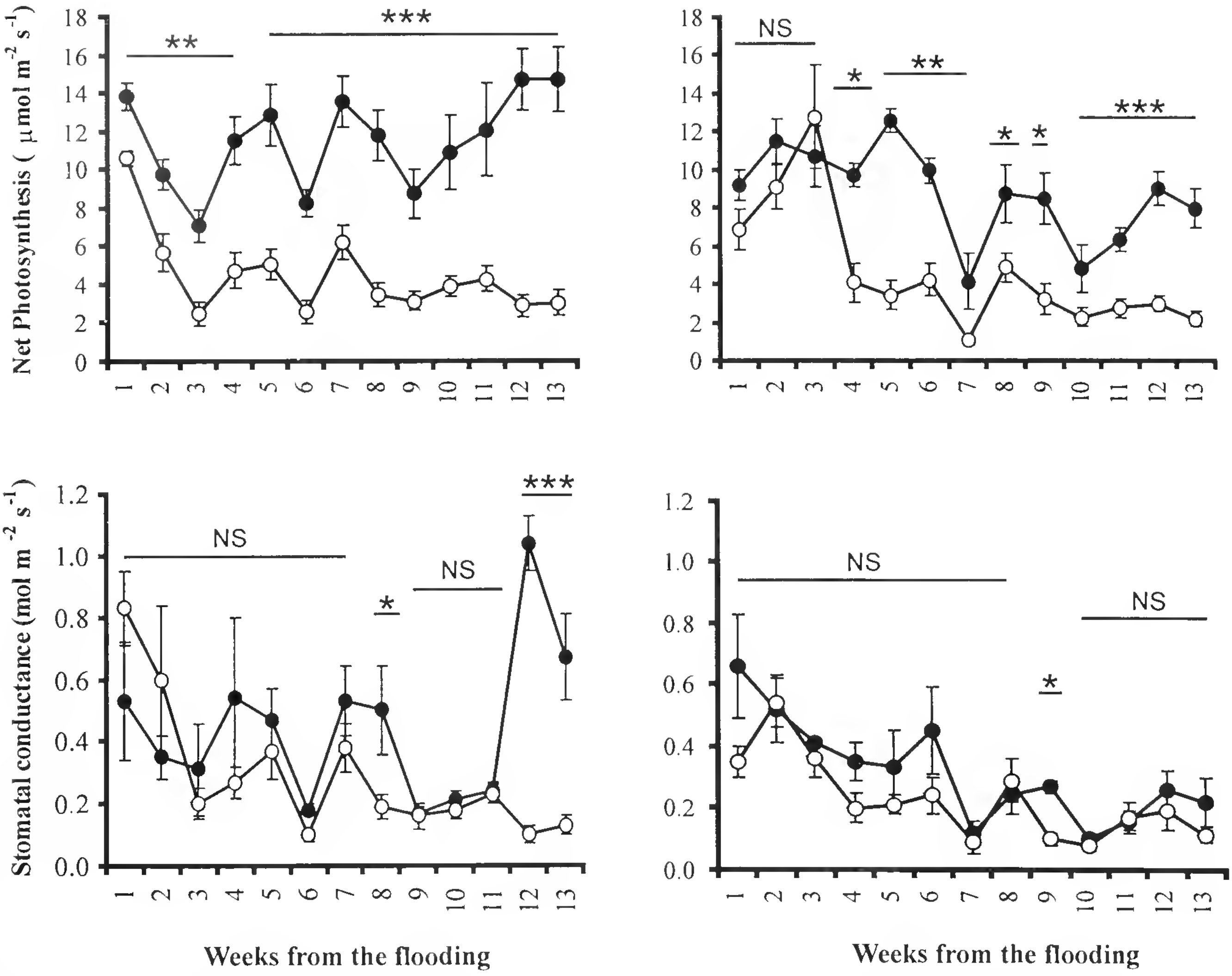

Figure. 1. Net photosynthesis (top), and stomatal conductance (bottom) rate for 6 weeks following flooding on 13 (left) and 17 (right) week-old seedlings of *E. victrix*; controls (●) and flooded (o). NS indicates no significant difference; * indicate samples are significantly different at $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

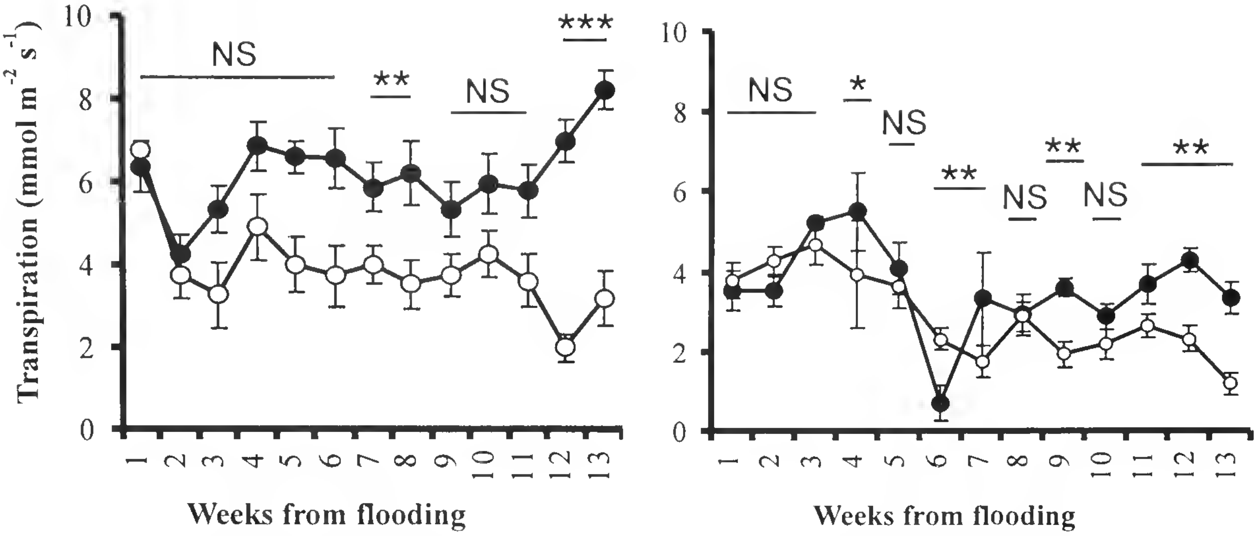

Figure 2. Transpiration rate, for 6 weeks following flooding on 13 (left) and 17 (right) week-old seedlings of *E. victrix*; controls (●) and flooded (o). NS indicates no significant difference; * indicates significant differences at $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Leaf colour changed from 16 days after waterlogging. Leaves initially became reddish-brown; some became yellowish after 32 days. After 47 days, submerged stems had begun to show splitting in the 17-week set. Adventitious root development was observed from 42 days in the 13-week old seedlings and from 62 days in the 17-week old plants. Mean total leaf areas (mm^2) of the 17-week plants at final harvest were; control 789 ± 424 (SD) and flooded 1063 ± 427 (SD). Flooded seedlings shed an average of two leaves each. New leaf formation appeared to be continuous in both flooded and control plants but was more prolific in flooded plants.

In all four-seedling age sets, the mean shoot height at harvest did not differ significantly between control and flooded seedlings (Tables 1 and 2). There was no significant difference in shoot dry weights even though

Table 1

Harvest details of 4- and 8- week old *Eucalyptus victrix* seedlings after flooding. $^*P < 0.05$; $^{**}P < 0.005$; $^{***}P < 0.001$; NS = not significant. Data are mean ± SE.

Treatment	Age	n	Shoot height (cm)	Shoot dry weight (g)	Root length (cm)	Root dry weight (g)	Stem diameter (mm)	Number of adventitious roots
Flooded	4	11	12.91 ± 0.95	0.80 ± 0.08	26.40 ± 1.80	0.41 ± 0.70	3.16 ± 0.37	14.72 ± 1.01
Unflooded	4	4	10.88 ± 0.58	0.59 ± 0.05	57.40 ± 5.70	1.01 ± 0.07	2.20 ± 0.13	0.00
Flooded	8	12	21.90 ± 1.34	2.42 ± 0.29	23.26 ± 6.22	0.94 ± 0.19	5.68 ± 0.33	13.41 ± 1.16
Unflooded	8	4	21.77 ± 5.11	1.83 ± 0.45	40.50 ± 7.00	2.54 ± 1.40	3.70 ± 0.56	0.00
P values								
Flooding			NS	NS	***	***	***	***
Age			***	***	**	***	***	NS
Flooding x Age			NS	NS	*	NS	NS	NS

Table 2

Harvest details of 13- and 17-week old *Eucalyptus victrix* seedlings. $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; NS = not significant. Data are mean ± SE.

Treatment	Age	n	Shoot height (cm)	Shoot dry weight (g)	Root length (cm)	Root dry weight (g)	Stem diameter (mm)	Number of adventitious roots
Flooding	13	12	16.66 ± 0.99	1.54 ± 0.21	20.56 ± 2.28	3.02 ± 0.75	4.70 ± 0.23	10.00 ± 1.04
Unflooded	13	4	16.20 ± 0.75	0.84 ± 0.17	38.75 ± 1.63	2.33 ± 0.75	3.05 ± 0.64	0.00
Flooded	17	7	22.09 ± 2.22	4.71 ± 0.39	27.19 ± 1.02	8.17 ± 1.50	7.40 ± 0.78	10.14 ± 1.40
Unflooded	17	4	21.05 ± 1.80	4.41 ± 0.31	27.78 ± 3.10	4.37 ± 0.68	4.31 ± 0.29	0.00
P values								
Flooding			NS	NS	***	NS	***	***
Age			**	***	NS	**	**	NS
Flooding x Age			*	NS	**	NS	NS	NS

13-week old flooded seedlings have almost twice the mean weight of the control (Table 1). Root length, root mass, stem diameter and number of adventitious roots were significantly different ($P < 0.0001$) in 4 and 8- week old seedlings (Table 1). However, there was no significant difference in shoot height or dry mass. Harvest data of 13- and 17-week old seedlings indicated that flooding was associated with significant differences ($P < 0.0001$) in root length, stem diameter and number of adventitious roots (Table 2). A significant interaction between flooding condition and seedling age was observed in shoot height and root length.

At harvest, all original root systems on waterlogged plants were soft and black, in stark contrast to the white-cream coloured adventitious roots. Flooding had the greatest effect on original seedling roots. The older sets the roots of flooded seedlings were black and decaying at the end of the experiment (32 weeks after). Just above the dead roots, prolific white adventitious roots were clearly observed in the 8 week seedlings.

Flooding tolerance

No plants died during the flooding experiment. Increase in height of specimens of all three *Eucalyptus* species subject to waterlogging was consistently slower than the controls (Table 3). Height growth of *E. victrix* was least affected by waterlogging, and no significant differences were observed for either *E. victrix* or *E. leucophloia*.

The number of intact leaves decreased within two weeks from initiation of waterlogging, particularly for *E. terminalis* (Table 3). At this stage, *E. leucophloia* and *E. victrix* showed symptoms of leaf epinasty in flooded seedlings. Leaf number increased for *E. victrix* for the first 23 days after flooding, followed by a gradual decline. Flooding effects were almost similar towards the end of the experiment for both *E. terminalis* and *E. leucophloia* where both species had reduced numbers of leaves attached to stems. At the end of the experiment (65 days after flooding) adventitious roots was found only for waterlogged *E. victrix* (3.60 ± 1.44, n = 9) with none formed in either *E. leucophloia* or *E. terminalis*.

Differences in shoot dry mass due to flooding were significant for both *E. leucophloia* ($P = 0.05$) and *E. terminalis* ($P < 0.001$; Table 4). The effect was most pronounced for *E. terminalis*; differences between waterlogged and control seedlings were also significant for *E. victrix* ($P = 0.022$). Analysis of whole plant dried mass indicated significant differences for all three species. The effect was more severe for *E. terminalis*. Analysis of shoot:root ratio showed differences for all three species.

Transpiration rates of *E. victrix* and *E. leucophloia* were similar between flooded and unflooded plants after 9 days (Fig 3). However, after 23 days transpiration was significantly lower for flooded plants. Transpiration was subsequently reduced in flooded *E. terminalis* and *E. leucophloia* but remained steady for *E. victrix*.

Stomatal conductance was significantly different between flooded and control plants after 9 days of flooding (Fig 3) with rates between 4.2 and 6.8 mol m^{-2} s^{-1} for unflooded plants. The range was only 0.3 to 1.1 m mol m^{-2} s^{-1} in all three species for flooded plants. Stomatal conductance remained relatively low for flooded *E. terminalis* and *E. leucophloia* but in contrast stomata started to reopen for *E. victrix* (stomatal conductance increased from 0.8 to 2.7 mol m^{-2} s^{-1}) by 40 days after flooding, and increased further by 60 days.

Diurnal patterns of temperature and PAR are given in

Table 3

Effect of waterlogging on height (cm), number of leaves and leaf area parameters for *E. victrix*, *E. terminalis* and *E. leucophloia*. Data are mean ± SD of tallest seedlings (n= 10) from each species for height, number of leaves and leaf area, leaf length, width and length:width ratio. NS indicates means are not significantly different; significant differences at $P < 0.05^{*}$, $P < 0.01^{**}$, $P < 0.001^{***}$.

	E. victrix		*E. terminalis*		*E. leucophloia*	
	Flooded	Control	Flooded	Control	Flooded	Control
Height (cm)						
09 days	21.2± 4.3	21.6 ± 3.3^{NS}	20.9 ± 1.2	22.9 ± 1.6**	19.6 ± 2.9	18.4 ± 3.7^{NS}
23 days	23.7 ± 4.8	24.2 ± 3.1^{NS}	21.9 ± 1.0	24.5 ± 1.9**	19.7 ± 2.8	18.9 ± 4.1^{NS}
31 days	24.1 ± 5.3	26.4 ± 3.0^{NS}	20.6 ± 2.1	24.5 ± 1.8**	20.0 ± 3.0	19.6 ± 4.4^{NS}
38 days	24.1 ± 5.7	27.2 ± 3.3^{NS}	21.0 ± 3.0	24.8 ± 1.8**	20.0 ± 2.8	20.0 ± 4.2^{NS}
59 days	25.2 ± 5.6	28.2 ± 2.9^{NS}	21.1 ± 3.1	25.6 ± 1.8***	20.1 ± 2.8	21.4 ± 4.6^{NS}
Number of leaves						
09 days	17.3 ± 2.1	17.3 ± 3.9^{NS}	18.0 ± 3.6	21.7± 3.8**	20.8 ± 3.0	18.2 ± 4.4^{NS}
23 days	17.9 ± 2.5	19.2 ± 5.3^{NS}	17.9 ± 4.1	21.3 ± 4.5^{NS}	20.7 ± 2.7	21.8 ± 5.2^{NS}
31 days	17.2 ± 2.9	19.8 ± 5.3^{NS}	15.5 ± 5.1	21.4 ± 3.8**	18.2 ± 4.4	21.9 ± 5.0^{NS}
38 days	16.6 ± 1.6	21.3 ± 6.4*	15.0 ± 5.5	22.6 ± 3.9**	17.2 ± 3.1	23.3 ± 5.7**
59 days	15.5 ± 1.6	20.3 ± 5.7*	14.0 ± 4.9	21.9 ± 4.7**	13.2 ± 2.6	23.3 ± 5.1***
65 days	14.5 ± 3.0	19.1± 5.3*	12.9 ± 4.6	21.6 ± 6.4**	10.5 ± 2.6	23.6 ± 5.8***
Leaf area parameters						
Area (mm^2)	110. 5 ± 19.6	121.3 ± 10.3*	84.0 ± 21.7	102.6 ± 10.5*	113.4 ± 22.5	138.1 ± 38.5^{NS}
Length (mm)	34. 8 ± 5.8	38. 6 ± 3.8*	34.0 ± 25.6	33.6 ± 5.7^{NS}	24.7 ± 4.7	33.5 ± 4.0***
Width (mm)	16. 2 ± 2.2	17. 3 ± 1.7^{NS}	12.6 ± 3.4	17.2 ± 1.9**	20.1 ± 3.4	25.9 ± 3.6**
L:W ratio	2.1 ± 0.3	2.2 ± 0.15^{NS}	2.6 ± 1.5	1.9 ± 0.3^{NS}	1.2 ± 0.1	1.3 ± 0.0*

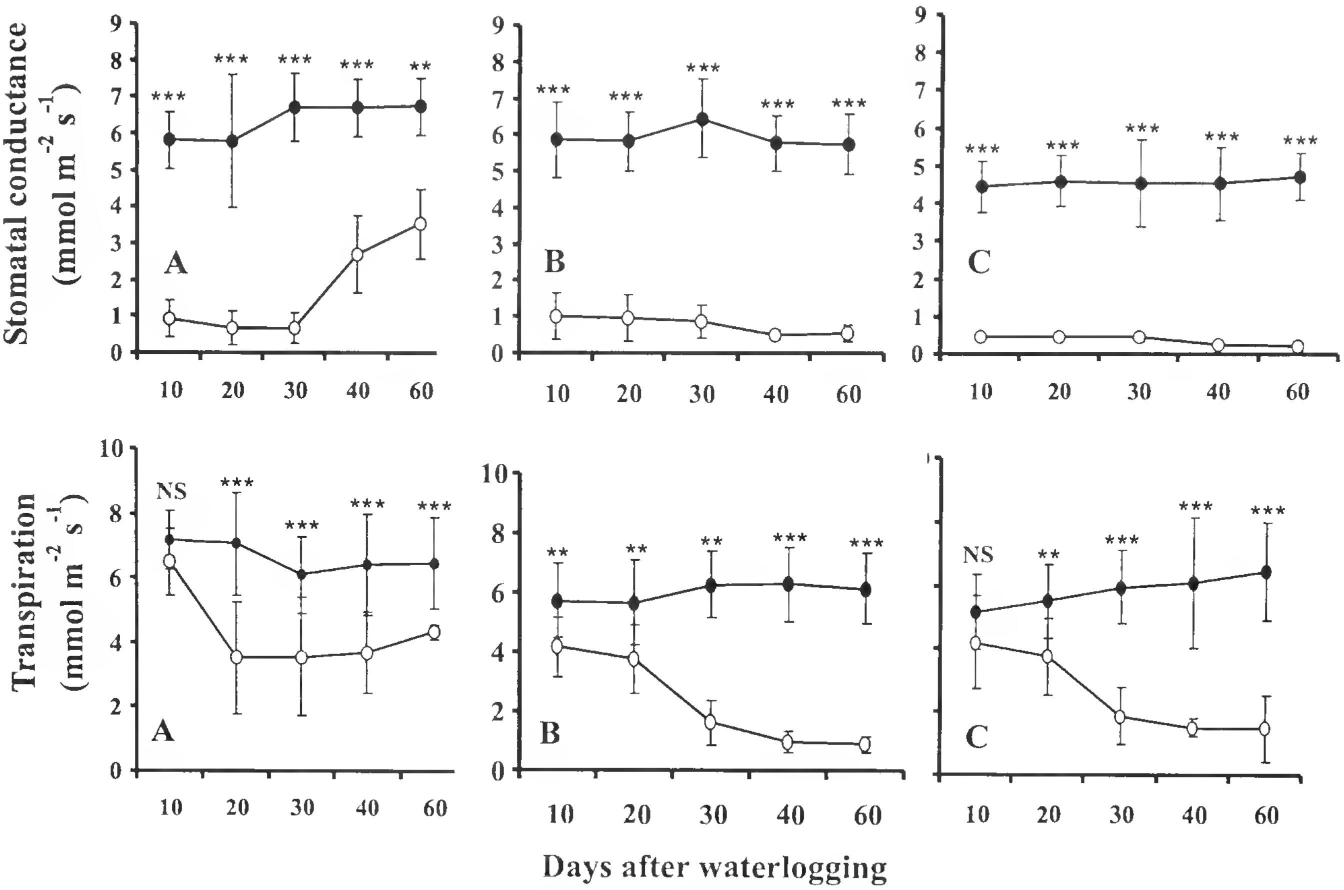

Figure 3. Changes in stomatal conductance and transpiration of *E. victrix* (A), *E. terminalis* (B) and *E. leucophloia* (C) of control (o) and flooded (•) and seedlings. The first measurements were taken 9 days after exposure to flooding. Vertical bars indicate standard error of means of five measurements. NS indicates no significant difference; * indicates samples are significantly different at $P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 4

Mean (± SD) of shoot dry weight, root dry weight, whole plant and shoot/root ratio of tallest seedlings from each of *E. victrix*, *E. terminalis*, and *E. leucophloia* seedlings after 65 days of waterlogging. Significant difference are $P < 0.05^*$; $P < 0.01^{**}$; $P<0.001^{***}$. NS indicates means are not significantly different.

	E. victrix			*E. terminalis*			*E. leucophloia*		
Attribute	Flooded (n= 10)	Control (n= 10)	*P*	Flooded (n= 10)	Control (n= 10)	*P*	Flooded (n= 10)	Control (n= 10)	*P*
Shoot dry wt(g)	2.66 ± 0.64	3.33± 0.54	*	1.51 ± 0.63	3.05 ± 0.84	***	2.55 ± 1.03	4.18 ± 1.66	*
Root dry wt(g)	0.64 ± 0.22	3.54 ± 1.29	***	0.37 ± 0.13	2.92 ± 1.10	***	0.53 ± 0.24	2.22 ± 0.88	***
Whole plant dry wt(g)	3.30 ± 0.73	6.87 ± 1.33	***	1.88 ± 0.69	5.98 ± 1.33	***	3.08 ± 1.18	6.41 ± 2.46	**
Shoot: Root ratio	4.77 ± 2.31	1.05 ± 0.41	***	4.37 ± 1.84	1.23 ± 0.66	***	5.66 ± 3.05	1.94 ± 0.50	**

Fig 4. Diurnal transpiration of flooded *E. leucophloia* and *E. terminalis* plants was significantly lower ($P < 0.001$) than for unflooded seedlings. For *E. victrix* a marginally significant difference ($P = 0.043$) was observed at 1200 hr. The difference in transpiration rate of flooded and control *E. leucophloia* and *E. terminalis* varied from 5-7 mmol m^{-2} s^{-1} at each sampling time (Fig 4).

The diurnal stomatal conductance of control plants (Fig 4) for all three species exceeded 1.5 m mol m^{-2} s^{-1}, and that of water-logged seedlings was between 1.0 and 1.5 m mol m^{-2} s^{-1} during the early part of the day. For both waterlogged and control plants, stomatal conductance declined progressively soon after sunrise. However, rates started to recover from 1500 hr. Differences were not significant between waterlogged and control plants of all three species. Although diurnal mean leaf water potential (Ψ) of waterlogged seedlings was consistently more negative than that of control plants, differences were only

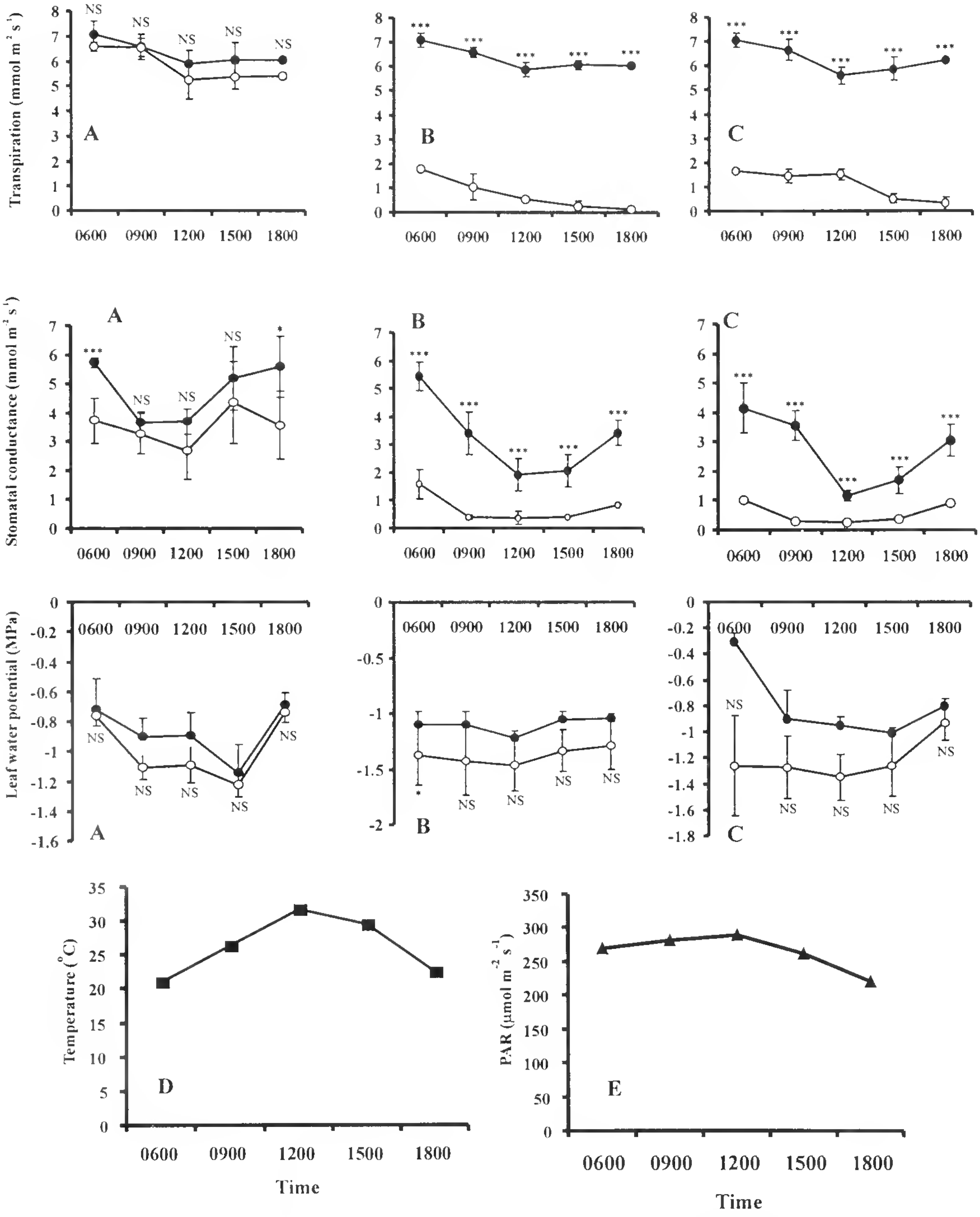

Figure 4. Diurnal patterns of transpiration, stomatal conductance and mean pre-dawn leaf water potential of control (•) and flooded (o) seedlings of *E. victrix* (A), *E. terminalis* (B) & *E. leucophloia* (C) after 65 days of flooding. Values are mean and standard error (n = 5). NS indicates no significant difference; * indicates samples are significantly different at $P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Temperature (D) and photosynthetic active radiation (E) are shown for the time of measurements.

significantly different for *E. leucopholia* at 0600 hr (P = 0.026) and *E. terminalis* at 1200 hrs (P = 0.002; Fig 4).

Within three weeks of waterlogging, leaf epinastic curvature was observed for waterlogged *E. leucophloia* and *E. terminalis* but not *E. victrix*. However, towards the end of the experiment this was observed for three *E. victrix* individuals. Between five and six weeks from waterlogging, 4 to 5 leaves of *E. terminalis* and *E. leucophloia* had turned a yellow-green colour (RHS Yellow Green Group C). Towards the end of the experiment, these leaves were bright yellow (RHS Yellow Group B). Many were dead and fell off the stem before harvesting. Most young leaves of waterlogged *E. victrix* seedlings were red-purple in colour (RHS Red Purple group A). In contrast, most of the newly flushed leaves from control seedlings were red (RHS Red Purple group A). Control plants had formed two to three small branches from the main stem, but no branches were produced on waterlogged seedlings for all three *Eucalyptus* species.

Stem hypertrophy (swelling) was observed only for waterlogged *E. victrix*. Three weeks after waterlogging, adventitious roots had also formed on the submerged portion of most *E. victrix* stems, and these floated just below the water surface. In contrast, neither *E. leucophloia* or *E. terminalis* waterlogged plants produced any adventitious roots. In most waterlogged plants, roots surrounded by soil had turned dark black. Most *E. victrix* waterlogged plant roots were decayed, with some remaining old roots being soft and presumed dead. During the harvest (65 days after flooding), *E. terminalis* and *E. leucophloia* water-logged plant roots were black.

Discussion

The genus *Eucalyptus* has adapted to different ranges of climatic and edaphic factors. Whereas no species grows in a permanently waterlogged condition, a few are able to grow in soil with some degree of waterlogging (Ladiges & Kelso 1977). The present study confirms the importance of adventitious root formation, at least in small *E. victrix*, as an adaptation to waterlogging. In addition, stem hypertrophy may also be considered an important adaptation in *E. victrix*. Production of adventitious roots was reflected in both rates of transpiration and stomatal conductance (Gomes & Kozlowski 1980a,b). Neither *E. terminalis* nor *E. leucophloia* produced any adventitious roots or showed stem hypertrophy when waterlogged. These species are presumed to be intolerant of waterlogging, as flood intolerant species seldom show any morphological changes and no recovery of gas exchange during the period of waterlogging (Tang & Kozlowski 1982). Species tolerant to the waterlogged condition often show reduced stomatal conductance and transpiration but recovered immediately after adventitious roots are formed (Gomes & Kozlowski 1980a,b). Hypertrophy (swelling) of the submerged portions of stems of *E. victrix* may assist with excretion of accumulated toxic compounds from the system (Gomes & Kozlowski 1986b). Production of adventitious roots may compensate for the death of older roots (Gomes & Kozlowski 1980a; Tsukahara & Kozlowski 1985).

Although no deaths occurred, waterlogging of *E. terminalis* and *E. leucophloia* reduced dry mass of both shoot and root. For both species, tips of lateral and tap roots had become very soft and some were visibly decaying. In addition, progressive decolouration was observed in a considerable number of leaves. It is emphasised that visual effects of waterlogging on these two species only started to become evident after 8-9 weeks. The rank of most flood tolerant to least tolerant is *E. victrix* > *E. leucopholia* > *E. terminalis*.

Adaptation to flooding by *E. victrix* is a combination of both morphological changes and responses (such as formation of adventitious roots and stem hypertrophy) and physiological adjustments (such as early stomatal closure and reduced transpiration rate). Further research is needed to study the effects of longer-term waterlogging on *E. terminalis* and *E. leucopholia*. Their absence from the floodplain is partially explained by the extent of detrimental effects and poor recovery following a period of waterlogging.

The process of adaptation to flooding by a single plant may require some time and transplanting shock is difficult to quantify (Megonigal & Day 1992). The use of seedlings of different ages clearly minimises initial root and shoot imbalances. The younger sets were of necessity not as well buffered to cope with flooding as seen for the lower root weights than shoot weights in 4- and 8-week seedlings compared with older sets. Established potted transplants of *E. victrix* appear to require 10-15 days for physiological adjustments. Younger, 14 cm height (13-week plants) are more sensitive than 19 cm height (17-week plants) in this respect. The relatively small mean height changes for all seedlings suggest that pot volume probably limited the expression of foliage material in the present study, whether plants were flooded or not.

Flooding may lead to much of the pre-existing root system being replaced with a new, morphologically distinct system (Hook 1984). Whether flood tolerant species can make continuous adjustments in root systems in response to periodic flooding is an interesting issue. Adventitious root development and intercellular air spaces are common responses to flooding. Adventitious roots are believed to confer tolerance to flooding (Gomes & Kozlowski 1980a; Kozlowski *et al.* 1991). Initiation of these roots is correlated with growth improvement in *E. camaldulensis* (Gomes & Kozlowski 1980a). Interestingly, the adventitious root material floated above the soil in the water tanks, although it is unclear whether this would be a useful adaptation in the field. Flooding of the Fortescue River valley is accompanied by considerable soil movement and it is possible that receding floodwaters could drop silt/clay material over any surface roots developed during a flood.

More detailed physiological analyses may have shown a change in transpiration rate in older flooded seedlings closer to the time at which adventitious roots had become visible, as seen for 4-month old *Fraxinus pennsylvanica* flooded seedlings (Gomes & Kozlowski 1980b). The production of adventitious roots is mainly due to flooding injury but may also be associated with ethylene production. Production of ethylene in unflooded plants has been associated with leaf epinasty (Denny & Miller 1935) and stem thickening (Zimmermann & Hitchcock 1933). Artificial application of ethylene releasing chemicals produces symptoms similar to those of flooding (Abeles 1973; Kawase 1974). Increased stem diameter may follow absorption of water by the bark. In *Eucalyptus globulus*, 10 days after flooding, the submerged portion of the stem had swollen (Gomes & Kozlowski 1980a). Similar observations apply to *E. viminalis*, *E. ovata* and *E. robusta* (Ladiges & Kelso 1977; Clemens & Pearson 1977).

Plant reactions to waterlogging vary with the duration, season, and tolerance to the stress (Ranney & Bir 1994). Root to shoot ratios may be expected to decrease in response to prolonged flooding (Megonigal & Day 1992). Although flooding time was equally long for all aged seedlings tested, *E. victrix* root/shoot ratios increased in the 17-week plants and decreased in response to flooding. In flooded conditions the soil becomes oxygen limited, in turn limiting physiological activity. Water and nutrient supplies through roots are reduced and the normal hormonal balance governing root shoot development can be disturbed (Kozlowski 1982). Flooded plants had a greater leaf area than control plants, at least for older plants, and leaf production did not appear inhibited by flooding. We hypothesised that a high seedling root/shoot ratio for *E. victrix* is an adaptation to drought. Despite its habitat being a floodplain, long dry periods occur each spring and longer droughts (with no flooding) are not uncommon. There is probably a change-over step when seedlings are large enough to permit sufficient bulk of new roots to replace those killed by the effects of flooding and this is associated with attained plant size at the onset of flooding. Alternatively, as all flooded plants had similar mean numbers of adventitious roots, perhaps the process simply requires more time in younger plants.

Observation suggests that seed dispersal of *E. victrix* occurs mainly in hot weather in summer (February to March), coincident with the greatest likelihood of rain (Florentine 1999). When capsules are ripe they dry rapidly, shedding the light seed that may blow some distance away. Germination is rapid at an optimum temperature of ~35-40 °C (Doran & Boland 1984) and is mainly effective in seedling production when seed falls onto moist sites just drying out from summer rain or flooding. The possibility of further flooding is high and this may lead to seedling submergence. The interest in this study was whether small seedlings of *E. victrix* can survive flooding. Field evidence suggests that established plants of 1-2 m can survive flooding but also that large numbers of summer germinating seedlings do not survive the following dry spring. The evidence obtained here suggests that seedlings of this species are remarkably tolerant of flooding, although total immersion has not been trialled.

In conclusion, there were significant difference in flood adaptations and response in gas exchange of 13- and 17- week old seedlings. In contrast, another two eucalypts were affected by flooding. This may explain why these species are absent from the floodplain area where *E. victrix* forms a unique patch of woodland. However, the relative impact of drought on *E. victrix* seedlings and the other species studied in this experiment has not been well documented. It will be worthwhile to examine those species and how they response to drought conditions.

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Terrestrial small mammals of the Abydos Plain in the north-eastern Pilbara, Western Australia

R A How & N K Cooper

Western Australian Museum, Francis Street, Perth WA 6000
email: ric.how@museum.wa.gov.au; norah.cooper@museum.wa.gov.au

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Abstract

Repeated surveys over three years of the 1500 km^2 Abydos/Woodstock Reserve, in the Pilbara of Western Australia, recorded 14 species of small terrestrial mammals including four endemic to the broader Pilbara area. Five species were captured frequently throughout the study. Captures of the dasyurids *Dasykaluta rosamondae* and *Ningaui timealeyi* increased when juveniles entered the population following seasonal breeding. Captures of the saxicoline rodent, *Zyzomys argurus*, showed relatively small fluctuations whereas populations of two other rodents, *Pseudomys hermannsburgensis* and *Mus musculus*, had 40 to 50 fold increase in captures between troughs and peaks, with peaks for both species occurring 18 months after the first of two major rainfall events. Species showed marked differences in their response to capture in Elliott and pitfall trap types; consequently, assemblage composition was compared in only eight habitats where both types were employed. The small mammal assemblage adjacent to a rocky breakaway differed to that on alluvial soil adjacent to the major creek, and to those in several *Triodia*-dominated habitats on the Abydos sandplain. The number of small mammal species and individuals in *Triodia*-dominated habitats decreased markedly after fire while similar habitats that remained unburnt over the same period showed an increase in both species and capture rates of individuals.

Keywords: dasyurid, rodent, trapping, capture rate, annual variation, habitat preference, fire response

Introduction

Several recent studies have evaluated or collated information on the demographic response of small mammal species to temporal changes in environmental variables across much of the extensive arid and semi arid landscapes of Australia (Masters 1993; Predavec 1994; Dickman *et al.* 1995, 1999, 2001; Carthew & Keynes 2000). There have also been important attempts to evaluate and explain changes in mammalian populations in response to environmental modifications imposed by European settlement (Morton 1990; Stafford-Smith & Morton 1990). Temporal and regional variations of murid rodent populations examined for over a decade have been synthesized by Dickman *et al.* (1999), who showed that the majority of species had a strong positive correlation between numbers and preceding rainfall. The nature of this correlation varied temporally for different species. Dasyurid marsupial populations showed less marked temporal changes, and these were generally correlated with changes in environmental variables other than rainfall (Masters 1993; Dickman *et al.* 2000). Arid regions cover 55 percent of Australia (Williams & Calaby 1985) but detailed studies of small mammal species have focused on populations in central and eastern Australia with only How *et al.* (1991) reporting on species in Western Australia.

Despite the large area and extensive development in the Pilbara there have been few attempts to systematically document the faunal diversity of the region on a systematic basis (Dunlop & Sawle 1980; How *et al.* 1991). As part of a three-year survey to document the faunal diversity of the Woodstock and Abydos stations, data were gathered on the composition and structure of numerous vertebrate assemblages in the area (How *et al.* 1991). These data provided baseline information on biodiversity for future management of the area (Berry *et al.* 1991) and were the first examination of seasonal and annual variation of vertebrate populations in one of the least known regions of arid Western Australia.

Agricultural and biological research has elevated Woodstock Station to the forefront of scientific understanding of the Pilbara region. Classical research on the ecology of the euro (Ealey *et al.* 1965; Ealey 1967a,b,c), vegetation (Burbidge 1943, 1945, 1959) and the effects of fire and grazing (Suijendorp 1955, 1967, 1980) provide unique information on arid zone ecology. The native mammal fauna has been documented over the last 50 years through collections lodged in the Western Australian Museum by numerous research scientists and by several studies on species biology (Woolley 1991a,b). Species whose first known records are from Woodstock Station include *Dasykaluta rosamondae* (Ride 1964), *Ningaui timealeyi* (Archer 1975), *Pseudomys chapmani* (Kitchener 1980) and *Pseudantechinus roryi* (Cooper *et al.* 2000); it is the type locality of *D. rosamondae* and *P. roryi.* At the completion of the Western Australian Museum survey in 1990, 31 species of mammals in 13 families had been recorded from the area, including four species (*Dasycercus cristicauda, Lagorchestes conspicillatus, Macrotis*

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lagotis, *Pseudomys chapmani*) that were listed as threatened taxa at that time (How *et al.* 1991).

In this study we examine the composition and habitat relationships of the small mammal assemblage on the Abydos Plain and document demographic changes for the more-frequently captured species over a three-year period.

Methods

Study area

The Abydos and Woodstock Stations cover an area of over 150 000 hectares of the northern Pilbara, 150 km south of Port Hedland. They cover the upper reaches of the Yule and Turner Rivers that drain north-westerly across a major physiographic unit of the Pilbara, the Abydos Plain (Fig 1). In 1882 two leases were granted which were to form the basis of Abydos Station, while a stone homestead was built on Woodstock Station in 1883/84 (Bindon 1979). Discovery of gold at Tambourah induced the Woodstock lessee to use the homestead as an inn until around 1898 when sheep grazing again became the primary land use. Grazing continued until the lease was taken over in 1945 by the Western Australian Department of Agriculture, which conducted research on the impacts of both grazing and fire on the vegetation of the region. In 1978 Abydos/Woodstock was vested in the Western Australian Museum and in February 1991 the vesting of the reserves was transferred to the indigenous people of the Mumbultjari Corporation.

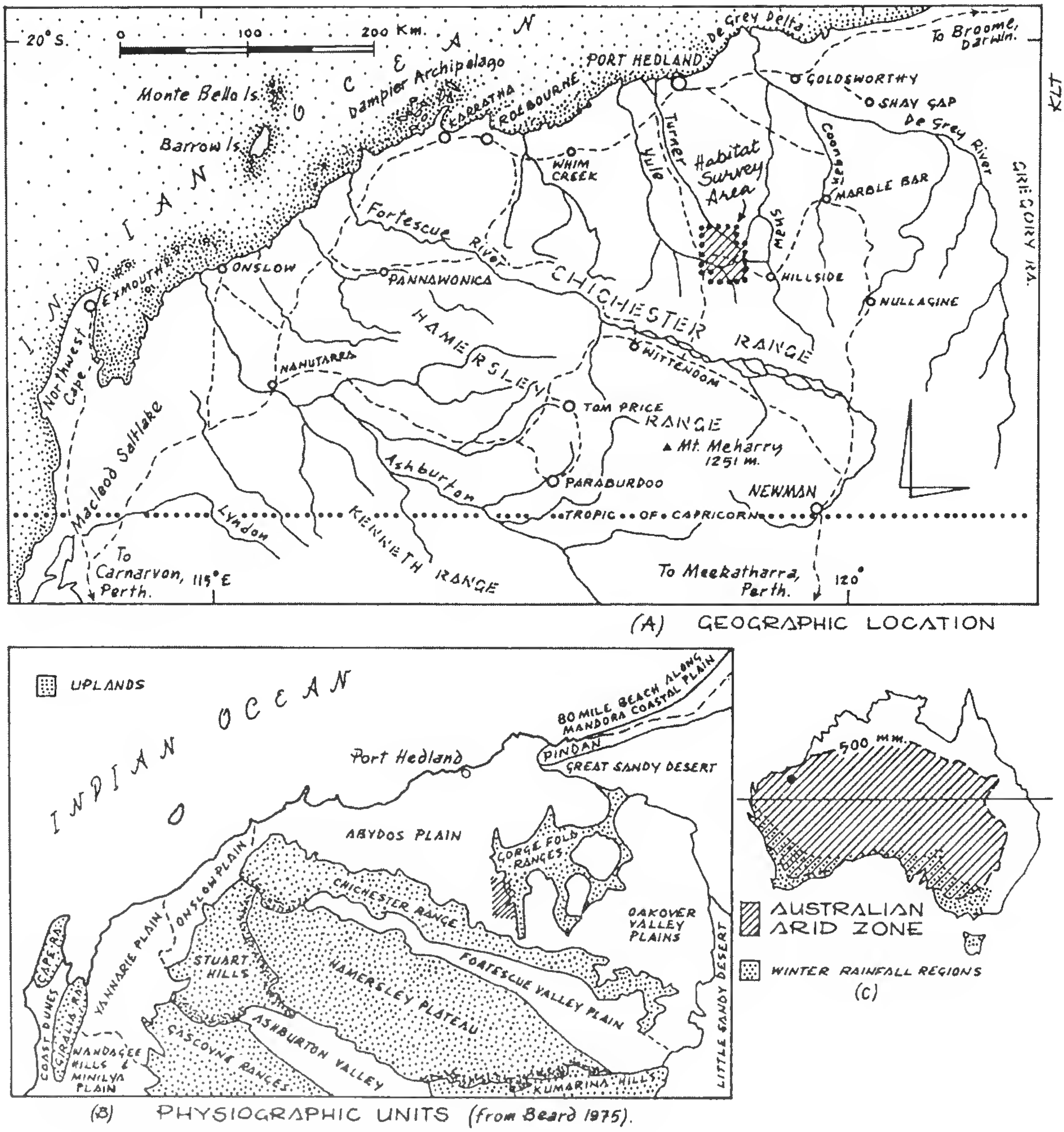

Figure 1. Geographic location of the Woodstock-Abydos Station study area and major physiographic units of the Pilbara region, including the Abydos Plain (after Tinley 1991a).

Table 1

Monthly and total rainfall registered at Woodstock Station for each month between January 1987 and October 1990.

Years	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	total
1987	95.2	78.8	0	0	4.8	0	8.5	0	0	0	0	23.0	210.3
1988	61.9	10.0	252.2	8.0	109.2	0.8	0	49.7	0	0.4	1.9	72.4	566.5
1989	63.4	227.0	0.4	46.2	9.0	117.9	2.3	0	0	0	4.0	11.2	484.4
1990	79.2	6.6	0	0	0	3.4	0	0	0	0			

The long-term climatic averages for the region are presented by Tinley (1991a). Over the three years of this study, rainfall showed significant seasonal and annual variation (Table 1). Major episodic rainfall events in March 1988 and February 1989 resulted in the flooding of Coorong Creek and all other ephemeral streams and drainage lines in its catchment.

Sampling sites and climate

The regional landforms and vegetation of the Abydos/Woodstock Reserve were described in detail by Tinley (1991b) and formed the basis for selecting sampling sites for the study of small mammals.

Eight sampling sites were selected to represent the major habitats identified on the sands of the Abydos Plain, while an additional 20 sites were selected to sample the granite tors on the Abydos Plain and adjacent rocky escarpments of the George Fold Ranges. The eight major sampling sites were:

WS1	*Eucalyptus camaldulensis*, *Melaleuca leucadendra* 5-8 m tall, 35% canopy cover, over *Acacia* sp 1-2 m tall, *ca* 5% canopy cover over *Cenchrus ciliaris* <0.5 m tall, *ca* 90% canopy cover. Site is narrow belt of riverine woodland on edge of Coorong Creek. Soil is deep alluvium.
WS2	*Acacia pyrifolia*, 2-3 m tall, 3% canopy cover, *Hakea suberea*, 2-3 m tall, <0.5% canopy cover and *Acacia* sp 2-3 m tall, <0.5% canopy cover over *Triodia* spp (2) *ca* 0.5 m tall, 80% canopy cover. Soil coarse sandy loam with granite bedrock at 30-40 cm and located 200 m from Coorong Creek. Site was burnt in January 1990.
WS3	*Triodia* spp <1 m tall *ca* 60% canopy cover with occasional *Acacia* spp as emergents. Soil red sandy loam in an ephemeral drainage line. Site was burnt in January 1990.
WS4	*Acacia pyrifolia*, 2-4 m tall, *ca* 5% canopy cover, over *Acacia ancistrocarpa*, 1.5-2 m tall, 50%-70% *Triodia* spp canopy cover. Occasional ephemerals after rain. Soil red sandy loam, >60 cm deep. Site was burnt in January 1990.
WS5	*Triodia secunda* and *T. longiceps* <0.5 m tall, *ca* 70% canopy cover. Soil white sandy silt over clay.
WS6	*Acacia orthocarpa*, 3-4 m tall, *ca* 7% canopy cover, and occasional *A. pyrifolia*, over *Triodia lanigera ca* 0.5 m tall, 50% canopy cover. Soil is skeletal red granitic sand.
WS8	*Eucalyptus terminalis*, 3-5 m tall, *ca* 2% canopy cover, over oval leaf wattle 1-1.5 m tall, *ca* 2% canopy cover, over *Triodia ca* 0.5 m tall, *ca* 40% canopy cover. Site includes valley between, and the steep slopes of calcrete mesas. Valley soil is calcareous clay loam.
WS10	*Acacia* sp 1.5-2.5 m tall, <0.5% canopy cover, *Hakea* sp 1.5-2.5 m tall, <0.5% canopy cover, over *Acacia* sp <1m tall, *ca* 3% canopy cover, over *Triodia* sp <0.5 m tall *ca* 60% canopy cover. Deep red loamy sand. Extensive surface water after heavy rain.

Fires were frequently seen around the study area, and small areas on the eastern edge were burnt in January and February 1989. In January 1990 lightning strikes started numerous small fires, three of which burnt out sampling sites WS2, WS3 and WS4 and several hundred hectares of the surrounding areas.

Sampling methods

The eight lines of fenced pitfall traps each comprised a 50-m long 30-cm high flyscreen mesh fence that crossed six pitfall traps inserted 600 mm into the substrate. Pitfall traps were generally made of 175 mm diameter PVC pipe 600 mm deep, but at several sites where the soil was less than this depth, piping was replaced with 400 mm deep conical pits. At each of the eight sampling sites a line of 15 Elliott Type A traps, baited with universal bait, were set 15 m apart and within 50 m of the fenced pitfall trapline. Fifteen Elliott Type B traps were used on rockpiles along with Type A traps. Traps were checked shortly after dawn and again in the late afternoon each day.

Sampling occurred in summer (February- March) and spring (September- October) in each of the three years, while three additional sampling periods examined activity at other times of the year. The nine surveys were undertaken between 21-31 March 1988, 2-9 May 1988, 22-30 September 1988, 9-17 February 1989, 16-24 April 1989, 16-24 September 1989, 26 February-7 March 1990, 25 July-2 August 1990 and 24 October-1 November 1990.

Regular trapping was undertaken on all surveys except May 1988, when only the fenced pitfall traplines were used, and April 1989 when, principally, Elliott traplines distant from the regular sampling sites were set. Only Elliott traps were set in areas where the substrate was either too rocky for fenced pitfall lines (screeslopes, rockpiles) or subject to seasonal inundation (creek beds).

All individuals captured were identified, measured and weighed to determine body mass. Voucher specimens were taken of all species.

Over all habitats and the nine sampling periods, there were 8131 Elliott trapnights and 2484 pitfall trapnights. Pitfall traplines were open on 58 days of the 74 days over which trapping occurred (Table 2).

Analyses

Least squares regression and analysis of variance were performed using the Statistix (1996) software package. Comparison of means between classes were made using Least Significant Differences with $\alpha = 0.05$. Assemblage analyses were carried out using the NTSYSpc (2000) program with UPGMA clustering of the Bray-Curtis index.

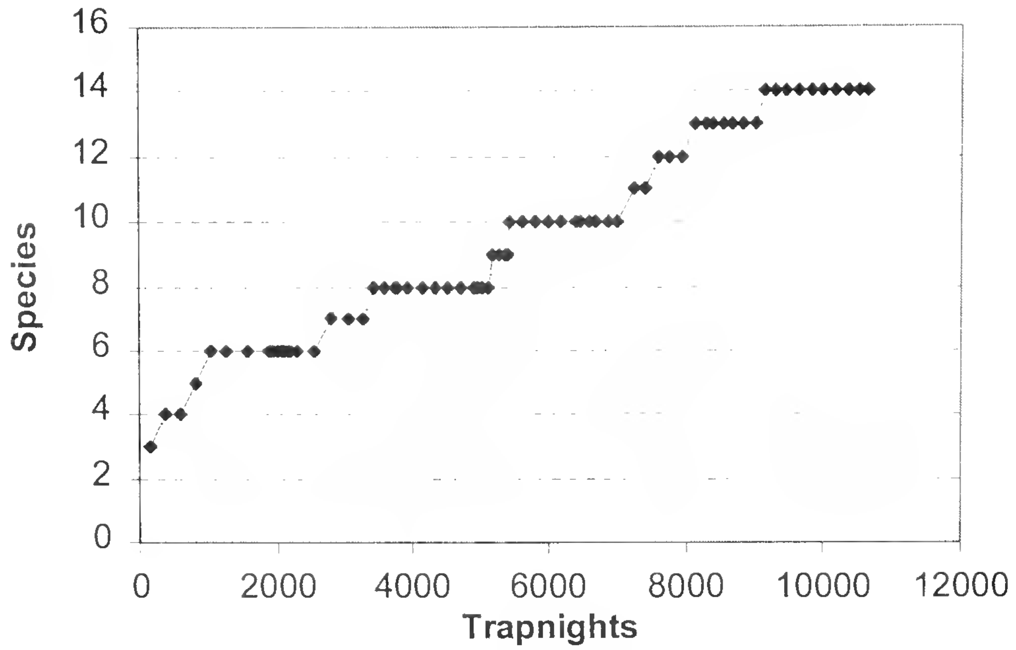

Figure 2. Cumulative number of terrestrial small mammal species captured for all trapnights between March 1988 and October 1990.

Results

Species

Fourteen species of small terrestrial mammals recorded on the Abydos Plain and associated landforms included nine dasyurid marsupials (*Dasyurus hallucatus*, *Dasycercus cristicauda*, *Dasykaluta rosamondae*, *Ningaui timealeyi*, *Planigale* sp, *Pseudantechinus roryi*, *Pseudantechinus woolleyae*, *Sminthopsis macroura*, *Sminthopsis youngsoni*) and five murid rodents (*Mus musculus*, *Pseudomys delicatulus*, *Pseudomys chapmani*, *Pseudomys hermannsburgensis*, *Zyzomys argurus*). Four species (*Planigale* sp, *S. macroura*, *S. youngsoni*, *P. delicatulus*) were recorded for the first time on the Abydos Plain. Recording of new species towards the end of the 74 trapping days (Fig 2), indicates that additional species may still be found in the area.

Three groups of species can be recognised on the basis of their response to capture in different trap types; those preferentially caught in Elliott traps (*D. hallucatus*, *S. macroura*, *P. woolleyae*, *P. chapmani*, *Z. argurus*), those preferentially caught in pitfall traps (*D. cristicauda*, *N. timealeyi*, *Planigale* sp, *S. youngsoni*, *P. delicatulus*) and those caught in both types of trap (*D. rosamondae*, *P. roryi*, *P. hermannsburgensis*, *M. musculus*) but more frequently in Elliotts (Fig 3). Four species (*S. macroura*, *S. youngsoni*,

Table 2

Number of captures of small mammal species in pitfall and Elliott trap types on the Abydos Plain during nine sampling periods between March 1988 and October 1990. Total number of pitfall/Elliott traps set during each sampling period is also presented.

	1988			1989			1990			total
	Mar	May	Sep	Feb	Apr	Sep	Mar	Jul	Oct	
D. cristicauda	0/0	0/0	0/0	0/0	0/0	0/0	1/0	0/0	0/0	1/0
D. hallucatus	0/0	0/0	0/0	0/0	0/4	0/3	0/3	0/0	0/1	0/11
D. rosamondae	2/1	0/0	4/5	0/1	0/0	5/3	1/18	1/1	0/9	13/38
N. timealeyi	4/0	5/0	4/0	4/0	0/0	12/0	3/0	1/0	3/0	36/0
Planigale sp	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/0
P. roryi	0/0	0/0	0/0	0/0	0/1	0/0	0/0	1/5	0/3	1/9
P. woolleyae	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/1	0/1	0/2
S macroura	0/0	0/0	0/1	0/0	0/0	0/0	0/0	0/0	0/0	0/1
S. youngsoni	0/0	0/0	0/0	0/0	0/0	0/0	1/0	0/0	0/0	1/0
M. musculus	0/3	0/0	0/15	0/6	0/2	3/75	0/8	0/2	0/4	3/115
P. chapmani	0/0	0/0	0/0	0/0	0/0	0/4	0/1	0/1	0/0	0/6
P. delicatulus	0/0	0/0	2/0	1/0	0/0	0/0	0/0	0/0	0/1	3/1
P. hermannsburgensis	2/2	0/0	0/1	4/2	0/0	3/40	2/6	7/14	1/15	19/80
Z. argurus	0/10	0/0	0/7	0/0	0/1	0/9	0/19	0/10	0/11	0/67
Total terrestrial mammals	25	5	39	18	8	157	63	44	49	408
Trap nights	324/1560	282/0	312/1240	318/1240	24/448	240/1017	432/1167	216/782	336/1017	2484/8131

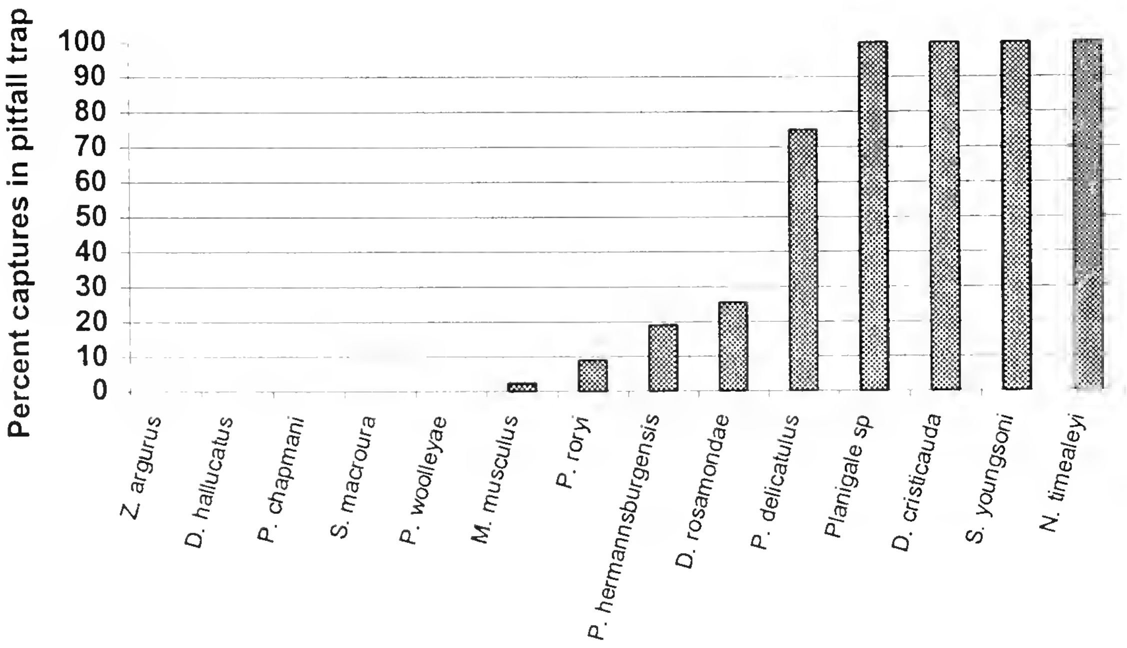

Figure 3. Percentage of captures of each species made in pitfall traps.

Planigale sp and *D. cristicauda*) were represented by a single individual in the regional assemblage. The capture rate of all small mammal species over all species, sites and sampling periods averaged only 3.84 per hundred trapnights (Table 2). The 8131 Elliott trapnights resulted in the capture of 330 individuals of 10 small mammal species and the 2484 pitfall trapnights in the capture of 78 individuals of 9 species.

Five species recorded during most sampling periods (*D. rosamondae, N. timealeyi, M. musculus, P. hermannsburgensis, Z. argurus*) provided information on temporal variation in body mass, population capture rates and reproductive status. These five species were examined for sexual dimorphism in body size, determined by head-vent length, and body mass. Only *N. timealeyi* showed sexual dimorphism, with males significantly larger (P = 0.0045) and heavier (P = 0.0003) than females. The mean body mass for adult females of each species during the study is presented in Table 3. No significant changes occurred in body mass of adult female *D. rosamondae* or *N. timealeyi* throughout the survey. For *Z. argurus*, highest female mass occurred in March 1988 compared to September 1988, 1989 and October 1990. Female *P. hermannsburgensis* had higher body mass in March 1990 than July 1990, September 1989 and October 1990. The highest body mass of *M. musculus* females occurred during February (Table 3).

Capture rates of these five species were generally less than one individual per 100 trapnights throughout the survey. Capture rates during both May 1988 and April

Table 3

Body weight (grams) of adult females of the five common small mammals of the Abydos Plain. Data for each sampling period are presented as mean ± standard deviation with sample size in parentheses.

	D. rosamondae	*N. timealeyi*	*M. musculus*	*P. hermannsburgensis*	*Z. argurus*
March 1988	-	4.8±2.0(2)	10.5(1)	12.0±1.4(2)	45.0±3.6(6)
May1988	-	4.5±1.0(3)	-	-	-
September 1988	27.0(1)		11.7±3.8(7)	-	32.9±8.4(4)
February 1989	-	3.3±0.3(3)	18.5±2. 8(3)	12.6(1)	-
April 1989	-		-	-	-
September 1989	28.5±0.7(2)	5.1±0.1(2)	9.6±2.6(31)	9.9±2.2(19)	34.4±11.0(6)
March 1990	29.0±4.2(2)	4.4±1.9(3)	12.0±0.9(3)	13.5±3.2(3)	36.3±9.4(8)
July 1990	-	3.5(1)	-	9.4±2.8(11)	35.7±1.2(3)
October 1990	22. 5±2.9(8)	6.0(1)	9.0±2.2(3)	10.0±0.7(5)	34.7±6.6(7)
Significant Differences (P<0.05)			Feb89>Oct90, Sep89, Mar88, Mar90, Sep88, Jul90	Mar90>Oct90, Sep88, Jul90	Mar88>Oct90, Sep89, Sep88

Table 4

Capture rates of the five common small mammal species of the Abydos Plain during major sampling periods presented as number of captures per 100 trapnights. The percentage change from March 1988 (taken as 100%) is given in parentheses. Only periods when both trap types were employed are evaluated for determining variation = peak/trough capture rates.

	Mar-88	Sep-88	Feb-89	Sep-89	Mar-90	Jul-90	Oct-90	Variation
Trapnights	1884	1552	1218	1257	1599	998	1353	
D. rosamondae	0.16(100)	0.58(364)	0.08(52)	0.64(399)	1.19(746)	0.20(126)	0.67(418)	14.9x
M. musculus	0.16(100)	0.97(607)	0.49(309)	6.21(3897)	0.50(314)	0.20(125)	0.30(186)	38.8x
N. timealeyi	0.21(100)	0.26(121)	0.33(154)	0.95(450)	0.19(88)	0.10(47)	0.22(104)	9.5x
P. hermannsburgensis	0.21(100)	0.06(30)	0.49(232)	3.42(1611)	0.50(235)	2.10(991)	1.18(557)	57.0x
Z. argurus	0.53(100)	0.45(85)	0	0.72(135)	1.19(224)	1.00(189)	0.81(153)	2.6x

1989 are not regarded as representative of population trends as both trap types were not used during these sampling periods. The change in capture rates of the five species between sampling periods is summarised in Table 4 and the percentage change between March 1988 and each subsequent sampling period is also documented. The first sampling period of March 1988 coincided with the end of a three-year dry spell and numbers of all species were expected to be at a minimum. *D. rosamondae* capture rate was highest in March 1990, when a relatively large number of juvenile individuals was caught, and lowest in February 1989. The highest capture rate of *N. timealeyi* occurred in September 1989 and the lowest in July of 1990. The capture rates of these two species of dasyurid and the rock rat (*Z. argurus*) showed relatively small variation throughout the survey, with peaks and troughs varying between 2.6 and 14.9 times (Table 4). Peak activity of *M. musculus* and *P. hermannsburgensis* occurred in September 1989, when capture rates were 39 times and 57 times greater than during troughs in March 1988 and September 1988, respectively. *Mus musculus* also showed an increase of 600 percent in capture rate between March 1988 and September 1988 while capture rates of *P. hermannsburgensis* declined to 30 percent over the same period (Table 4). Spearman rank correlation showed no significant concordance of pattern for any of the five species between seasonally ranked capture rates and adult body mass, indicating that no species attained maximum capture rates at the time of best body condition.

A female *D. rosamondae* collected in September 1989 was in oestrus. Three juveniles were captured in March 1988, one in February 1989 and sixteen (8 females, 8 males) in March 1990. These juveniles had an average body weight of 18.9 ± 2.7g compared with 29g for two adult females captured in the same season. No adult males were trapped in February or March of any year. Female *N. timealeyi* with 5 pouch young were trapped in March 1988 and March 1990. The average crown-

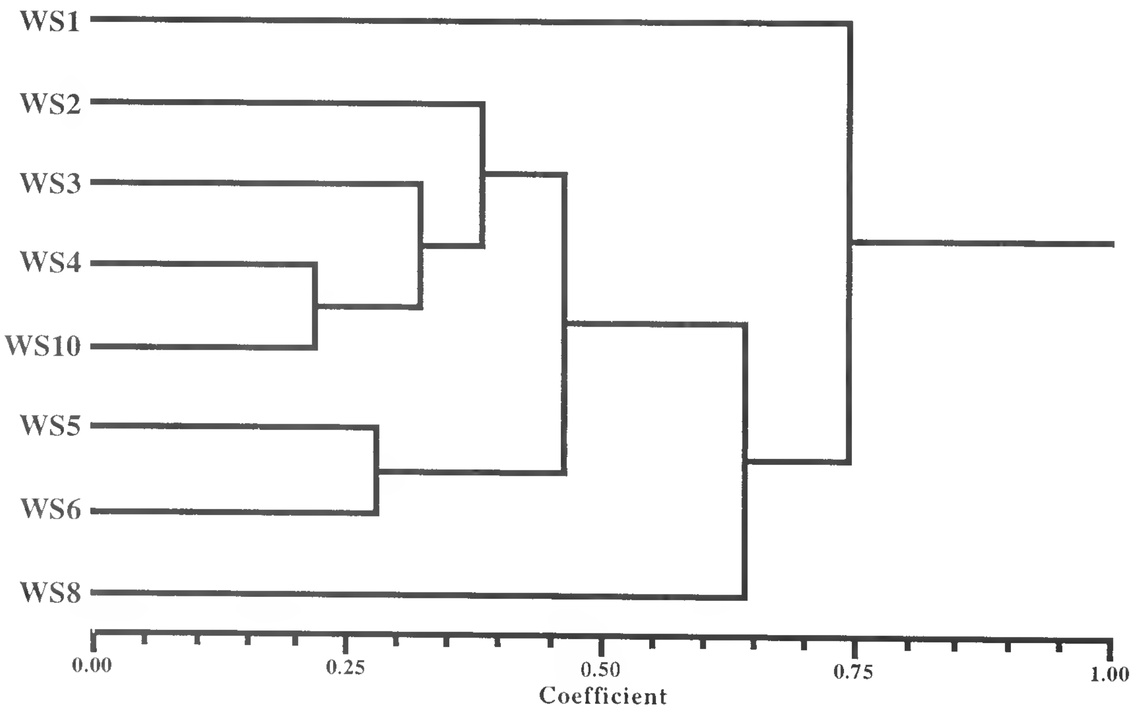

Figure 4. Dendrogram of similarity between the eight major habitats surveyed based on their small mammal assemblages. Bray-Curtis similarity indices were clustered using UPGMA.

Table 5

The number of captures of each small mammal species on each of the intensively trapped sampling sites on the Abydos Plain.

SITES	WS1	WS2	WS3	WS4	WS10	WS5	WS6	WS8
D. cristicauda	0	0	0	0	1	0	0	0
D. hallucatus	0	0	0	1	0	0	0	0
D. rosamondae	0	2	4	8	4	10	11	1
M. musculus	37	24	10	10	10	5	0	4
N. timealeyi	0	3	7	4	6	0	4	12
P. chapmani	0	0	0	0	0	0	0	0
P. delicatulus	1	0	0	1	0	0	0	1
P. hermannsburgensis	0	10	3	13	21	8	11	2
P. roryi	0	1	0	1	1	0	0	0
P. woolleyae	0	0	0	0	0	0	0	1
Planigale sp	0	0	0	0	0	0	0	1
S. macroura	0	0	0	0	0	1	0	0
S. youngsoni	0	0	0	0	1	0	0	0
Z. argurus	0	0	0	0	0	0	0	4

rump length for each litter was 8.6 mm. Adults were caught in each trip (except July 1989 when no pit-traps were open) and juveniles were caught on all trips except July 1990 and September 1988. Pregnant *P. hermannsburgensis* were trapped in February 1989, September 1989 and March 1990, but parous females were trapped on all other trips except for October 1990 when adult females were neither pregnant nor parous. Female *Z. argurus* were pregnant on each spring and summer sampling. Pregnant *M. musculus* were caught on almost all trips between February 1989 and March 1990 and over 30 juveniles were captured in September 1989.

Habitat relationships

Several taxa were confined, or predominantly restricted to, specific habitats when all sampling techniques and habitats were considered. All *P. chapmani* were caught in Elliott traps on pebble mounds on the scree slopes of the George Fold Range adjacent to the Abydos Plain, while the majority of *D. hallucatus, P. roryi, P. woolleyae* and *Z. argurus* were trapped in Elliott traps on or adjacent to the granite tors and rockpiles. All three *Pseudomys* species were captured in Elliott traps on a single pebble mound on scree slopes.

Comparisons of small mammal assemblages were confined to the eight habitats where both trap types were employed due to the varied capture responses of individual species to differing trap type (Fig 3). The similarity between these eight habitats based on their small mammal assemblages is presented in Fig 4. Three clusters are recognisable at greater than 50% similarity. These conform to three discernibly different habitat groups among the eight compared. Bunchgrass on the deep alluviums adjacent to Coorong Creek (WS1) is markedly different to sites located on the broad sandplain dominated by *Triodia* species and occasional *Acacia* shrubs (WS2, WS3, WS4, WS5, WS6 and WS10) and the loams adjacent to the only calcrete breakaway sampled (WS8). Only two species (Table 5) were recorded at WS1, *M. musculus* and *P. delicatulus*. Three species were trapped only at WS8 (*P. woolleyae, Planigale* sp, *Z. argurus*). *Mus musculus* was numerically dominant (Table 5) at WS1 and WS2 with all captures at other sites occurring on or after the major population eruption of September 1989.

The small mammal species and individuals caught in three *Triodia*-dominated sandplain sites before and after the burn in January 1990 (WS2, WS3, WS4) and those caught in three other *Triodia*-dominated sites that remained unburnt throughout the study (WS5, WS6, WS10) are summarised in Table 6. Fewer species and individuals were trapped in burnt sites after the fire, while in the 'control' sites more species and individuals were trapped in the three sampling periods after the January 1990 fires than in the six sampling periods before it. Three species were caught in Elliott traps in recently burnt areas (Table 6); all in traps placed in unburnt *Triodia* patches within 50 metres of the burnt fenced pitfall traplines. No individuals were pitfall trapped in recently burnt areas and there was no evidence of mass migration into unburnt habitats after fire.

Table 6

Mammal species and individuals caught on three Abydos Plain sampling sites (WS2, WS3, WS5) before and after they were burnt in January 1990, and three 'control' sites (WS5, WS6, WS10) that remained unburnt throughout the study.

	Burnt Sites		Unburnt Sites	
	Pre1990	Post1990	Pre1990	Post1990
Trapnights	2019	940	1723	996
D. hallucatus	1	0	-	-
D. cristicauda	-	-	0	1
D. rosamondae	14	0	6	19
N. timealeyi	14	0	8	2
P. roryi	0	2	0	1
S. macroura	-	-	1	0
S. youngsoni	-	-	0	1
M. musculus	41	3	13	2
P. delicatulus	1	0	-	-
P. hermannsburgensis	9	17	25	15
Total Species	6	3	5	7
Total Individuals	80	22	53	41
Individuals per 100 trap nights	3.96	2.34	3.08	4.12

Discussion

Fourteen species of terrestrial small mammal have been recorded from the Abydos Plain. This represents a diverse community when compared with other locations in central Australia (Masters 1993), the southern Pilbara (Dunlop & Sawle 1980; Anstee, Hamersley Iron, personal communication) and the eastern Pilbara (P Kendrick, CALM, personal communication). Included in this diverse assemblage are four species (*D. rosamondae, N. timealeyi, P. roryi, P. chapmani*) endemic to the Pilbara and regions immediately adjacent, while the distribution of *Z. argurus* in arid Australia is confined to the Pilbara and adjacent offshore islands (Fleming 1996). Despite over 50 years of scientific investigation of the Woodstock and Abydos Stations, four small mammal species were recorded for the first time during the study and it is probable that additional species will be recorded (Fig 2) with greater sampling effort. An examination of the distribution of mammal specimens in the Western Australian Museum collection indicated that other rodents (*e.g. Notomys alexis, Pseudomys desertor, Leggadina lakedownensis*) and a dasyurid marsupial (*Sminthopsis longicaudata*) could occur on the Abydos Plain.

Two of the five species captured regularly through the study, *D. rosamondae* and *N. timealeyi*, are endemic to the Pilbara region and there have been no previous studies of their natural populations. A recent synthesis of information on a third Pilbara endemic, *P. chapmani*, has led to that species being removed from Western Australia's Threatened Fauna list (Start *et al.* 2000).

Reproduction

Both of the commonly captured dasyurid marsupials had broadly seasonal patterns of reproduction. *Dasykaluta rosamondae* has a male die-off in October, and up to eight young are weaned in February and March (Woolley 1991b). It is the only dasyurid in arid Australia that has a synchronised annual male die-off. This was confirmed during this study when a male, in 'poor condition' and losing fur, was caught by hand during the day in late October 1990, and by the absence of adult males but the presence of numerous juveniles in the population during February and March sampling periods. The observed reproductive status of *N. timealeyi* on the Abydos Plain complements earlier studies (Dunlop & Sawle 1982; Kitchener *et al.* 1986) that determined females had six teats and a breeding peak between September and March; adult males were present in the population throughout the year. Dickman *et al.* (2001) showed breeding occurring in late winter and spring in field populations of the dasyurids *S. youngsoni* and *D. cristicauda* in the Simpson Desert.

The three frequently trapped rodent species on the Abydos Plain had markedly different reproductive patterns and potential. Both *Z. argurus* and *P. hermannsburgensis* have four teats (two inguinal pairs) while *M. musculus* has 12 teats (three inguinal and three pectoral pairs) (Watts & Aslin 1981) and thus a greater reproductive potential. *Zyzomys argurus* showed evidence of reproductive activity in most sampling periods and juvenile and sub-adult animals were present throughout the study. This contrasts with populations of this species in Arnhem Land (Begg 1981) and the north Kimberley (Bradley *et al.* 1988) where peak reproductive activity occurred at the end of the wet season (April) with populations in the north Kimberley also showing major temporal and spatial changes in abundance (Bradley *et al.* 1988). *Pseudomys hermannsburgensis* has the potential to breed at any time of the year (Breed 1982, 1990) and reproductive activity was apparent in most sampling periods on the Abydos Plain. The reproductive potential of *M. musculus* has been well documented in Australia over many years and in numerous areas (Newsome 1969; Chapman 1981; Singleton & Redhead 1991; Masters 1993). The presence of adult female *M. musculus* in reproductive condition during all sampling periods on the Abydos Plain illustrates the species' latent reproductive ability and its capacity to respond quickly to improved environmental conditions.

Population fluctuations

The commonly captured rodents and dasyurid marsupials on the Abydos Plain also showed different fluctuations in numbers caught over the three-year study. Neither of the dasyurid species showed large population fluctuations despite two consecutive summers with above average rainfall (Table 4). Variation in capture rates for both dasyurids are more readily explained by the introduction of juveniles into the population after seasonal reproductive events. Masters (1993) also found only slight increases in dasyurid populations over three-years at Uluru and showed they contrasted with rodents in their demographic correlates with environmental variables; only one dasyurid had 'cumulative deviation from mean rainfall' as a significant positive correlate with numbers, while the populations of the four rodent species showed significant correlation with previous rainfall (Masters 1993). Dickman *et al.* (2001) described capture rates of all dasyurid species in the Simpson desert as low, 'as in many other studies of arid zone dasyurids', and showed that capture rates were associated with different environmental variables in each of the three species they studied.

Capture rates of *M. musculus* and *P. hermannsburgensis* were 40-50 times higher in the peaks than the troughs on the Abydos Plain. However, *Z. argurus*, like the two dasyurids, had small changes in capture rates throughout the study. Decreased abundance of *Z. argurus* populations occurred during April in both Arnhem Land (Begg 1981) and the north Kimberley (Bradley *et al.* 1988). No captures of this species were made in the study area during February 1989, while in April 1989 a single juvenile was captured. The highest capture rates of *M. musculus* and *P. hermannsburgensis* occurred in September 1989, some 18 months after major rainfall in March 1988 and seven months after the equally heavy summer rains of February 1989. There was no population eruption in *P. hermannsburgensis* within the first 12 months after the major post-cyclonic rains of March 1988; however, by September 1989 capture rates were over 50 times that of the preceding September (Table 4). Capture rates increased six times in *M. musculus* from March 1988 to September 1988 and to nearly 39 times by the following September. The contrast in species responses to the first post–cyclonic rainfall in March 1988 can be seen by the fact that *P. hermannsburgensis* capture rates declined to 30 percent by September 1988 while *M. musculus* had increased by 600 percent over the same period (Table 4).

Dickman *et al.* (1999) collated information on long-term population changes for four rodents (*M. musculus, N. alexis, P. hermannsburgensis, P. desertor)* in arid Australia and showed that they erupted after significant rainfall periods but remained in low numbers or were absent during droughts. Population peaks occurred two months after rain for *M. musculus*, but between three and 10 months after rain for *N. alexis, P. hermannsburgensis* and *P. desertor*. Numerical changes between population peaks and troughs for all rodent species were several orders of magnitude and all species disappeared from the trap record on some occasion (Dickman *et al.* 1999). Dickman *et al.* (1999) also modelled the relationship between the cumulative mean rainfall residual (CMRR) and small mammal abundance to show that, for most species, there was a strong positive correlation between rodent population peaks and the impact of earlier rainfall events. However, not all populations in all areas followed their predictive model. *P. hermannsburgensis* populations erupted at Uluru in 1993-94 in the absence of significant rainfall while *P. hermannsburgensis, N. alexis* and *P. desertor* populations failed to respond to the significant summer rains of 1986-87 in the Tanami Desert area. They suggested that variation in numerical responses both within and between species may result from differing reproductive potential of the species, lower starting densities (possibly maintained by predation) or differences in resource states for species between study areas. Predavec (1994) also indicated that population structure in desert rodents fluctuated by 40 times between the peaks and troughs with a lag of four months between a rainfall event and peak density. *Mus musculus* populations at Uluru required prolonged exposure to wet conditions after an extended drought before showing major population peaks (Masters 1993). Similar responses in activity of *M. musculus* were encountered during this study.

On the Abydos Plain, the drought-breaking rains of March 1988 did not precede peak capture rates in any of the five common species either two months (May 1988) or six months (September 1988) later, although lag times of two to six months led to significant increases in rodent populations in central and eastern arid areas of Australia (Predavec 1994; Dickman *et al.* 1999). A second, major summer rainfall event on the Abydos Plain in February 1989 had little impact on rodent populations by April 1989. However, by September 1989 capture rates of both *M. musculus* and *P. hermannsburgensis* had peaked at around 7–12 times the levels noted in February of 1989, and between 40 and 50 times those of population troughs some 12 to 18 months previously. Changes in capture rates of the saxicoline rodent *Z. argurus* and the dasyurids *D. rosamondae* and *N. timealeyi* were far less than these over the three years of sampling. The former occurs in the less variable environments associated with granite tors and rock outcrops, while the latter marsupials have differing yet seasonal reproductive patterns (Lee *et al.* 1982) that are not conducive to eruptive population responses to improved environmental conditions.

Differences between arid zone dasyurids and rodents also extend to diet. A study of 16 species of arid rodents (including several species examined in this study) concluded that the dietary pattern was 'overwhelmingly' omnivorous (Murray *et al.* 1999) while the diets of six arid zone dasyurid species (Fisher & Dickman 1993) were almost exclusively insectivorous. The most obvious initial environmental response to major rainfall in arid areas is the flush of new vegetative growth, generally followed by seeding in grasses and an increase in invertebrate activity. Our studies on the Abydos Plain included an examination of invertebrate diversity (Harvey & Waldock 1991) that increased in the first six months following rain (M Harvey, WA Museum, personal communication), a pattern of increase similar to that documented by Fisher & Dickman (1993). Increased invertebrate activity increases prey availability for insectivorous marsupials; however, being seasonal breeders with fixed litter sizes (based on the number of teats), their demographic response will be restricted to either improved survival of pouch young or recently independent juveniles.

Body mass

Our examination of body mass changes of the five frequently trapped small mammals showed no significant changes occurred for adult female *N. timealeyi* or *D. rosamondae* during the study, even though invertebrate abundance increased after major rainfall at the start of the study. For *Z. argurus*, maximum female body mass was recorded in the populations during March 1988, the period during which major post-cyclonic rainfall broke a three-year long dry spell (Tinley 1991a). *Pseudomys hermannsburgensis* females were heaviest during March 1990 when body mass was significantly higher than during either the population peak of September 1989 or the declining populations of July and October 1990. The peak body mass of female *M. musculus* occurred during February 1989, immediately after the second above average summer rainfall and prior to the population peak of September 1989.

Habitat associations

In both arid and semiarid regions of Western Australia's eastern Goldfields, rodents were preferentially trapped in box traps while dasyurid marsupials were more frequently caught in fenced pitfall traps (How *et al.* 1984). Our study has shown major differences between species in their response to capture in different trap types for the Pilbara area (Fig 3). Consequently, only habitats where both trap types were employed were used to interpret assemblage structure (Table 5) and species habitat associations (Fig 4).

Three major habitat groupings were recognised for the terrestrial small mammal species. The deep alluvial soils and tussock grasses adjacent to Coorong Creek contained only *M. musculus* and a single *P. delicatulus*, while the most diverse assemblage was recorded on calcareous clay loams covered by *Triodia* adjacent to a calcrete breakaway. The third group of habitats included all six sampling sites that were dominated by *Triodia* and *Acacia pyrifolia* (Table 5). Although *M. musculus* were present throughout the study area, they were most abundant in the tussock grass banks associated with Coorong Creek; captures away from this habitat occurred when populations were at a peak and individuals appear to have expanded into the surrounding *Triodia* habitats. In central Australia, *M. musculus* is a poor coloniser of

Triodia-dominated habitats and only survives in those habitats in wet years (Masters 1993).

The largest variety of habitats sampled during the study were in or adjacent to rocky slopes of the George Fold Ranges and the abundant granite tors on the Abydos Plain; these habitats were sampled using only Elliott traps. The Western Pebble Mound Mouse, *P. chapmani*, was restricted to the rocky slopes associated with the George Fold Ranges, while the majority of captures of *D. hallucatus, P. roryi, P. woolleyae* and *Z. argurus* were made in and around the granite tors. The granite tors of the Abydos Plain were focal habitat for many faunal species (How *et al.* 1991) including several small mammals, two species of macropod, four bats and numerous snakes and lizards. The capture of three *Pseudomys* species in sympatry on a pebble mound on the scree slopes illustrates that both *P. hermannsburgensis* and *P. delicatulus* will move onto rocky substrates.

Numbers of most small mammals were generally lowest on the Abydos Plain at the commencement of the study in March 1988, a sampling period that occurred at the end of a three year long dry spell and during heavy rain associated with a post-cyclonic depression. We did not detect changes over the study in predator populations although numerous predatory species were present including introduced (fox and cat) and native (*D. cristicauda, D. hallucatus*) mammals, various raptors, monitors and snakes (How *et al.* 1991). Competition between granivorous species that use the abundant seed-set of *Triodia* and *Acacia* following major rainfall has not been evaluated as a mechanism influencing rodent population responses to increased food availability. The granivorous bird guild on the Abydos Plain showed a change in flock size and dispersion over the study (How *et al.* 1991) that differed between species but, overall, reflected a change to more aggregated and larger flock sizes with increasing time since major rainfall events. Rabbits, a key agent in competing with native species and altering environments in arid Australia (Morton 1990), were absent from the study site. They have been infrequently recorded in the north-eastern Pilbara where shallow soils are unsuitable for burrow systems and *Triodia* spp are unsuitable for forage (King 1990).

Fire response

The response of rodents to fire in arid Australia has been well documented (Friend 1993; Masters 1993; Southgate & Masters 1996; Sutherland & Dickman 1999). Our data show that, in *Triodia* dominated habitats where similar assemblages occur, fewer species and fewer individuals were trapped in habitats following fire than in habitats that remained unburnt throughout the study (Table 6). However, there was no indication that the widespread but small-scale burns of February 1990 had any discernable impact on total mammal populations, several of which were declining following peaks in capture rates across the Abydos Plain.

Fires were not considered to have had a significant impact on the eruptive response of rodent populations at either Uluru or Tanami study sites by Dickman *et al.* (1999) as they preceded the onset of the eruptive cycle. Additionally, it has been shown that many mammal species exhibit large-scale movements in *Triodia* communities of the arid zone (Dickman *et al.* 1995, 2001) that would enable them to avoid or move quickly through small-scale burn patches. Fire has been suggested as a major management technique for maintaining the diversity of small mammal assemblages across a mosaic of successional communities at Uluru (Masters 1993). The fires on the Abydos Plain could similarly assist in maintaining the small mammal diversity by leaving refugia for species and developing an array of successional habitats across the landscape.

The diverse assemblage of terrestrial small mammals sampled during this three year study in the arid north-eastern Pilbara showed well defined habitat preferences in most species, differing species responses to trap types and highly variable responses to changing environmental conditions following major rainfall events. Two rodents exhibited very high rates of capture about 18 months after the first major post-cyclonic rain, although most of the remaining 12 species had low rates of capture throughout the study. Continued sampling is likely to increase the number of species known from this environmentally heterogeneous area.

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Morphology and origin of three bornhardt inselbergs near Lake Johnston, Western Australia

J A Bourne & C R Twidale

Department of Geology & Geophysics, Adelaide University, Adelaide SA 5005
email: rowl.twidale@adelaide.edu.au

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Abstract

Three domical inselbergs or bornhardts, Disappointment, McDermid and Bank Rocks, located near the Hyden-Norseman road in the south-eastern corner of the Yilgarn Craton, are described and analysed. All are basically similar in origin, being due to differential fracture-controlled subsurface weathering followed by the stripping of the weathered mantle. Disappointment Rock is older and topographically more subdued than either McDermid or Bank Rocks; it is located further from the Lake Johnston valley and has not been as greatly exposed. McDermid and Bank Rocks display spectacular flared slopes, whereas those developed at Disappointment Rock probably remain hidden by the lateritic regolith. All three Rocks display a similar range of minor forms, some due to subsurface weathering, others to weathering after exposure of the rock surface, yet others to contrasted rates of weathering on wet and dry surfaces. Some are due to protection against water attack, others reflect bedrock characteristics, and yet others the effects of gravity. Recent earth movements, as evidenced in neotectonic landforms, have affected all three residuals.

Keywords: Yilgarn Craton, bornhardt, origin, age, palaeodrainage, granitic landforms, Disappointment Rock, McDermid Rock, Bank Rock

Introduction

Like many other cratons, the Yilgarn Block of the south-west of Western Australia is characterised by plains interrupted by ranges or, in areas of granitic outcrop, domical hills or bornhardts. Hyden Rock is well known for the high concave, or flared, slope - Wave Rock - exposed on its northern flank, but most of the other granite hills scattered over the Yilgarn remain undescribed. Yet many features typical of granite outcrops, including some of particular interest, are exposed on them. The purpose of this paper is to give an explanatory account of three bornhardts, Disappointment, McDermid and Bank Rocks. They are located on either side of Lake Johnston, near the south-eastern margin of the Craton (Fig 1). The evolution of the bornhardts, and of the assemblages of minor features developed on them, can be deduced from the regional setting and the local evidence. It is hoped that this account will entice natural scientists to them, for they have much to offer the interested lay person as well as the specialist geologist or geomorphologist.

The evolution of the landscape in that part of the Craton is first reviewed. Some comments on the evolution of bornhardts and of the more common minor forms are presented by way of background, but also with reference to the development of the bornhardts as gross forms. This is followed by an account of the detailed evolution of each of the three bornhardts.

Landscape evolution of the Lake Johnston area

The region under review is underlain by Archaean gneisses and granites with intruded basic dykes and sills (Doepel *et al.* 1972; Gower & Bunting 1976). Following the disappearance of the Late Palaeozoic ice sheets which occupied all or most of what is now southern Australia (BMR Palaeogeographic Group 1992) much of the Lake Johnston area was reduced to low relief and subjected to intense weathering, probably under humid tropical conditions. This resulted in the formation of an iron-rich lateritic regolith (*e.g.* Jutson 1914; Walther 1915; Prider 1966; Maignien 1966; Mulcahy 1973). Remnants of this palaeosol are preserved on higher ground immediately west of Lake Cowan, westwards almost to the Lake Johnston depression, and beyond into the Hyden district. There it is preserved in plateaux, as it is also in the Corrigin and Brookton areas, between Hyden and Perth and, more extensively, in the Darling Range east of Perth.

The ferruginous pisolitic zone of primary or *in situ* laterite is iron-cemented and 0.5-2.0 metres thick. It is overlain by a sandy A-horizon and underlain by pallid and mottled clay-rich kaolinised bedrock. The complete profile is at least 30 metres thick and up to 50 metres in places. Ironstone pisolites ('pea gravel') mixed with clay and derived from the erosion of the primary laterite are widespread on slightly lower slopes. Some valleys associated with the laterite surface carry a fill of silicified debris (including silcrete blocks and boulders) which at some sites, as for example at The Breakaway (Fig 2), give rise to sheer, even overhanging bluffs capped by silcrete.

The major remnants of laterite developed on Precambrian rocks are separated by north-south trending

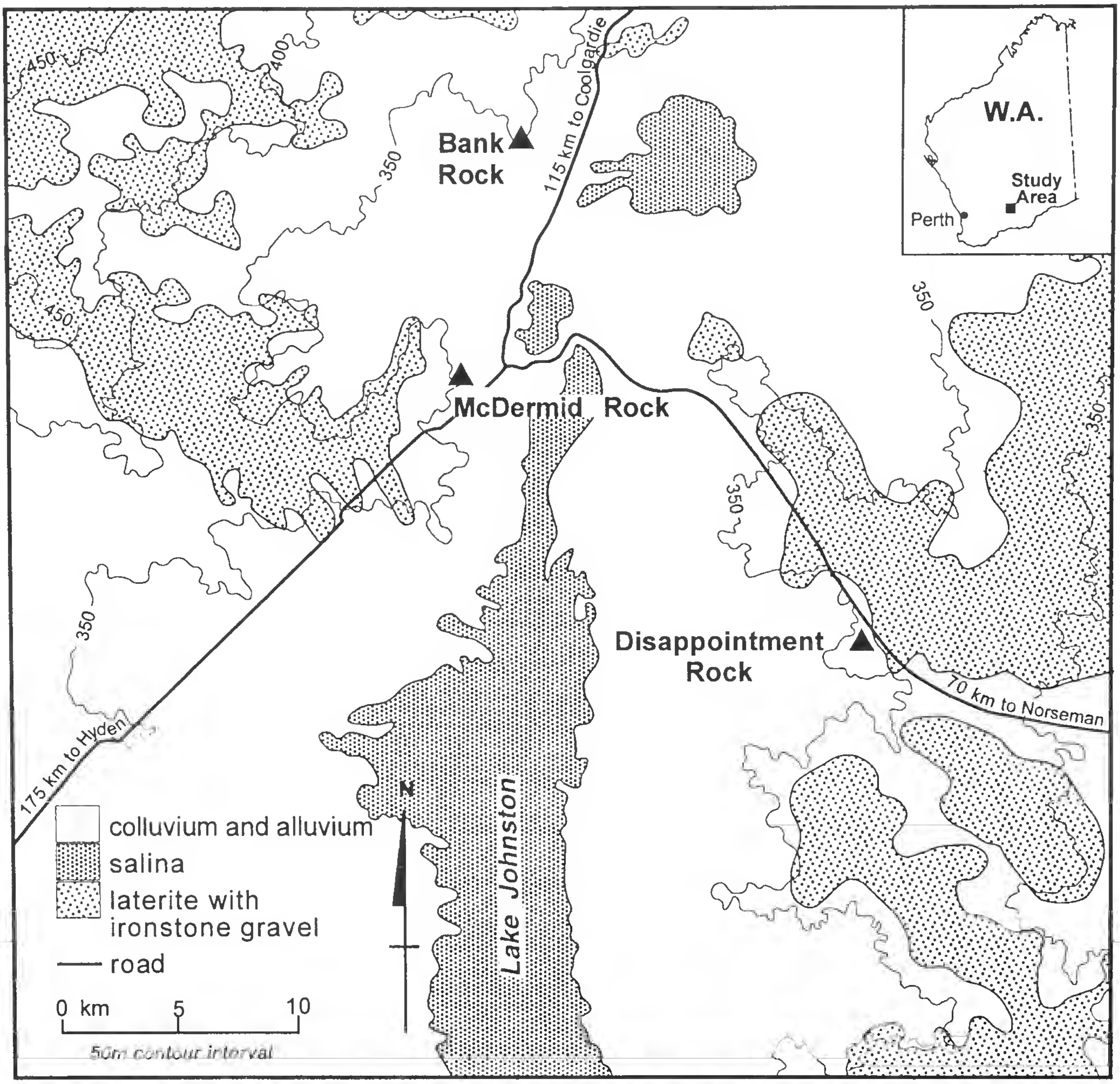

Figure 1. Location map and generalised surficial geology of the Lake Johnston area. The positions of the three inselbergs discussed are shown.

major valleys that are palaeodrainage lines (see *e.g.* Clarke 1994a), which with the onset of aridity in later Cainozoic times were abandoned, blocked and disused. These palaeoriver systems are now occupied by strings of salinas or salt lakes. The Lefroy channel, which embraces Lake Johnston, intervenes between Disappointment Rock on the one hand and McDermid and Bank Rocks on the other.

The palaeochannels have a complex history, for the rivers responsible for their incision originally flowed north and east. The Cowan drainage system, of which the Lefroy arm is tributary, was diverted southwards prior to the Jurassic as a result of the development of the Jarrahwood Upwarp, a south-west to north-east trending rise between what are now Norseman and Kambalda (Clarke 1994a). The valleys became shallow arms of the sea during the Eocene, about 60 million years ago. These estuaries persisted until the Miocene, about 20 million years ago, when aridity set in causing surface drainage to be dismembered. Gypsum and gypsiferous deposits accumulated in the valley floor resulting in the salt pans that are such eye-catching features of the present landscape.

Though it was not diverted southwards, the original Lefroy river probably eroded its channel and created a valley incised below the lateritised plain in the Eocene, about 60 million years ago. The implication is that the lateritic plain is older than the Eocene but it postdates the late Palaeozoic glaciation. It is of later Mesozoic -

Figure 2. The Breakaway is a valley bounded by cliffs, some of them overhanging, as seen here, and eroded in mottled kaolinised granite capped by silcrete. The steepness of the cliffs is due to seepage and sapping at the base of the slope.

later Jurassic and Cretaceous - age (Clarke 1994b; Twidale & Bourne 1998).

Origin and age of bornhardt inselbergs

Terminology

The three granite hills discussed in this paper are all inselbergs, for they each stand in isolation and rise abruptly from the surrounding plains. But all are also essentially domical and for this reason are referred to as domical inselbergs or bornhardts, after the German explorer of that name whose accounts of such features in what is now Tanzania (Bornhardt 1900) prompted Willis (1934) to suggest that his name be given to domical inselbergs.

Morphology

Bornhardts are common throughout the Yilgarn Craton. They are convex-upward hills which display varied radii of curvature and stand at various heights above the surrounding plains. All are domical by definition, but they vary in precise geometry and morphology as well as complexity. Some, like Disappointment Rock, take the form of hemispheres or *meias laranjas* (half oranges), others are elongate domes or turtlebacks, low whalebacks (*dos de baleine*), or asymmetrical elephant rocks (*dos d'elephant*), mostly, as at McDermid and Bank Rocks, with clefts due to the weathering and erosion of fractures. Yet others stand tall in relation to plan diameter to give sugarloafs or turrets, like Quarbabing Hill, some 43 km south-west of Corrigin (and the well-known Sugarloaf of Rio de Janeiro). Taking examples from the south-eastern Yilgarn Craton, some, like Frenchmans Peak, consist of a single dome but most, including Peak Charles, comprise two or more juxtaposed forms. Hyden Rock consists of three domes at once separated and linked by major fracture zones (Twidale & Bourne 1998, 2001), and McDermid Rock, The Humps and Boyagin Rock each include several linked domes. Platforms like Bottle Rock, some 45 km east of Hyden and just north of the Hyden-Norseman road, and several unnamed examples standing flush with the plains around the three residuals discussed here, are regarded as the crests of compartments as yet unexposed. Regardless of their varied areas, elevations, relief amplitude and geometry, however, all these outcrops have many gross characteristics and minor features in common.

The plan outlines of these bornhardts are determined by systems of steeply-dipping, orthogonal fracture systems due to stress and shearing. Their profiles are coincident with sets of sheet fractures which are traditionally attributed to erosional offloading and so are frequently referred to as offloading joints (Gilbert 1904), though in many instances they are more likely due to the same compressional stresses that caused orthogonal fracture systems to develop in the rock (Merrill 1897; Twidale 1964; Vidal Romani *et al.* 1995; Twidale *et al.* 1996).

Origin

The bornhardts are invariably developed on compartments of massive rock, *i.e.* rock with few open partings, and they are upstanding because the scarcity of open fractures offers few avenues for water penetration in what is an impermeable crystalline rock. By contrast, the surrounding plains have been worn down because the granite was well fractured and weathered by contact with water seeping down from the surface. That the granite of the hills is massive is readily demonstrated by walking over the outcrops and noting that the fractures are few and commonly many metres, even tens of metres, apart. It is more difficult to demonstrate rock structure beneath the plains for exposures are few. However, where excavations have been made (dams, tanks) the rock is found to be altered, possibly with corestones, tens of centimetres in diameter, preserved in the weathered granite or grus. The size of the corestones provides a general guide to the original fracture spacing in the bedrock (*e.g.* Twidale 1982a, pp 89 *et seq*). Similarly, boulders (exposed corestones) are frequently found standing in isolation or in small clusters on the plains, and again their dimensions give an indication of fracture density.

Three points need to be made about this interpretation. First, in the study area the evidence is fragmentary and to that extent unsatisfactory, but at some few sites on Dartmoor, south-western England (Jones 1859; Twidale 1982a, p 132), in peninsular India (Büdel 1977, p 109), in Namaqualand, Western Cape Province, South Africa (Vidal Romani & Twidale 1998, p 193) and at Ucontitchie Hill, north-western Eyre Peninsula (Twidale 1964, 1971, pp 52-53) where excavations have been sunk at or near the base of granite hills, fracture contrasts of the kind postulated are observeable.

Second, why are there contrasts in fracture density? The bornhardts are developed on massive blocks. The major fractures are shears from which fractures are propagated by continued dislocation so that the present bornhardts can be viewed as forming the cores of otherwise shattered blocks (Weissenberg 1947; Twidale 1980).

Third, it might be argued that the fracture density beneath the present plains is irrelevant, and that it is the contrast between the granite of the bornhardt and of the rock adjacent to it but now eroded, that is germane to the argument. Blès (1986) has compared fracture density at the surface with that at depth, and found that they are similar at any given site. If surface density is an indicator of density vertically below, is it not reasonable to suggest that it is also an indicator of the density in the rock vertically above, in the compartment that has now been eroded to produce the plain (Twidale 1987)?

Thus the compartments of granitic rocks on which bornhardts are developed resisted weathering and erosion and remain upstanding because they are massive with few open partings. When did this two-stage mechanism, involving differential subsurface weathering and then the stripping of the weathered mantle and exposure of the projecting compartments as bornhardts, take place?

Age

The age of the bornhardts of the south-eastern Yilgan Craton can be deduced from their topographic relationship to the Cretaceous lateritic land surface. Some, like the higher domes of The Humps and Boyagin Rock, stand higher than the local remnants of laterite, and are therefore at least as old as the duricrusted surface. The crests of other bornhardts, such as Waycott Picnic Rock, west of Corrigin, stand at a similar elevation as the laterite preserved on adjacent mesas (in the instance cited, Jingaring Hill) and are construed as Cretaceous platforms, which have however been left high in the relief by subsequent erosion of the surrounding weathered bedrock. Others, however, are more complex with crests higher than the laterite but most of the residual lower.

Granitic bornhardts located on the Gawler Craton, on north-western Eyre Peninsula, South Australia, though domical overall are stepped in detail, with steep slopes or steps separating gently sloping areas, platforms or treads. The steps display flared slopes indicative of former hill-plain junctions, and it has been suggested that the tiered morphology of the residuals is due to their having been exposed in stages. In other words that phases of stability during which subsurface weathering (including the formation of flared forms at the then hill base) alternated with phases of erosion and lowering of the plains around the hills (Twidale & Bourne 1975; Twidale 1982b; Bourne & Twidale 2000). Many of the bornhardts of the Yilgarn Craton are similarly stepped, and the hypothesis of episodic exposure seems compatible with the local evidence.

Such residuals as Boyagin Rock in the Darling Ranges, east of Perth, and King Rocks near Hyden, consist of a smaller dome rising from a larger. These crestal areas stand higher than the local remnants of the lateritised surface and are thus at least of Cretaceous age. The highest crest of bornhardts, like Hyden Rock, may have been exposed as platforms or very low domes in the lateritised plain but they are essentially due to post-Cretaceous erosion of the surrounding areas. Hyden Rock displays two 'treads' lower than the highest crest. They are partly bounded by flared slopes and represent stages in the post Cretaceous lowering of the plains. In general terms the ages of the residuals (in this context, when they were exposed as landforms) can be gauged according to their location within major catchments; Eocene near major palaeochannels, Miocene in headwater reaches and so on (*see* Salama 1997; Twidale *et al.* 1999a), but with variations and phases of exposure according to proximity to major channels, and possibly also the effect of rock barriers or river incision. In addition, besides plains shaped by rivers, weathering at the base of the regolith simultaneously creates another platform at the lower limit of effective weathering, or weathering front (Mabbutt 1961a); what is referred to as double 'planation' (Büdel 1957). The development of the Old and New Plateaux of the Yilgarn Craton (Jutson 1914; see also Mabbutt 1961b) is a good example, with the weathering front later exposed to give the New Plateau, originating at the same time as the Old Plateau was being shaped.

Comparisons

Of the three inselbergs under review, the whole of Disappointment Rock stands higher than the laterite that

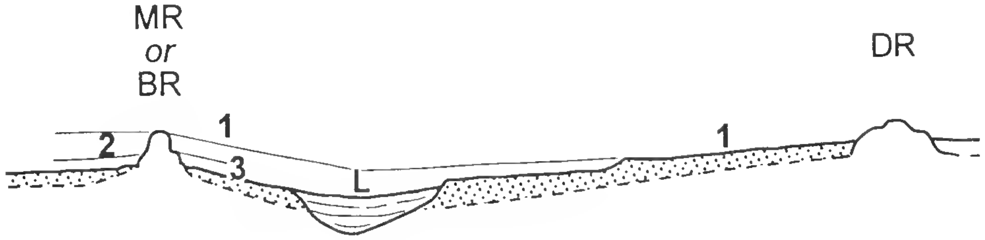

Figure 3. Suggested development of inselbergs in the Lake Johnston area. (L) indicates the Lefroy palaeochannel with Lake Johnston. (1) Cretaceous times with weathered (lateritised) land surface with Disappointment Rock (DR) already exposed and standing as an inselberg on the plain. (2) River incision along Johnston drainage line, stripping of weathered mantle, and exposure of uppermost domes of McDermid (MR) and Bank (BR) Rocks. (3) Further stripping near the valley and exposure of lower levels of McDermid and Bank Rocks, while Disappointment Rock remains basically unchanged.

caps the adjacent plain and which is there exposed in borrow pits (Fig 3). Thus the residual is at least of Cretaceous age. The bornhardt comprises a dome-on-dome form with a distinct break of slope between the two, and the higher dome is the older, in the sense that it was exposed earlier than were the lower slopes.

McDermid and Bank Rocks are more distinctly tiered (Fig 3), with steeper flanks than Disappointment, suggesting that because of their proximity to a major water course subsurface moisture attack was more pronounced. Several minor and possibly localised levels can be detected on each, but on McDermid Rock the upper dome rises from a level of some 355 m, which can tentatively be taken as an old plain level below which a regolith and associated flared slopes and platforms developed. This may have been the lateritic regolith in which case the upper dome is of Cretaceous age and the lower forms are younger, being either a weathering front exposed by the erosion of the regolith or having evolved on the surface so exposed. The convergence of flared slopes on the northern slope suggests localised erosion.

A similar construction can be placed on Bank Rock, where the main dome rises from a gently sloping area at about 380 m bounded by flared slopes. In both instances a regolith some 10-15 m is implied, which is less than the maximum revealed in the deeper valleys but which is comprehensible in terms of having developed on resistant rock masses.

Minor landforms developed on bornhardts

The various minor landforms developed on bornhardts can be classified according to their origin. Some were initiated at the weathering front when the host mass was still below the land surface but was in contact with groundwaters. Some were formed after the exposure of the hill. Others are due to localised contrasts between exposed and regolith-covered areas. Some are an expression of structures in the granitic host rock and yet others are tectonic and are due to earth movements. Yet others owe their existence to protective mechanisms and factors (for reviews *see* Twidale 1982a; Campbell 1997; Vidal Romani & Twidale 1998; Twidale & Vidal Romani 2002).

Subsurface origin

Subsurface moisture attack by way of solution, hydration and hydrolysis preferentially alters mica and feldspar to clay, leaving quartz in micro-relief and producing a rough surface called pitting (Twidale & Bourne 1976). This is a sure sign of relatively recent exposure of the surface through the removal of soil, regolith or slabs of rock.

At a slightly larger scale, small hollows (alveoles, or collectively honeycomb weathering) form at the weathering front. The septa separating alveoles are areas of algal colonisation but whether the plants protect and thus preserve the septa or whether the algae take advantage of a suitable niche is not clear. Pecking denotes a group of slightly larger and more widely separated hollows, again due to localised moisture attack at the weathering front. Neither alveoles nor pecking carries the same implication of recent exposure as pitting.

Chemical reactions at the weathering front may cause concentrations of salts of silicon, iron and manganese. Certainly such concentrations can be seen at exposed fronts (*e.g.* Twidale 1986) but it has been surmised that continued precipitation of such salts could cause space problems and the disruption of the rock surface into small (1-20 cm diameter) plates defined and delimited by fractures. When weathered and enlarged these fractures produce polygonal patterns. Examples of polygonal patterns, which are well displayed at King Rocks, near Hyden, and at Dundas Rocks, about 22 km south of Norseman (Fig 4A), have been noted on recently exposed corestones in the Snowy Mountains. On the other hand, these features may also have formed on exposed surfaces.

Rock basins (or gnammas) are depressions in the bedrock surface and are one of the most common and widely distributed of all granitic forms. Many are initiated as shallow saucer-shaped depressions where moisture has exploited clusters of such susceptible minerals as micas and feldspars, but many form at the intersection of fractures. After exposure they become differentiated according to the structure of the granite and the slope of the surface (Twidale & Corbin 1963). On gentle slopes hemispherical pits form in massive isotropic rock, but shallow flat-floored pans, frequently with overhanging sidewalls, develop in laminated granite which allows more rapid lateral rather than vertical moisture attack. On steep slopes (greater than about 20 °) the basins are asymmetrical with open downslope sides, and are called armchair-shaped hollows. Where pits have penetrated through the base of a slab or sheet structure runoff entering the pit flows through the base, a swirling motion develops and a

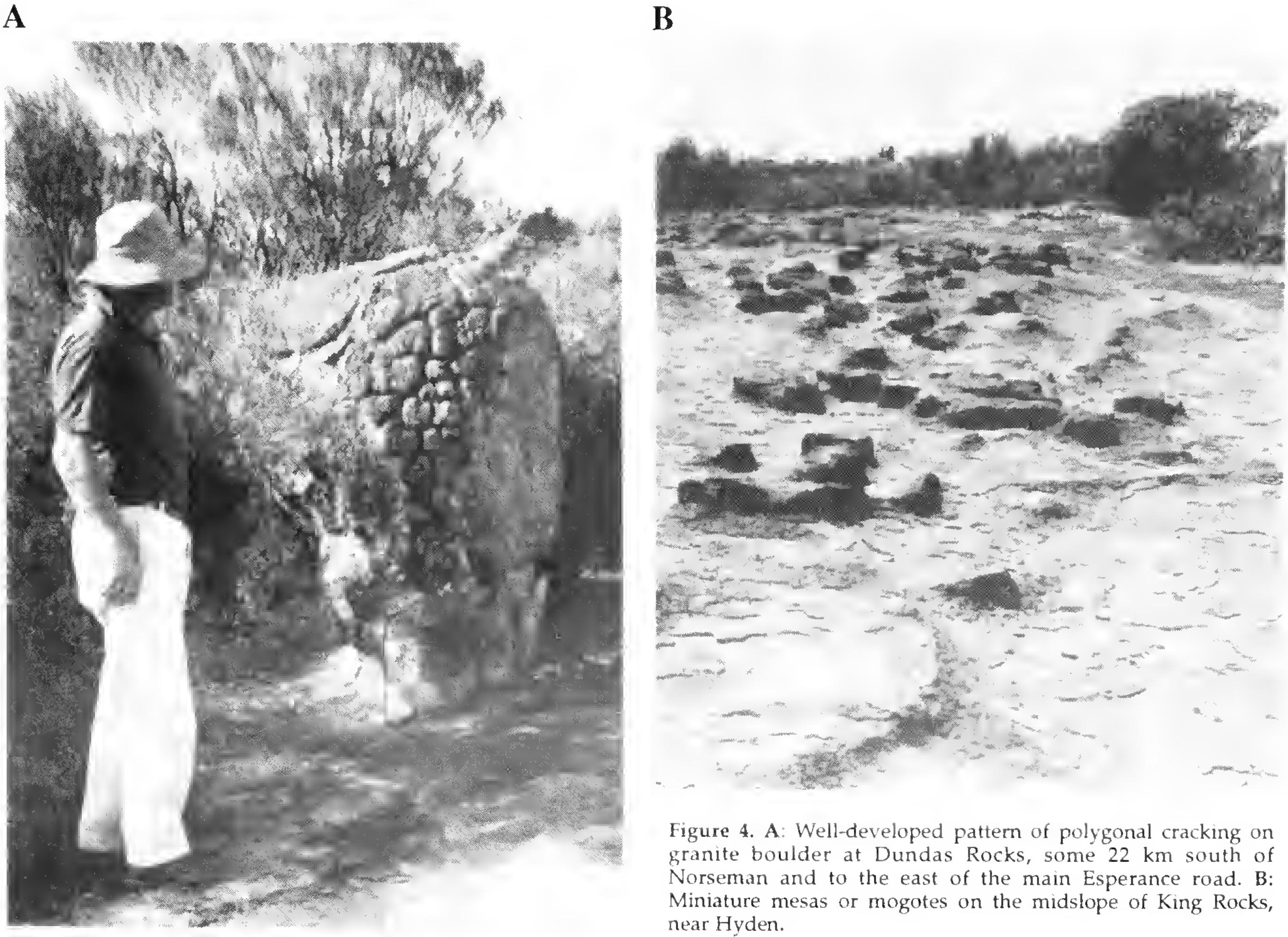

Figure 4. A: Well-developed pattern of polygonal cracking on granite boulder at Dundas Rocks, some 22 km south of Norseman and to the east of the main Esperance road. B: Miniature mesas or mogotes on the midslope of King Rocks, near Hyden.

cyclindrical hollow is formed. A particularly large example some 6 m long and 3 m wide and at least 2 m deep is developed on Beswick Rock, near Corrigin. Basins formed along fractures tend to be elongate in plan and when carrying water look like eyes; and for this reason they are known in south-east Asia as 'water eyes' (*e.g.* Tschang 1962).

Water running along the weathering front erodes linear channels in the rock surface. Such channels are known as gutters. Those exploiting fractures are straight and are called *Kluftkarren* or (in the USA) slots. Water running or seeping into the soil or regolith at the margins of an exposed rock mass (whether a dome or bornhardt or a block or boulder) infiltrates into the regolith. It alters the rock with which it is in contact both vertically and laterally. In this way, it creates a concavity just below the land surface. When exposed as a result of the erosion of the regolith and lowering of the plain level, such concavities are known as flared slopes (Twidale 1962). The shoulder between the convex slope above and the concavity below marks the former hill-plain junction. Long-continued subsurface weathering around a block or boulder can eventually produce an hourglass or pedestal rock (Twidale & Campbell 1992).

Sheet structures begin to break down into orthogonal or quadrangular blocks when still beneath the land surface, probably as a result of moisture penetrating along and weathering incipient partings.

Subaerial or epigene origin

After exposure of blocks and boulders, various types of gnammas evolve from saucer-shaped depressions, as described above, and gutters extend and develop. Some new ones are formed below seepages issuing from patches of regolith that may survive on gentler slopes, as for instance on hill crests: decantation flows and gutters. Blocks and boulders are attacked from below partly by moisture persisting in the sheltered parting beneath the block, but mostly by salt crystallisation (exudation, haloclasty) which exerts enough force to rupture even strong rocks like fresh granite (Buckley 1951; Evans 1969). Books of flakes are a manifestation of such salt weathering as is some granular disintegration, but either or both produce alcoves and shelters at the exposed ends of sheet structures and enclosed hollows or tafoni in blocks and boulders, and the outer shell or visor is indurated by iron oxides and silica, possibly related to lichen growth.

Exploitation of the partings defining polygonal cracking (*qv*) to the extent that the residual cores of polygons are widely separated, produces mogotes or miniature mesas, excellent examples of which can be seen at King Rocks, near Hyden (Fig 4B), and at The Granites, Mt Magnet (Twidale *et al.* 1999b).

Contrasts between exposed and covered surfaces

Some granite forms are due to contrasted rates of weathering on exposed and covered rock surfaces, for exposed surfaces are dry and are comparatively stable whereas a rock surface carrying a regolithic cover is longer in contact with moisture and therefore is weathered more rapidly. Both rock doughnuts and rock levees can be explained in this way (Twidale 1993).

Protection – the 'umbrella' effect

A block or boulder shelters the immediate surface on which it rests against rain and hence weathering (Twidale & Bourne 2000a). But water drips on the adjacent surface from the block, augmenting that which falls directly on it, thus causing rapid weathering and hence erosion. Thus a shallow moat is formed around the base of the block. In this way the area beneath the block comes to be higher than its immediate surrounds, forming a plinth on which the perched block or boulder stands.

Petrology

Bornhardts themselves are structural forms, and many minor features are due to the exploitation by agents of weathering and erosion of weaknesses, or contrasts, in the country rock. Fracture patterns give rise *Kluftkarren*, and water eyes. Compositional variations denote differences in susceptibility to weathering and cause the development of micro ridges and depressions, many of them in parallel and forming 'tramlines', as for instance on Kirk Rock and Hyden Rock, some of them irregular as at Boyagin Rock (Twidale & Bourne 2001, p 61). Pitting, as previously mentioned, is due to differential weathering at the crystal scale. Porphyritic texture implies large crystals of one mineral set in a matrix of finer minerals. On Hyden Rock, for example, feldspar phenocrysts have resisted weathering and project to give a pronounced rough surface. The ancient granitic rocks are criss-crossed by veins and sills, most of which were injected along fractures. They vary in composition, some consisting of quartz, others of feldspar, and yet others are a mixture of the two. Some are composed of fine-grained granite or aplite, others of coarse-grained pegmatite. Some aplites are bordered by pegmatite. The veins vary in thickness between a millimetre or so to more than two metres. Some are steeply inclined, others dip gently into the granite.

Tectonic forms

Though the cratons located far from plate boundaries are tectonically stable compared to plate margin locations, no part of the Earth's surface is entirely stable. Earthquakes are frequently recorded in the Australian cratons (*e.g.* Gordon & Lewis 1980; Bowman 1992; Twidale & Bourne 2000b). They result in such tectonic features as fault scarps, A-tents or pop-ups and displaced wedges (Twidale & Sved 1978), related to compressional stress. Orthogonal patterns of fractures and plates develop on sheared surfaces. Shaking gives rise to displaced slabs and blocks and may also contribute to the formation of split rocks, though they are mainly due to gravity. As they are due entirely to earth movements they are called tectonic forms, and as they postdate the Miocene, neotectonic.

Gravity

Gravity is the force behind several of the forms already mentioned. Water infiltrates into soil under gravity and is instrumental in pushing the weathering front further below the land surface. Linear flows of water along the front scour gutters. Also, any blocks and boulders that include a latent steeply-inclined fracture may be split as a result of the fracture being weathered, thus weakening cohesion between the two parts. Gravity eventually causes one or both of the imperfectly supported parts to pull apart and the block or boulder to split in two.

Inselbergs of Lake Johnston area

Not all of these minor forms are found on any one residual, but many are found on almost all. Despite

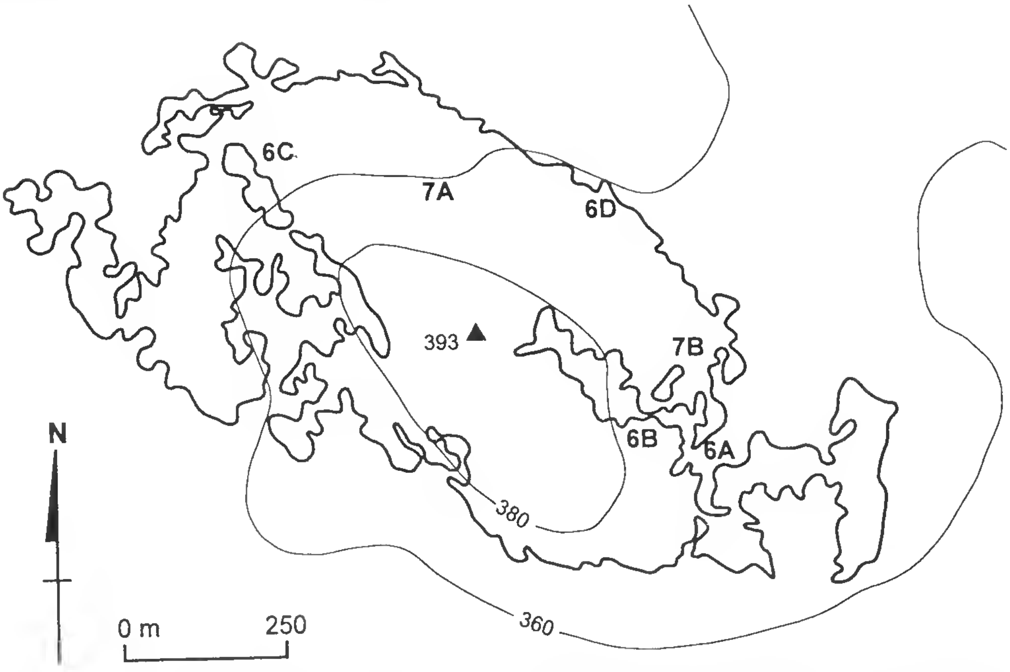

Figure 5. Plan outline of Disappointment Rock. Heavier line indicates outline of granite outcrop; finer lines, contours in metres above sea level; and numbers and letters, positions of landforms shown in Figs 6 and 7. (Drawn from air photographs and topographic map data).

A

B

Figure 6. Some notable landforms on Disappointment Rock. **A**: Large A-tent. **B**: Tilted block with indurated surface visible top right. Note the 'window' just below the induration. **C**: The differential weathering and erosion of pegmatitic intrusions result in oversteepened slopes. Here on the western slope of the dome, the linear scarp is related to a moderately steeply dipping sill, and the break of slope to the right is associated with discrete masses of pegmatite. **D**: Low flared slope with rock basins, or gnammas, developed in laminated granite.

C

D

Figure 6. (cont.)

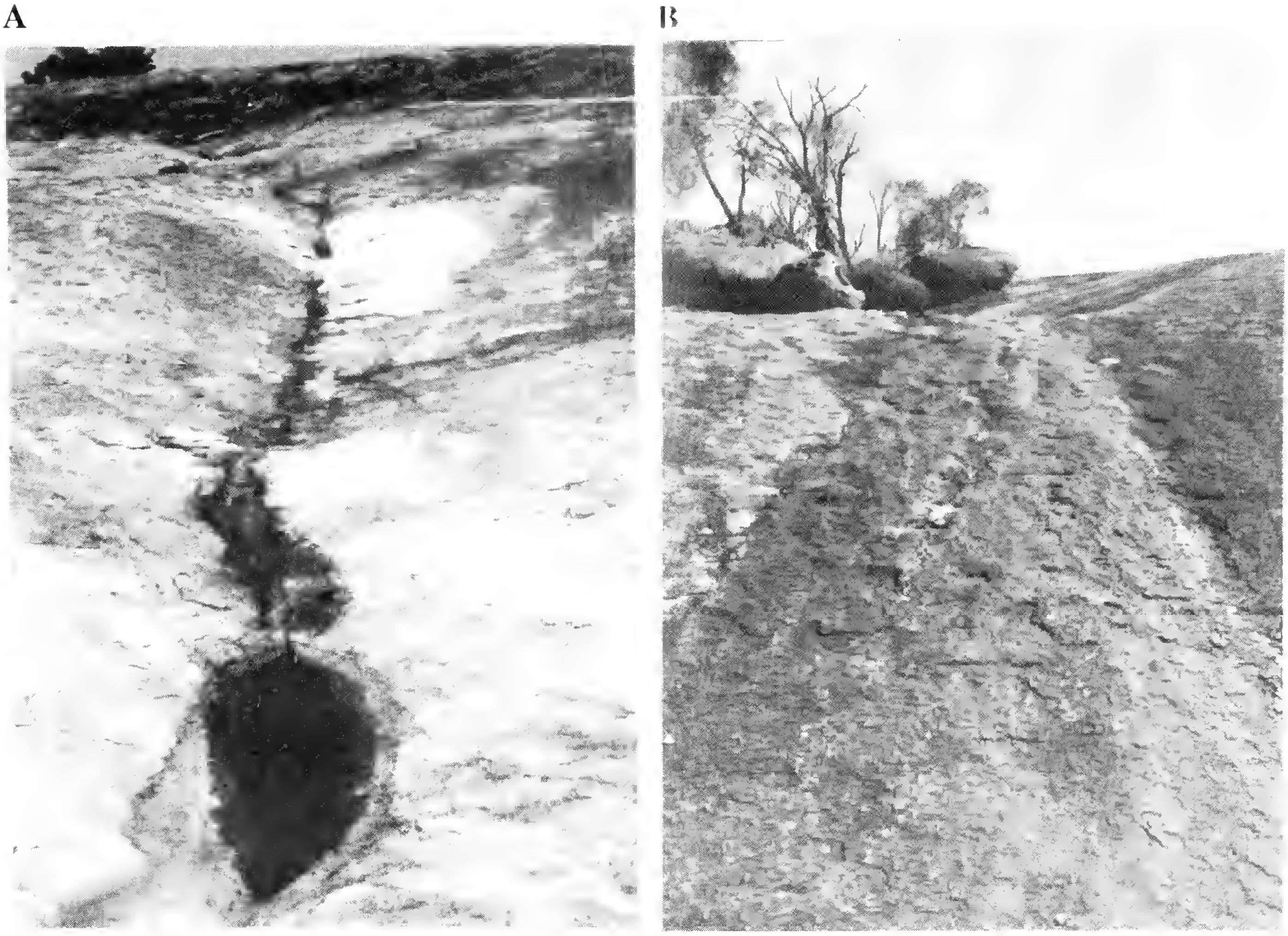

Figure 7. Water weathering and deposition, Disappointment Rock. **A**: Lenticular pits, or water-eyes, developed along a fracture-determined cleft. **B**: Slightly raised (or inverted) algae-coated floor of gutter or *Rille* on flank of inselberg. It drains from a soil-filled and vegetated armchair-shaped hollow (top left).

many common features and attributes every bornhardt is individual, with particular forms of note. This is illustrated by our account of three bornhardt inselbergs, Disappointment, McDermid and Bank Rocks, close to the Lake Johnston palaeochannel, and near the Hyden-Norseman road. A brief account of each is given below with features of special interest highlighted and illustrated. The granite in which they are developed is of Archaean age, *i.e.* more than 2.5 billion years old. The hills rise abruptly from a broadly rolling plain ranging in elevation from about 320 m above sea level in the Lake Johnston valley, to more than 380 m in the sand plain to the east of the valley and 400 m plus to the west (Fig 1).

Disappointment Rock

Disappointment Rock is located about 80 km west of Norseman and stands about 200 m south of the Hyden-Norseman road. Of the three bornhardts under review, this is closest to being characteristic of the standard Yilgarn type, for in plan it forms an irregularly oval whaleback of large radius, with a crest that stands about 393 m above sea level (Fig 5). Rising only 35-40 m above the adjacent plains, relative to its diameter (1.25 km x 0.6 km) its flanks appear gentle and smooth. Its surface is scored by basins and gutters, and blocks and boulders are scattered over the rock surface.

Many small fault scarps, trending 100 °, 40 ° or 10 °, are preserved low on the eastern and the western slopes. A large A-tent (trend of crestal fracture 0 °), the largest yet recorded in Western Australia, occurs on the eastern midslope (Fig 6A) and a tilted block is preserved high on the eastern slope (Fig 6B). A good example of a complex (in the sense of including offset sectors) fracture-controlled valley or *Kluftkarren* can be seen to the east of the access track. Along it are developed several of the lenticular basins known as water-eyes (Fig 7A). Here, and on McDermid Rock, pegmatitic sills have been preferentially weathered to produce breaks of slope (Fig 6C) and linear clefts. Notably large (up to 28 cm diameter) phenocrysts of feldspar are exposed in the northern slope, as are good examples of vegetational (tree root) disruption of surficial plates. In addition, however, Aboriginal people tilted and then released slabs in an effort to trap lizards, and some of the displacements evident today may be relic from such activities.

Small flared slopes are exposed in several sectors around the base of the residual but just east of the entry to the Rock they are low but overhanging. They are scored by basins in the walls of which laminated rock typical of the weathering front is exposed, suggesting that the gnammas have formed after the exposure of the flares (Fig 6D). Armchair-shaped hollows with soil and vegetation are well-developed and several of the gutters (or *Rillen*) that drain the dome originate in, or flow through, such depressions. Those that do tend to carry a protective veneer of black algal remains in the channel floors and some are inverted in consequence (Fig 7B). Some gutters have been diverted along fractures and veins resulting in dogleg bends. Large boulders with tafoni occur just to the west of the entry bay and hourglass rocks resulting from subsurface weathering all around blocks and boulders are also found at various sites on the Rock.

McDermid Rock

McDermid Rock which lies west of Lake Johnston, some 100 km from Norseman and about 1.5 km north of the main Hyden-Norseman road, consists of five juxtaposed domes separated from one another by fracture-controlled clefts, *Kluftkarren* (Fig 8). The highest dome stands 373 m above sea level and some 35-40 m above the adjacent plains. In plan, the residual, which extends 1.25 km south-west to north-east and 0.36 km north-west to south-east, is clearly defined by steeply dipping fractures with a south-west to north-east zone forming the south-eastern margin of the upland and with cols developed on roughly north-west to south-east trending fractures separating the four easterly domes. The most westerly dome meets the adjacent dome, the highest, in a NNW-trending fracture. Strong ENE offset, or *en echelon*, trends define the northern flanks of three of the easterly domes. In profile, the dome morphology reflects the development of arcuate-upward sheet fracture sets within the fracture-defined blocks. Pegmatitic and aplitic sills, some of them intersecting, are preferentially weathered to produce linear valleys.

The overall morphology of McDermid Rock is tiered with steep slopes, or steps, many of them concave or flared, separating gently sloping treads. The basal flares on the south-western margin are simple but those on the north-eastern flank of the highest and largest dome are sloping and intersect, suggesting that the erosional

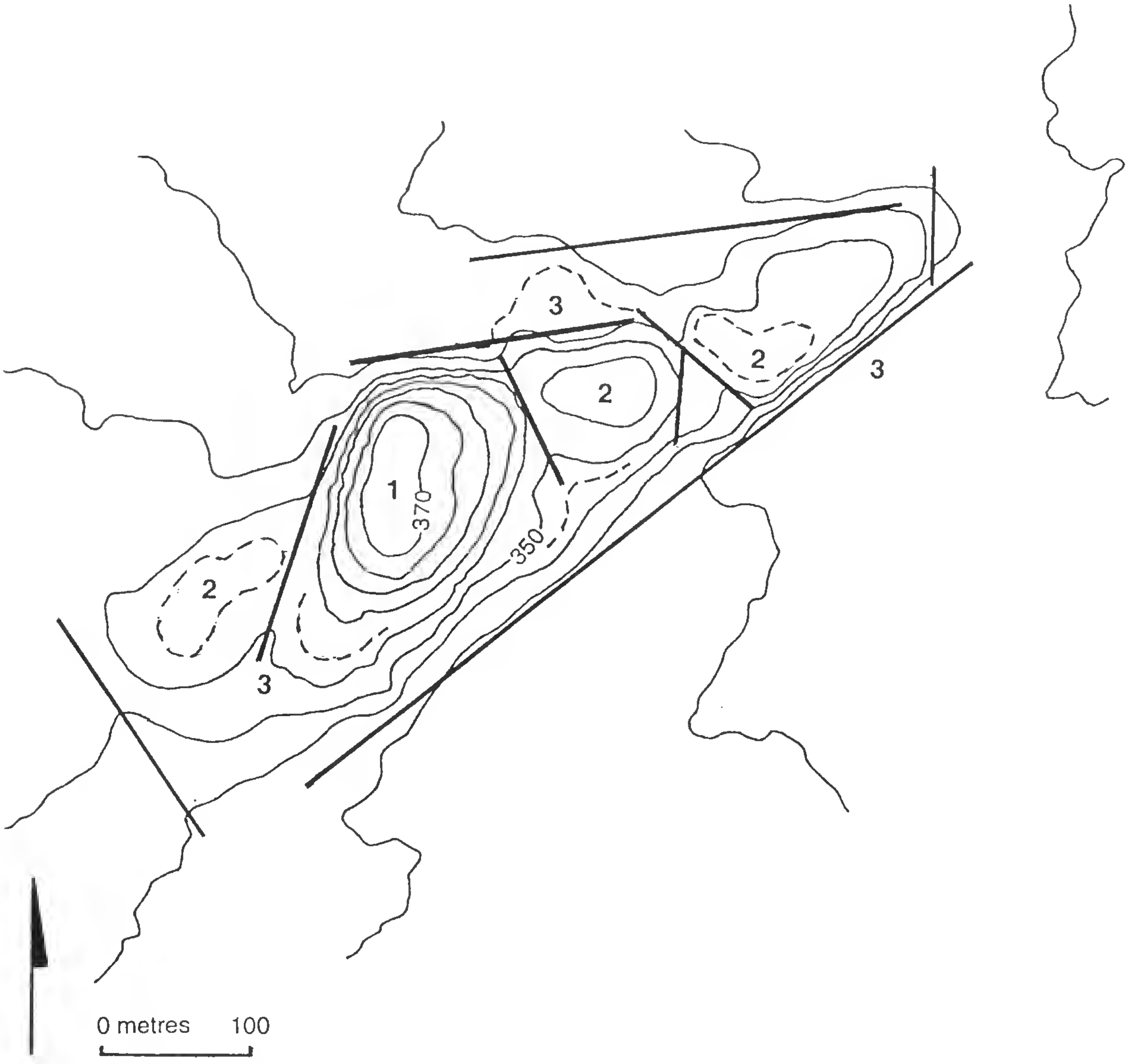

Figure 8. Plan of McDermid Rock showing contours (continuous lines; 4 m intervals) and form-lines (dashed lines), major fractures (heavy lines), and prominent domes, numbered 1-3, with 1 highest and 3 lowest. (Adapted from map drawn by McMullen, Nolan & Partners Surveyors, WA).

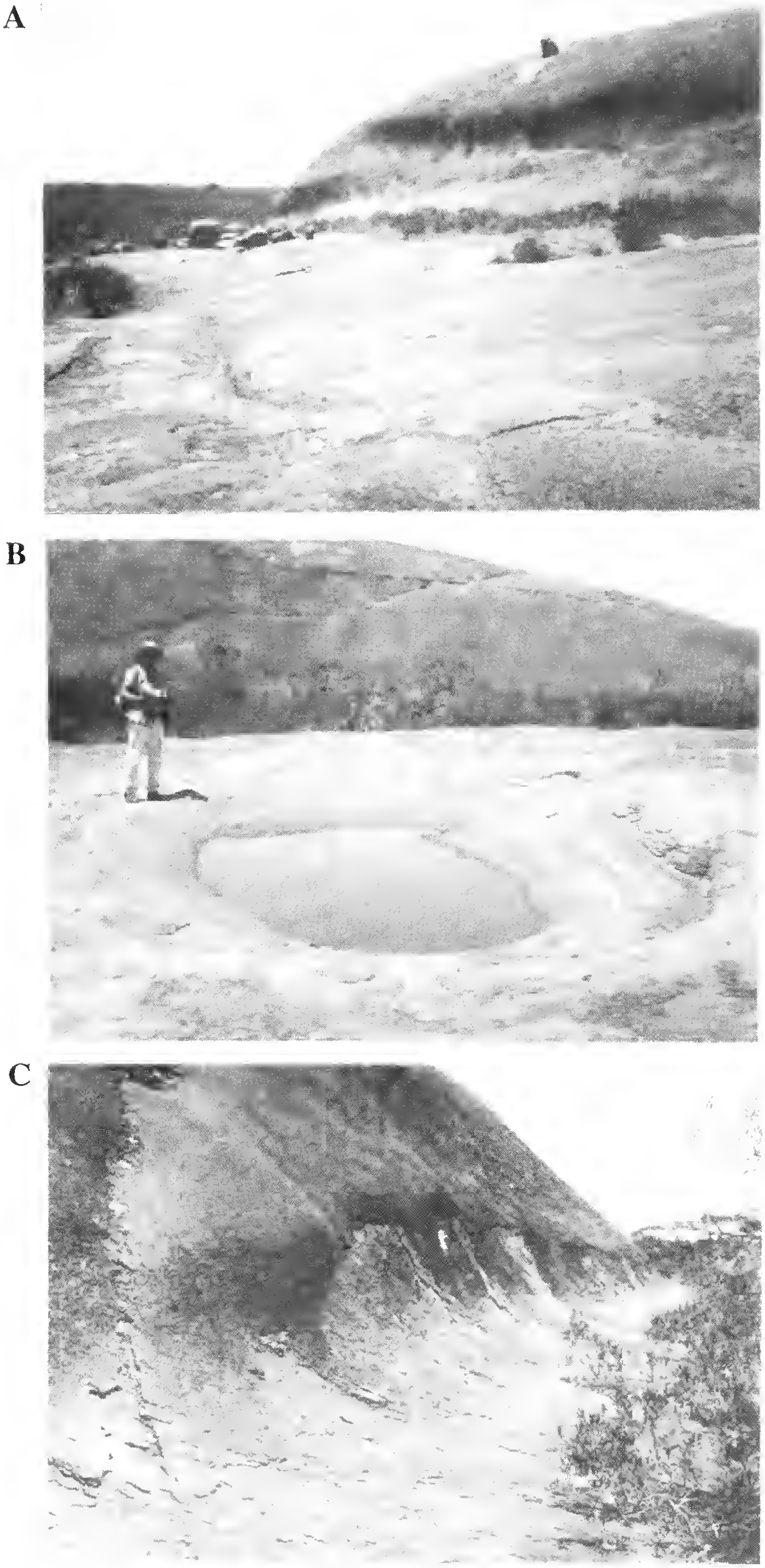

Figure 9. Some notable landforms found on McDermid Rock. **A**: Part of the north-western flank of McDermid Rock showing flared slopes converging to the north-east (right). Note also the perched boulder, and platform with several more perched blocks, some on plinths. **B**: Shallow flat-floored gnamma, or pan, located within a larger diameter pan. Note the intersecting pegmatite and aplite sills on the backing slope. **C**: Flared slope of recent origin is a lighter colour because there has not been enough time for substantial colonisation by algae. It meets an older slope above in a distinct ledge, or break of slope. Note the pegmatite sill exposed on the slope to left of view.

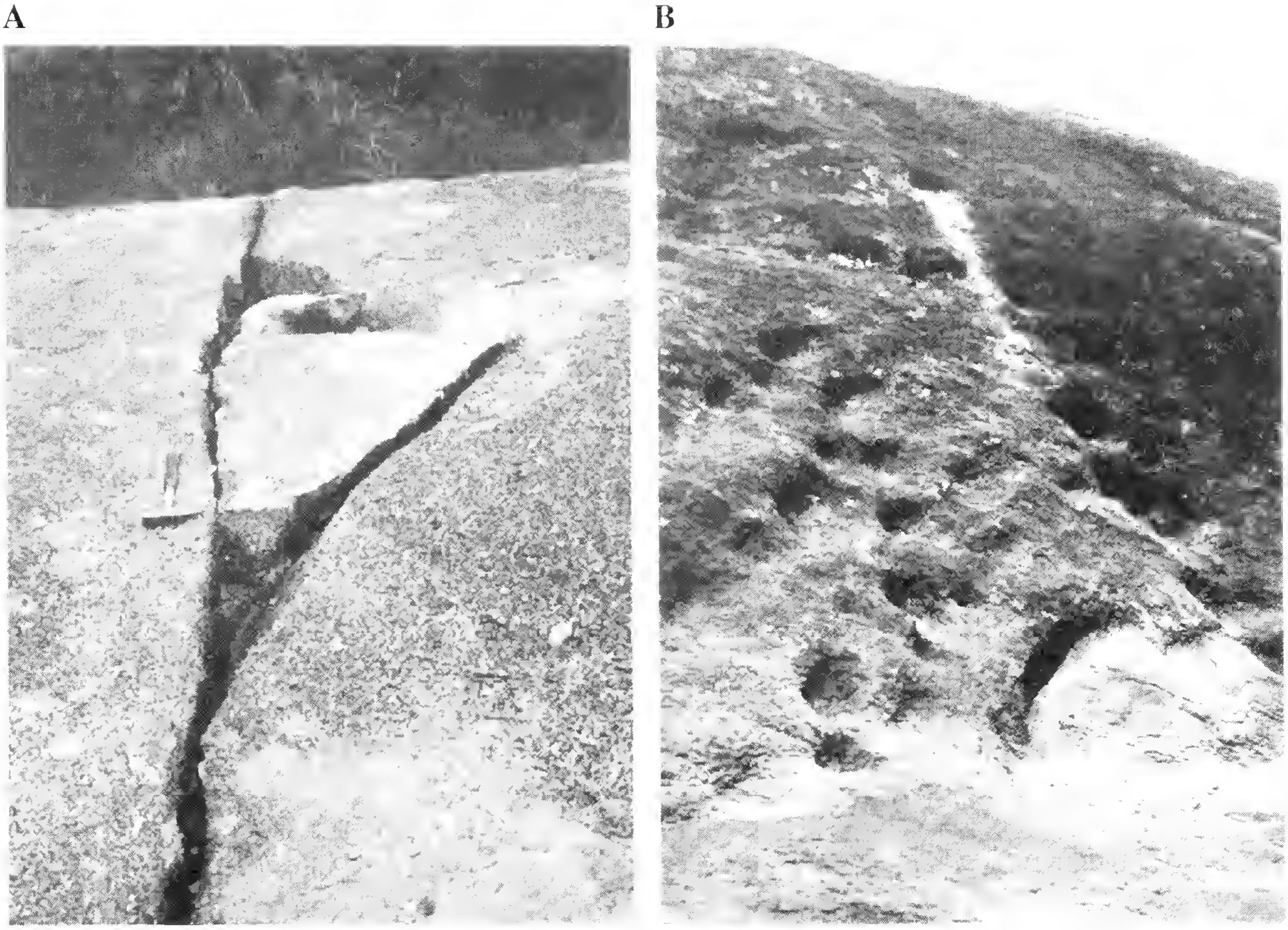

Figure 10. A: Recent fault scarp with splinter on McDermid Rock. B: Pecking on northern slope.

chronology of the plain on that side of the residual was more complex than that to the south (Fig 9A). Bearing in mind that the flared forms indicate the former piedmont zone and that the shoulder between the upper convexity and the lower concavity marks the hill-plain junction, it can be suggested that, following the development of the uppermost flared zone the adjacent plain was lowered to the north and another flare formed in relation to this newer, lower, and sloping plain surface.

Features of note include a recent fault scarp (Fig 10A); rock basins or gnammas with distinct basin-in-basin form and spectacular pegmatite sills (Fig 9B); evidence that some gnammas are initiated by the exploitation of clusters of susceptible minerals; curious small depressions or pecking on the steep north-western face (Fig 10B); perched boulders, platforms and multiple flared slopes (Fig 9A), including some that are clearly of relatively recent origin (Fig 9C).

Bank Rock

Bank Rock is located some 10 km north of McDermid Rock and some 2.5 km west of the Coolgardie road. It

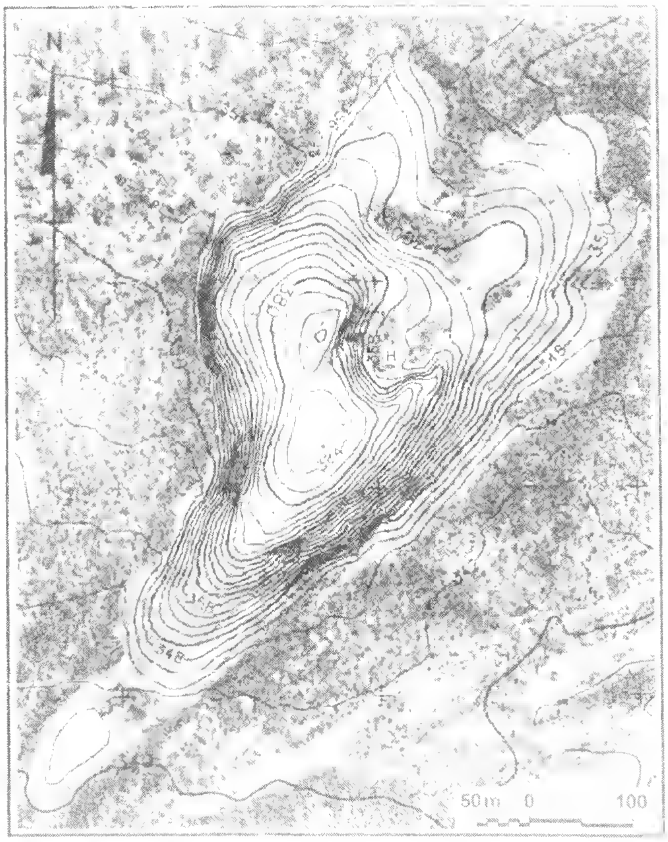

Figure 11. Bank Rock: topography, indicated by two metre form lines, superimposed on vertical aerial photograph. Note that the crosses are part of the form-line plot. (Extract from photo-map drawn by McMullen, Nolan and Partners Surveyors, WA).

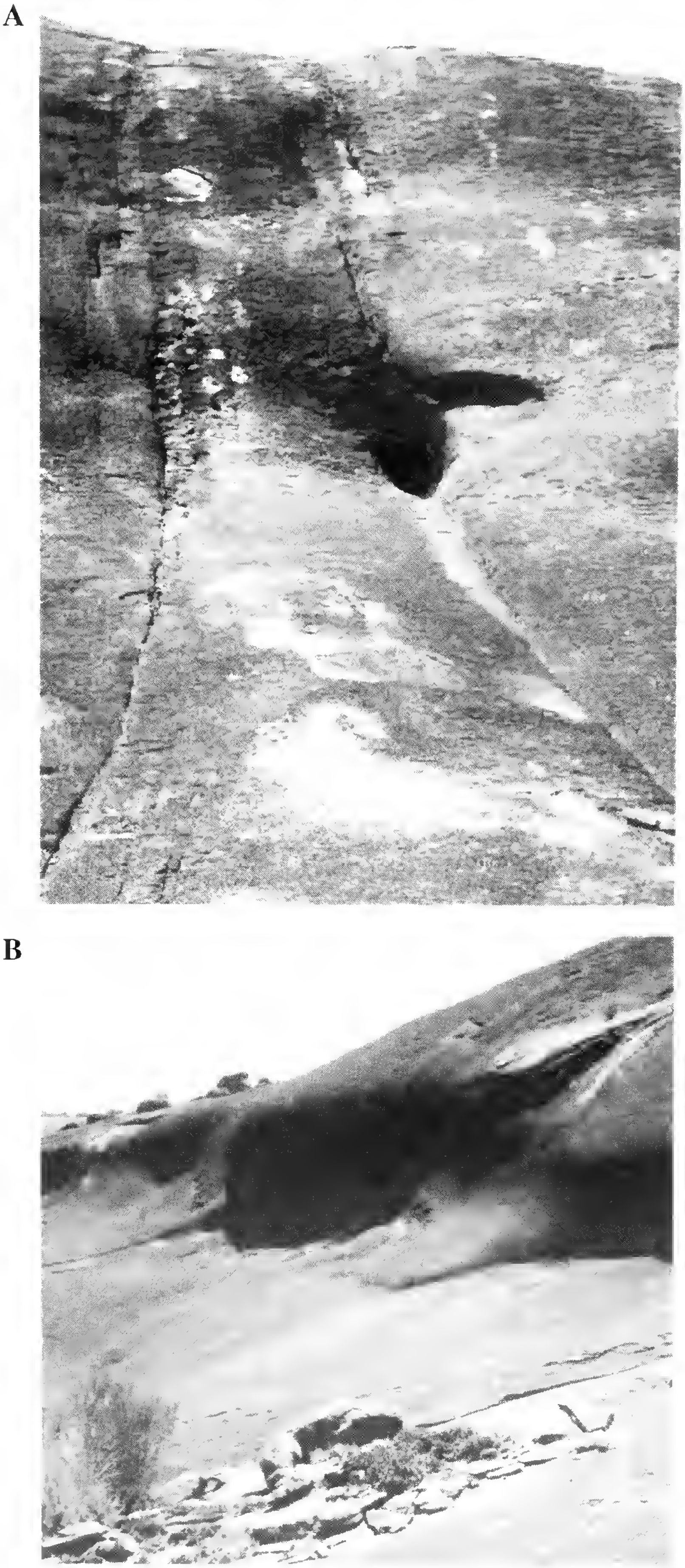

Figure 12. Bank Rock. **A**: Parallel joints, some offset, with quartz injections and water-eye developed; note also pecking on upper slope. B: Flared slopes arranged *en echelon* on western side of the residual.

A

B

Figure 13. Other notable features found on Bank Rock. **A**: Head of large armchair-shaped hollow (H on Fig 11) with flared sidewalls and large split boulder at its western margin. **B**: Wedge, triangular in cross-section and due to shearing along a sheet fracture. **C**: Broken and disturbed sheet structure just below crest on the western flank; in the foreground is a small perched boulder standing on a plinth. **D**: Face of disturbed slab with slickensides and recrystallisation indicating that the slabs here have split along an old fault plane. **E**: Boulders derived from the breakdown of a sheet structure and with tafoni and alveolar weathering developed. **F**: Elongate A-tent on south-western basal slope.

Figure 13. (cont).

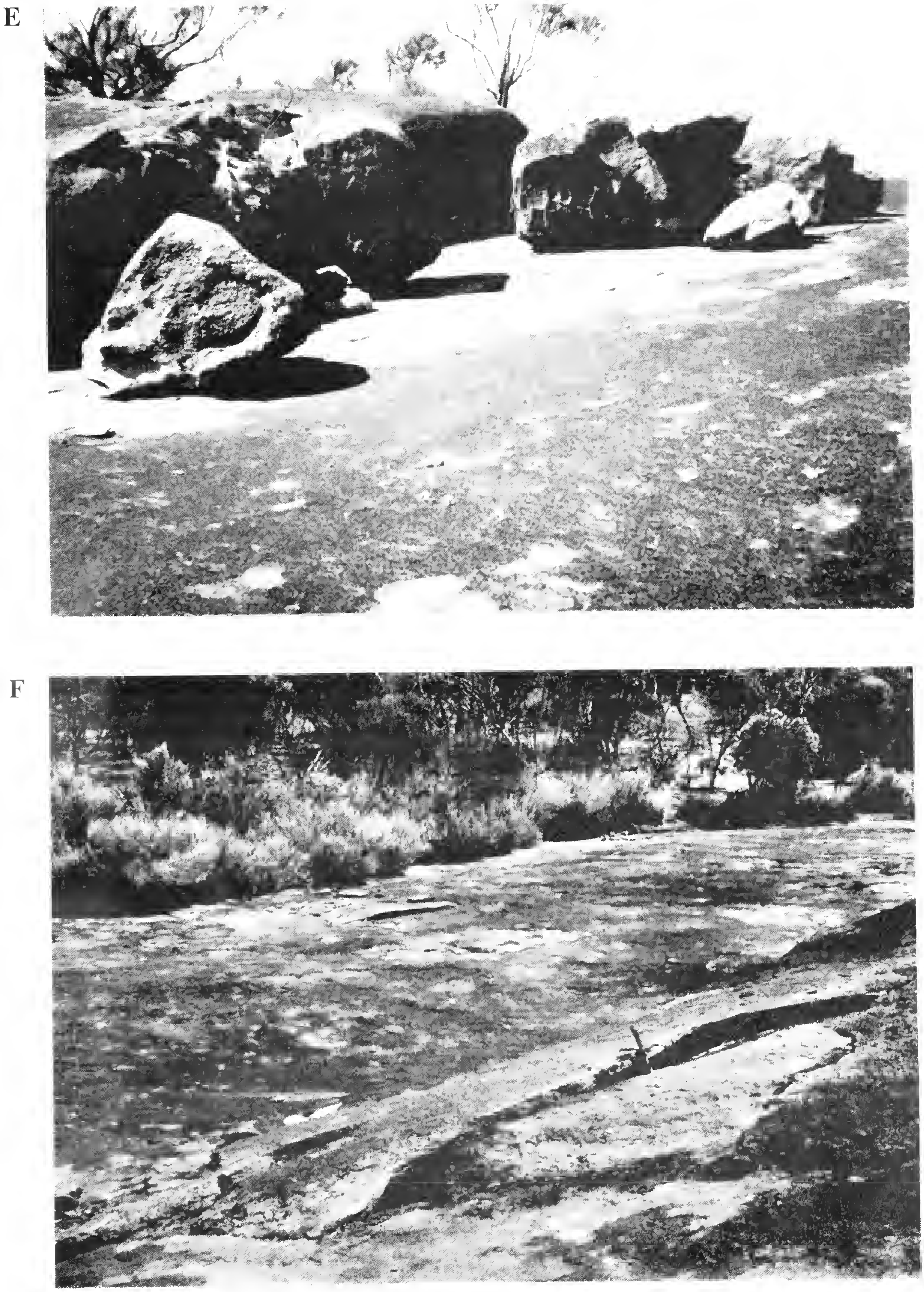

Figure 13. (cont).

(Fig 11) is elongate but triangular in plan form, with a length of some 0.87 km south-west to north-east and 0.4 km at its widest point, from north-west to south-east, at its north-eastern extremity. Like McDermid Rock it is clearly defined by steeply-dipping fractures trending south-west to north-east. Many of the fractures within the upland can be traced long distances (Fig 12A), and many are exploited by weathering to give *Kluftkarren*. The northern and southern flanks are scored by flights of flared forms, most of them inclined. On the eastern flank this geometry can be related to foliation in the bedrock but on the south-western appears to indicate that, as happens at present at some sites, the hill-plain junction was not level, and that, following the formation of the higher zone of flares, the plain was lowered, simultaneously exposing the first-formed concavities and initiating the development of the new lower zone of intense scarp-foot weathering. Closely spaced *en echelon* flared slopes suggest repeated localised lowerings of the hill-plain junction (Fig 12B).

In addition to flights of flares, notable features include a huge armchair-shaped hollow and related collapse and splitting of a large boulder (Fig 13A) and a triangular wedge associated with sheet structure (Fig 13B). Perched and hourglass boulders can be seen at various sites and other minor features of note include a massive aplite sill on the crest of the Rock, disturbed slabs developed in a thick slab or sheet structure (Fig 13C) including an exposure of fault plane with recrystallisation, polishing, fault steps, and slickensides (Fig 13D); tafoni (Fig 13E); and numerous small A-tents (Fig 13F) and perched blocks on plinths. Rather poor remnants of polygonal cracking, including isolated mogotes, are preserved on one sheet structure on the midslope.

Concluding remarks

The relationship of the three bornhardts with the (Cretaceous) palaeosurface and associated palaeosol and the evidence, such as it is, of zones of massive and well-fractured rock, sustain the suggestion that the residuals are essentially two-stage or etch forms (Falconer 1911). No nascent bornhardts have yet been exposed in quarries and other excavations, as they have in Africa and on Eyre Peninsula (*e.g.* Boyé & Fritsch 1973; Twidale 1982a, pp 142-143; Vidal Romani & Twidale 1998, pp 169, 194), but the occurrence of many bornhardts lower in the local landscape than weathered lateritic remnants is consistent with this interpretation (*cf* Lister 1987).

All three are two-stage forms and have been exposed in phases. McDermid Rock is the most obviously stepped with areas of low rolling topography or treads separated by steep flared steps, but sets of multiple flares occur also on the flanks of Bank Rock. At Disappointment Rock, an episodic exposure is suggested by topographic breaks at midslope most of the way round the hill, though the topography cannot be described as obviously stepped.

At Disappointment Rock the dome stands higher than the primary laterite exposed a short distance to the east, so that the bornhardt is at least Cretaceous in age, and the presence of a break of slope between an upper and lower dome suggests that the former may be even older. The age of the crests of McDermid and Bank Rocks is less clear because of their distance from lateritised remnants. They stand closer to the palaeochannel, and their being in wetter sites may account for the more pronounced weathering and resultant greater relief. In particular the contrast between the steeper bounding slopes typical of these two bornhardts and the gentle basal slopes with only a few low flared sections found on Disappointment Rock can be explained in these terms.

Disappointment Rock stands about 15 km from the Lake Johnston valley and has not yet been dissected; the lateritic cover remains essentially in place, and hence any pronounced bedrock concave marginal forms that are developed are not yet exposed. At Disappointment Rock the few, low, flared basal slopes that are revealed can be attributed to a combination of marginal weathering, volume decrease, and compaction, plus runoff and flushing of fines (*cf* Ruxton 1958), leading to localised surface subsidence around the perimeter of the outcrop (*cf* Clayton 1956). On the other hand, McDermid and Bank Rocks stand only some five kilometres from the old channel. The adjacent plains have been dissected and the results of scarp-foot weathering have been exposed. Whereas the exposure of Disappointment Rock appears to have taken place in two major stages, the multiplicity of flared forms and their sloping and intersecting geometries at McDermid and Bank Rocks suggest that many more changes in water table, possibly related to fluctuations in river level, find expression on the lower bornhardts located west of the Lake Johnston valley.

These three quite accessible inselbergs together display a wide range of granite landforms, with excellent examples of several, and uncommon evidence concerning the origin of a few. They also illustrate the evidence and argument that can be used to determine the origin and age of such residuals. In addition, the contrasted gross morphology of Disappointment Rock on the one hand, and McDermid and Bank Rocks on the other highlight the importance of location in relation to water, the major agent of weathering in shaping bornhardts. The upper zones of Disappointment Rock also appear to be sufficiently old to offer the possibility of their having been plant refuges. On the other hand all three bornhardts show clear evidence of recent earth movements: despite their location in crystalline rocks of the shield sectors of the Yilgarn Craton, they are affected by tectonic disturbances.

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Foraging profile of a Salmon Gum woodland avifauna in Western Australia

H F Recher[1] & W E Davis Jr[2]

[1]School of Natural Sciences, Edith Cowan University, Joondalup WA 6027 Australia. hjrecher@pacific.net.au

[2]College of General Studies, Boston University, Boston MA 02215 , USA

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Abstract

During studies of the foraging ecology of birds in the western Goldfields of Western Australia in Spring 1997, 63 species were recorded. The majority were resident and insectivorous, but we estimate that about 25% were migratory or nomadic. Our interpretation of the data is that migrants and nomads had aggregated in the area in response to an abundance of nectar and insects, following good rains in autumn and winter. In addition, there were seven species of raptors, possibly attracted by the numerous nectar-feeders. Ground-foragers dominated the avifauna, but many species foraged in the shrub and canopy layers by gleaning and snatching insects from the foliage. Feeding on flying insects was also prominent and accentuated by the availability of flying termites (Isoptera) at dusk. In contrast, bark was a poorly used foraging substrate compared with other woodlands that have been studied. Differences in community-wide foraging profiles can be explained by temporal and spatial variation in the kinds and abundance of prey (including nectar), but have important implications for the conservation of woodland bird communities. Conserving woodland birds requires large and multiple reserves on a supra-landscape scale, and the restoration of ground substrates and vegetation: both are necessary if all parts of the avifauna, nomads, migrants and residents, are to be conserved.

Keywords: foraging ecology, birds, Salmon Gum, woodland, Western Australia, conservation

Introduction

Prior to European settlement, Salmon Gum (*Eucalyptus salmonophloia*) formed extensive woodlands throughout the Wheatbelt and Goldfield regions of Western Australia where it occurred in association with other eucalypts (Boland *et al.* 1984) including Black Morrel (*E. melanoxylon*), Gimlet (*E. salubris*), Redwood (*E. transcontinentalis*), Red Morrel (*E. longicornis*) and York Gum (*E. loxophleba*). Within the Wheatbelt, eucalypt woodlands have been extensively cleared and continuous Salmon Gum woodlands remain only in the Goldfields and along the mulga-eucalypt line at the northern limits of the Wheatbelt.

Although the avifauna of remnant eucalypt woodlands in the Wheatbelt has been extensively documented (*e.g.* Kitchener *et al.* 1982; Saunders 1989; Cale 1990; Saunders & Ingram 1995; Arnold & Weeldenberg 1998), there are few descriptions of the bird communities and their ecology in the woodlands of the Goldfields or along the mulga-eucalypt line. As these communities may retain components of the avifauna lost from remnant vegetation in the Wheatbelt, details on species composition and the use of resources by birds in these habitats are important in understanding patterns of species loss from remnants and for designing reserve systems with the capacity to sustain all elements of the avifauna.

In this paper, we describe the breeding season foraging ecology of birds in Salmon Gum woodlands in the western Goldfields at the eastern limits of the Wheatbelt. Our objective was to document the foraging profile of the avifauna in a brief period and thereby avoid changes in resource abundance. Changes in foraging behaviour over time can blur differences between species and confuse analyses of community-wide foraging patterns (*e.g.* guild structure). Although information on seasonal and year to year patterns of abundance, breeding cycles and population sizes is necessary for a complete analysis, foraging data identify essential resource requirements for birds and can be used to develop revegetation programmes to maximise conservation benefits.

Methods

Study area and vegetation

From September 12 to 20, 1997, using the same procedures as Recher & Davis (1998), we sampled woodlands at 12 sites along 20 km of the Great Eastern Highway centred on Yellowdine (31° 17' S, 119° 39' E; ~ 400-450 m asl). Each site was about 10 ha in area. Data on foraging birds were obtained within woodlands dominated by Salmon Gum, Gimlet, Red Morrel and mallee eucalypts. The shrub layer, 1-4 m tall, was floristically rich and multiple-layered with *Acacia, Cassia, Dodonea, Eremophila, Exocarpus, Grevillea, Melaleuca* and *Santalum* species dominating. Mistletoes were common in the eucalypt canopy. Canopy vegetation ranged from

8 to 15 m in height with individual Salmon Gums to 18 m and morrels to 16 m. Small trees and mallees, which included Yorrell (*E. yilgarnensis*), Square-fruited Mallee (*E. callycogona*), Redwood and Gimlet ranged from 3 to 6 m in height. Among the mallees, Yorrell dominated and on the lower parts of the landscape formed extensive grassy woodlands with Gimlet. The result was a complexly structured canopy and subcanopy vegetation with considerable open space and variation in the composition and height of the dominant plants. The shrub layer was variable. In places, it was nearly continuous, but elsewhere was sparse. Ground cover was also variable, but floristically diverse and included species of *Atriplex*, *Brachycome*, *Maireana* and *Ptilotus*, as well as grasses. In places where shrubs were abundant, the soil was nearly bare, while sites with few shrubs were dominated by a nearly continuous growth of grasses and forbs. Throughout the study area, litter was sparse and wind driven into concentrations around the base of shrubs and trees, within clumps of mallee, against logs or where there was an accumulation of coarse woody debris. Coarse woody debris and logs were abundant throughout. On average, nearly 50% of the ground surface was bare.

Most of the area had been selectively logged prior to the 1970s but, as noted by Newbey *et al.* (1995), it was difficult to identify the effects on the vegetation. The most obvious changes resulted from the cutting of *Melaleuca* for posts, with many stands failing to recover. There was no sign of grazing by domestic stock, but macropods and rabbits appeared abundant.

Foraging Data

Foraging observations commenced shortly after sunrise and continued to dusk.

We began at a different site each day and changed sites during the day whenever we felt that we had sampled all available individuals. Some sites were visited on two or more occasions. Our objective in selecting different sites was to sample the range of habitats within the study area and our sites were allocated between the different plant associations in about the proportion that each occurred.

Foraging observations were recorded for all species of birds encountered. For each individual, we recorded up to five consecutive foraging manoeuvres following the procedures of Recher *et al.* (1985) as modified by Recher & Gebski (1989). We avoided recording data on the same individual on the same day by moving continuously and changing sites frequently. For some rare and/or difficult to observe species (*e.g.* Gilbert's Whistler, Chestnut Quail-thrush; species names of birds are given in Appendix 1), we recorded up to 20 continuous observations per individual. As our objective was to describe the foraging profile of the avifauna, multiple observations of individual birds increased the chance of recording infrequent or unusual behaviour (Recher *et al.* 1985), while also providing sufficient data for description. By recording behaviour from early morning to late afternoon, any changes in foraging activities associated with possible changes in food availability (*e.g.* emergence of flying insects near dusk, depletion of nectar near mid-day) are recorded and incorporated equally in the data.

Only foraging manoeuvres in which the bird obtained or attempted to obtain a prey item were recorded ('attack behaviour' of Remsen & Robinson 1990). For each of these, we recorded the species of bird, the substrate and height of the prey, and the manoeuvre used by the bird. Foraging manoeuvres were described following the terminology of Recher *et al.* (1985). However, in this paper we separate hawking manoeuvres into two types; 'hawk' in which a perched bird takes flight and captures a flying insect (equivalent to sally of Remsen & Robinson 1990), and 'sweep' in which airborne insects are caught on the wing by birds, such as swallows which forage in flight (after Mac Nally 1994). In addition, we use 'flitting' (after Crome 1978) to describe the behaviour of Willie Wagtails and Grey Fantails as they search for and pursue prey in the air and on the ground by short darts or runs, and short, twisting flights with the rapid changing of perches (see Cameron 1985). In previous papers, we described the behaviour of wagtails and fantails as 'hawking' and/or 'gleaning' (*e.g.* Recher *et al.* 1985; Recher & Davis 1997, 1998), but this does not adequately portray their behaviour.

For substrates we recorded the following categories; 1, Ground (including ground vegetation, litter, logs and coarse woody debris); 2, Bark (including small (< 2.5 cm diameter) and large (> 2.5 cm diameter) branches, and the main stem or trunk); substrates with loose or decorticating bark were recorded separately from other bark surfaces; 3, Foliage (including twigs, petioles, eucalypt seed capsules, and leaves); 4, Flowers; and 5, Air (for aerial prey). Dead substrates were distinguished from live substrates. The height of the prey taken was estimated to the nearest 0.1 m below 2 m and to the nearest 0.5 m above 2 m. Plants on which birds were foraging were identified to genus and, where possible, to species.

Species Abundances

An estimate of the number of individuals of all bird species was made at each site where we recorded foraging data. These estimates were made over one to several hours as a 'running tally' of birds detected during the collection of foraging data. Counts were conducted at different times of the day and under different weather conditions, although the weather was always fine and sunny. On most days, one count was done during the morning and a second during the afternoon at a different site. Although these estimates cannot be used as measures of absolute abundances or to compare population densities between species and sites, they indicate relative numbers and are an index of variation in the composition and species richness of the avifauna on the sites where we collected foraging data.

Data Analysis and Presentation

For each species we present the total number of foraging manoeuvres observed and the percentage use of substrates, prey-attack behaviours, and foraging heights based on these totals. Data from all sites are combined. Although substrates were recorded as finely as possible, sample sizes for many categories were too small for separate analysis and have been grouped as Ground, Bark (Branches & Trunk), Foliage, Flowers (nectar and insect feeding) and Air. Species were sorted into foraging

Table 1

Use of vegetation layers (%) and foraging height of birds in Salmon Gum woodlands at Yellowdine during September 1997.

Species (n)	Vegetation layer (m)				
	Ground 0–0.1	Shrub 0.2–1	Sub-canopy 1.1–5	Canopy >5	Height (m)*
Ground					
Chestnut Quail-thrush (49)	100	0	0	0	0(0.01)
Emu (20)	100	0	0	0	0(0)
Galah (25)	100	0	0	0	0(0)
Redthroat (30)	100	0	0	0	0(0.02)
Yellow-rumped Thornbill (77)	100	0	0	0	0(0.02)
White-browed Babbler (29)	83	7	10	0	0.3(0.8)
Rufous Treecreeper (169)	84	4	11	5	0.7(1.7)
Ground & shrub					
Willie Wagtail (132)	43	8	38	11	2.2(2.6)
Gilbert's Whistler (32)	22	59	19	0	0.6(0.6)
Chestnut-rumped Thornbill (191)	19	21	47	13	2.2(2.3)
White-eared Honeyeater (35)	11	3	77	9	3.5(2.7)
Grey Fantail (57)	9	7	84	0	3.4(1.5)
Ground & canopy					
Port Lincoln Parrot (106)	74	9	5	12	1.8(4.8)
Grey Shrike-thrush (11)	64	9	9	18	1.7(2.9)
Yellow-throated Miner (20)	50	0	25	25	3.4(4.2)
Red-capped Robin (50)	38	0	38	24	2.7(2.7)
Jacky Winter (76)	26	23	26	25	2.9(3.7)
Grey Butcherbird (34)	18	12	32	38	5.7(5.4)
Shrub & canopy					
Spiny-cheeked Honeyeater (104)	0	26	50	24	3.2(2.8)
Yellow-plumed Honeyeater (375)	0	1	61	38	4.8(2.8)
Broad-tailed Thornbill (155)	4	17	66	13	3.2(2.2)
Horsfield's Bronze Cuckoo (10)	0	0	70	30	5.2(1.5)
Brown Honeyeater (52)	4	6	75	15	3.5(2.7)
Brown-headed Honeyeater (51)	0	0	75	25	5(2.3)
White-fronted Honeyeater (59)	0	1	90	9	3.6(1.4)
Canopy					
Weebill (264)	0	2	73	25	4.3(2.1)
Red Wattlebird (54)	0	0	54	46	5.4(2.1)
Purple-crowned Lorikeet (218)	0	0	53	47	6(2.6)
Striated Pardalote (202)	0	0	46	54	6.2(3.1)
Black-capped Sittella (18)	0	0	33	67	7.1(3.2)
Black-faced Cuckoo-shrike (35)	0	0	14	86	7.6(2)
Above & within canopy					
Dusky Woodswallow (73)	0	0	12	88	15.3(9.6)
Tree Martin (124)	0	0	8	92	20.6(8.9)

*values are mean with standard deviation in parentheses

guilds based on percent use of foraging manoeuvres, substrates and foraging heights. The point of division was arbitrary, but generally grouped species using a particular height range, substrate, manoeuvre or combination of height, substrate and manoeuvre for 40% or more of recorded observations. Ten or more observations were recorded for 33 species (Table 1). Species for which we recorded fewer than ten foraging manoeuvres were not analysed.

Results

Species richness

Sixty-three species of birds were recorded within the study area (Appendix 1). The maximum number of species observed during a count was 36 and the minimum was eight (16 ± sd 8, n = 24). The wide variation in species number is partly due to differences between counts in the time of day, temperature and habitat. In early morning counts when temperatures were less than 20 °C (min 10 °C), more individuals and species were recorded than in counts later in the day or when temperatures were higher (max 28 °C). The greatest number of species were recorded in complexly structured Salmon Gum forest with four vegetation strata: ground (0 - 0.1 m), low shrub (0.2 - 1 m), mallee and tall shrub (1.1 - 6 m), and canopy eucalypts (> 12 m). Gimlet/Yorrell woodlands with a grassy ground vegetation and comparatively few shrubs had the fewest species of birds present.

An index of abundance (total number of individuals recorded during counts; n = 24) is presented in Appendix 1. However, most species were represented by few birds and the frequency with which species were recorded on counts (*i.e.* presence/absence) may be a better indicator of relative abundance. The distribution of species among sites was patchy and most species were only recorded on a small number of counts (Appendix 1). Nineteen of the 63 species (30%) were recorded on only 1 or 2 counts, while 32 (51%) occurred on five or fewer counts. Fifty-one species (81%) were recorded on 11 or fewer counts, while only five species (8%) occurred on 19 or more counts. No species was recorded on all counts (Appendix 1).

Foraging heights

Ten species (30%) took more than 50% or more of their food from the ground or from ground vegetation less than 10 cm in height (Table 1). Including ground-foragers, twelve species (36%) took 50% or more of their food from within 1 m of the ground.

Twelve species (36%), including Yellow-throated Miner and Red-capped Robin, foraged from the ground through the shrub and subcanopy vegetation into the canopy (Table 1). This includes species which foraged primarily on the ground, such as Rufous Treecreeper. The Grey Fantail also forages over this height range, but we did not record it foraging in the canopy during this study. Eighteen species (55%) took more than 40% of their food from shrubs and mallee eucalypts within a height range of 0.2-5 m. Only Gilbert's Whistler foraged predominantly (59% of foraging manoeuvres) in shrubs within a metre of the ground. Brown, Spiny-cheeked, White-eared, Yellow-plumed and White-fronted Honeyeaters took nectar from a variety of tall shrubs (mainly *Eremophila* spp) 1-1.8 m in height, and also visited flowering mallees 2.5-6 m in height. Most observations of Purple-crowned Lorikeets were of birds foraging on mallee blossom.

Eight species (24%), Black-faced Cuckoo-shrike, Brown-headed Honeyeater, Horsfield's Bronze Cuckoo, Purple-crowned Lorikeet, Red Wattlebird, Striated Pardalote, Weebill, and Yellow-plumed Honeyeater, foraged predominantly (> 95% of foraging manoeuvres) in the canopy (> 4 m) of mallees and other eucalypts. Black-capped Sittella foraged on the trunks of trees and stems of eucalypts from < 2 m to more than 13 m above

Table 2

Use of substrates (%) by foraging birds in Salmon Gum woodland at Yellowdine during September 1997. See Table 1 for sample sizes and Appendix 1 for scientific names.

Species	Substrate					
	Ground	Bark		Foliage	Air	Flower
		Branch	Trunk			
Ground foragers						
Chestnut Quail-thrush	100	0	0	0	0	0
Emu	100	0	0	0	0	0
Galah	100	0	0	0	0	0
Redthroat	100	0	0	0	0	0
Yellow-rumped Thornbill	100	0	0	0	0	0
White-browed Babbler	83	17	0	0	0	0
Rufous Treecreeper	80	9	8	3	0	0
Port Lincoln Parrot	74	0	12	7	0	7
Grey Shrike-thrush	64	9	0	0	17	0
Ground & foliage						
Yellow-throated Miner	40	0	5	55	0	0
Gilbert's Whistler	22	9	0	69	0	0
Chestnut-rumped Thornbill	18	9	2	62	6	3
Ground & aerial foragers						
Red-capped Robin	40	7	2	7	44	0
Willie Wagtail	34	0	0	12	54	0
Grey Butcherbird	33	10	7	14	36	0
Jacky Winter	29	3	11	4	53	0
Aerial foragers						
Tree Martin	0	0	0	0	100	0
Dusky Woodswallow	0	2	5	3	88	2
Grey Fantail	0	9	0	16	75	0
Foliage foragers						
Striated Pardalote	0	0	0	100	0	0
Horsfield's Bronze Cuckoo	0	0	0	100	0	0
Broad-tailed Thornbill	5	7	1	84	1	2
Black-faced Cuckoo-shrike	0	0	3	83	14	0
Weebill	0	5	0	78	1	16
Bark foragers						
Black-capped Sittella	0	96	4	0	0	0
Nectar foragers						
Purple-crowned Lorikeet	0	0	0	0	0	100
Brown Honeyeater	4	0	0	4	2	90
Spiny-cheeked Honeyeater	0	2	0	8	4	86
White-fronted Honeyeater	0	0	0	5	10	85
Yellow-plumed Honeyeater	0	3	1	23	12	61
Red Wattlebird	0	10	5	20	8	57
White-eared Honeyeater	12	3	9	15	9	52
Brown-headed Honeyeater	0	0	2	47	0	51

the ground. Tree Martins and Dusky Woodswallows foraged within and above the canopy.

Substrates

Nine species took 60% or more of their food from the ground, including litter, coarse woody debris, logs and ground vegetation (Table 2). Eight species took more than 50% of their prey from foliage, including five which took more than 75% of prey from foliage (Table 2). Seven species took more than 35% of their prey from the air. Aerial foragers fell into two groups. One group (ground and aerial foragers) took more than 25% of their prey from the ground, while the second group (aerial foragers) took more than 75% of prey from the air.

The Black-capped Sittella was the only species to forage exclusively on bark substrates (Table 2). Bark was little used by birds at Yellowdine and only five species, including the sittella, took 15% or more of their prey from branches or trunks. Other than the sittella, none took more than 17% of their prey from bark.

Nectar-feeders were a conspicuous component of the avifauna at Yellowdine. Seven honeyeaters and the Purple-crowned Lorikeet fed at flowers on more than 50% of observed foraging manoeuvres. Apart from the lorikeet, nectar-feeders also took food from foliage, bark and the air (Table 2). The Weebill, an insectivore, was observed feeding at flowers 16% of the time and appeared to be taking nectar, not insects. The observations (7%) of Port Lincoln Parrot foraging on flowers were of birds eating the soft base (cup) of the inflorescence.

Foraging manoeuvre

Probing and gleaning were the most common foraging behaviours used by birds at Yellowdine (Table 3). Eight species of nectar-feeders took more than 50% of their food by probing flowers for nectar. Four nectar-feeders gleaned extensively and took arthropods and alternative carbohydrates (*e.g.* lerp, honeydew) from foliage and bark. Nectar-feeders also hawked and snatched insects and on occasion hovered at flowers or foliage to feed (Table 3). Ground-foragers took most food by gleaning and probing the soil surface, litter and low ground vegetation. Five

Table 3

Use of foraging manoeuvres (%) by birds in a Salmon Gum woodland at Yellowdine during September 1997. See Table 1 for sample sizes and Appendix 1 for scientific names.

Species	Foraging Manoeuvre					
	Pounce	Probe	Glean	Hover	Snatch	Hawk
Nectar feeders						
Purple-crowned Lorikeet	0	100	0	0	0	0
Brown Honeyeater	0	90	2	4	2	2
Spiny-cheeked Honeyeater	0	87	7	0	2	4
White-fronted Honeyeater	0	85	3	0	2	10
White-eared Honeyeater	0	69	20	3	0	8
Yellow-plumed Honeyeater	0	61	24	1	2	12
Red Wattlebird	0	58	32	0	8	2
Brown-headed Honeyeater	0	53	43	4	0	0
Ground gleaners & probers						
Chestnut Quail-thrush	0	0	100	0	0	0
Emu	0	0	100	0	0	0
Galah	0	0	100	0	0	0
Port Lincoln Parrot	0	14	86	0	0	0
Yellow-rumped Thornbill	0	14	86	0	0	0
Redthroat	0	33	67	0	0	0
Rufous Treecreeper	0	37	63	0	1	0
Grey Shrike-thrush	0	45	45	0	10	0
White-browed Babbler	0	97	3	0	0	0
Foliage gleaners						
Horsfield's Bronze Cuckoo	0	0	100	0	0	0
Striated Pardalote	0	0	94	1	9	0
Weebill	0	8	58	14	18	2
Yellow-throated Miner	0	45	55	0	0	0
Foliage/ bark gleaners & snatchers						
Chestnut-rumped Thornbill	0	3	59	5	28	5
Broad-tailed Thornbill	0	0	59	3	37	1
Gilbert's Whistler	0	0	47	0	53	0
Black-faced Cuckoo-shrike	0	20	0	0	80	0
Bark gleaners						
Black-capped Sittella	0	25	75	0	0	0
Pouncers & hawkers						
Red-capped Robin	38	15	6	0	2	39
Jacky Winter	29	0	1	0	0	54
Grey Butcherbird	29	14	18	0	5	34
Hawkers						
Tree Martin	0	0	0	0	0	100
Dusky Woodswallow	0	0	0	0	10	90
Grey Fantail	0	0	11	0	14	75
Willie Wagtail	2	12	26	0	4	56

species of ground-foragers took more than 85% of their food by gleaning. These included the Emu, Galah and Port Lincoln Parrot, which appeared to feed mainly on foliage (soft leaves) and seeds, including entire seed pods (*e.g.* of *Acacia*). Three other ground-foragers took a third or more of their prey by probing, usually into and under litter and debris. White-browed Babblers foraged almost exclusively by probing for prey in litter, debris and under the bark of branches (Tables 2, 3).

The Black-capped Sittella took prey from on and under bark by gleaning and probing. This included flaking bark from branches to expose arthropods. Four species were primarily foliage-gleaners and took more than 50% of their prey in this way. Weebills also hovered and snatched prey from foliage and probed flowers. The Yellow-throated Miner probed and gleaned prey from foliage and also foraged on the ground (Table 2). Gilbert's Whistler and Chestnut-rumped and Broad-tailed Thornbills took prey from bark and foliage by gleaning and snatching, while Black-faced Cuckoo-shrikes foraged almost exclusively on large insects snatched from foliage in the canopy.

Three species, Red-capped Robin, Jacky Winter and Grey Butcherbird, took more than 25% of their prey by pouncing, but took the largest proportion of their prey by hawking (Table 3). A group of four species took more than 50% of their prey by hawking, Grey Fantails and Willie Wagtails by flitting and Tree Martins by sweeping. Dusky Woodswallows took flying insects by both sweeping and hawking, but also snatched prey from bark and foliage. Grey fantails also gleaned and snatched prey from bark and foliage, while Willie Wagtails took prey from the ground and ground vegetation by a combination of methods, but mainly by gleaning (Table 3).

Discussion

The pattern of resource use by birds in the Salmon Gum woodlands at Yellowdine is similar to that reported for wandoo (*Eucalyptus wandoo* and *E. accedens*) woodlands at Dryandra on the western margin of the Wheatbelt (Recher & Davis 1998). At Yellowdine and Dryandra, ground-foraging was a major component of community-wide foraging with 45% and 61% of species, respectively, taking 20% or more of their prey from ground substrates. Using data from other localities, another 19 species recorded at Yellowdine but for which there are fewer than ten foraging observations, are principally ground-foragers; Australian Magpie, Australian Raven, Brown Falcon, Common Bronzewing, Fan-tailed and Pallid Cuckoos, Grey Currawong, Nankeen Kestrel, Little Crow (*Corvus bennetti*), Major Mitchell Cockatoo, Magpie-lark, Pied Butcherbird, Red-backed and Sacred Kingfishers, Regent Parrot, Southern Scrubrobin, Tawny Frogmouth (*Podargus strigoides*), Wedge-tailed Eagle and White-winged Triller.

Foliage was the next most important substrate in both Yellowdine and Dryandra woodlands, with 30% and 49% of species, respectively, taking 20% or more of prey from foliage. Aerial foragers comprised 21% of species in both woodlands, but in wandoo woodland 30% of species foraged extensively on bark, whereas only one species (3%) at Yellowdine took more than 20% of its prey from bark. Nectar-feeders were frequent at Yellowdine with 24% of species foraging predominantly on nectar, but only 9% at Dryandra. Note that since species took prey from multiple substrates and used more than one foraging manoeuvre, percents of species can sum to more than 100.

Morris & Wooller (2001) studied the abundance and foraging ecology of small birds in Salmon Gum woodland near Kambalda, Western Australia (31° 12' S, 121° 38' E) from February 1981 to June 1982. They found that insectivorous birds were largely resident and that their abundances did not change greatly over the 18 months sampled. Numbers and species composition of honeyeaters were more variable. Morris & Wooller (2001) suggested that this reflected the 'temporal inconsistency' of eucalypt flowering on their study area. Nectar from *Eremophila* spp was also available during winter at Kambalda, but shrubs were dispersed and may not have been attractive to honeyeaters.

At Yellowdine, eucalypt and *Eremophila* nectar was abundant during September 1997. Although we did not measure nectar abundance nor score flowers, the amount of eucalypt and *Eremophila* blossom was one of the greatest we have encountered in 20 years of fieldwork in eucalypt woodlands in eastern and western Australia. With the exception of the Singing Honeyeater (*Lichenostomus virescens*), which was absent from Yellowdine, the same honeyeaters occurred at Yellowdine and Kambalda. The nectar dependent Purple-crowned Lorikeet was abundant at Yellowdine (Appendix 1), but absent at Kambalda. At neither location did Yellow-throated Miners forage for nectar (2% of observations at Kambalda). Of the remaining seven species of honeyeaters present at both locations, more than 50% of foraging observations at Yellowdine were of birds taking nectar from eucalypt and *Eremophila* flowers (Table 2). At Kambalda, only three species (Brown and White-fronted Honeyeaters and Red Wattlebird) were recorded nectar-feeding on more than 50% of observations. Instead, most honeyeaters foraged by gleaning and probing foliage and bark (Morris & Wooller 2001). At Yellowdine, gleaning or probing foliage and bark comprised more than 20% of foraging observations for White-eared, Yellow-plumed and Brown-headed Honeyeaters, and Red Wattlebird (Table 2).

The high incidence of nectar-feeding at Yellowdine relative to Kambalda and Dryandra reflects the large amount of blossom at Yellowdine during our observations and illustrates how nectar-feeders shift between substrates and habitats in response to changes in the availability of nectar and other energy-rich carbohydrates (*i.e.* lerp, manna and honeydew). Changes in the abundance and species composition of nectar-feeders, as well as movements between habitats, in response to temporal availability of nectar has been extensively documented (*e.g.* Pyke & Recher 1986, 1988; Pyke *et al.* 1993) and the differences in our observations from those a Kambalda fit this pattern. For example, at Kambalda, the White-eared Honeyeater took most of its food by gleaning and probing bark, but visited flowers extensively (> 20% of observations) in spring and summer when nectar was more abundant (Morris & Wooller 2001). Wilson & Recher (2001) found that Yellow-plumed Honeyeaters at Dryandra foraged primarily by gleaning lerp from eucalypt foliage, but during some sample periods foraged by gleaning and probing bark. At Yellowdine, Yellow-plumed Honeyeaters seldom foraged on bark (Table 2).

Although not reported for Kambalda (Morris & Wooller 2001), resident and migratory insectivores in Australian woodlands also exploit different prey and foraging substrates at different places and times (*e.g.* Recher *et al.* 1987; Recher 1989). For example, at Yellowdine, a number of insectivores hawked termites as these swarmed late in the day. This included species which normally take prey by pouncing to the ground, such as Red-capped Robin (Recher *et al.* 2002). Although the swarming of termites is a diurnal phenomenon, it is also seasonal and most likely to occur following rain when it is warm and humid (*e.g.* spring and early summer). The differences in foraging behaviour between the observations at Kambalda and ours at Yellowdine suggest substantial temporal variation in the spatial distribution, type and abundance of food resources in eucalypt woodlands. In Jarrah (*Eucalyptus marginata*) forest near Perth, there are significant changes in the abundance of canopy arthropods between seasons and years (Recher *et al.* 1996). Similar seasonal and annual differences have been demonstrated in the bark arthropod fauna in Jarrah forest and wandoo woodlands with significant changes in the pattern of bark foraging by birds (J Majer, C Norwood & H Recher, unpublished observations).

Although some individuals may be sedentary and remain resident, based on fieldwork at Yellowdine since 1997 and extensive studies in similar habitats elsewhere, we have reached the conclusion that a much larger number of insectivorous bird species in eucalypt and acacia woodlands are migratory or nomadic than is generally accepted; woodswallows, cuckoo-shrikes, trillers, pardalotes, whistlers and cuckoos are birds that appear to move seasonally between habitats and regions and aggregate wherever food is abundant. Thus, of the 63 species recorded at Yellowdine, we conservatively estimate that 16 (25%) present in 1997 were nomadic or migratory. In addition, we recorded seven species of hawks, all of which aggregate in areas of high food abundance and are also nomadic and migratory. More than a third of the bird species we observed at Yellowdine may therefore not be resident and censuses at another time may reveal a much poorer (or richer) avifauna. We suggest that the large number of nomads and migrants, which we recorded were present in response to abundant nectar and insects. Similarly, we suggest that raptors aggregated in the area in response to the abundance of honeyeaters and lorikeets on flowering eucalypts, as well as an abundant insect fauna. Obviously, our ideas and observations require confirmation, but the implications for regional and continental conservation are profound, if as we contend, our interpretation of the data is correct.

Conclusion

Salmon Gum woodlands in the western Goldfields sustain a rich and diverse avifauna. While the majority of species are resident and insectivorous (Morris & Wooller 2001; this study), a substantial proportion of individuals and species are migratory or nomadic. We suggest that these birds aggregate whenever food resources in the form of nectar, lerp, insects and other birds are abundant. This component of the avifauna may be especially sensitive to habitat loss and fragmentation that not only decreases the amount of available food making it difficult to locate patches of abundant food, but could result in absolute shortages in some seasons or years by chance alone. The natural temporal and spatial variability of the flowering of eucalypts (Davies 1976) makes this an increasingly likely event as habitat is diminished. We further suggest that it is not only nectar and carbohydrate-dependent species, such as honeyeaters, pardalotes and lorikeets, that may be affected, but also insectivorous species, such as woodswallows, martins, cuckoo-shrikes and trillers, and raptors. It appears to us that it is unlikely that the spatial and temporal variation in resources on which this avifauna relies can be accommodated in a conventional system of reserves sampling only a small part of the land area. Conserving woodland bird communities in the Goldfields and elsewhere therefore requires the retention of large areas of habitat as functional ecosystems between and within which the avifauna can move in response to a dynamic and shifting resource base.

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Appendix 1

An index of abundance of birds recorded at Yellowdine, Western Australia during September 1997. Abundances are the total number of individuals recorded during counts at all sites where foraging data were collected. The number of counts (n = 24) on which a species was recorded is shown in parentheses and is a measure of habitat breadth and relative abundance (frequency of occurrence). Species are listed in alphabetical order of English names, with scientific names after Johnstone (2001). *Daphoenositta pileata* (Black-capped Sittella) is retained as a species.

SPECIES		ABUNDANCE
Brown Goshawk	*Accipter fasciatus*	7 (5)
Australian Magpie	*Gymnorhina tibicen*	2 (2)
Australian Raven	*Corvus coronoides*	20 (11)
Black-capped Sittella	*Daphoenositta pileata*	7 (1)
Black-eared Cuckoo	*Chrysococcyx osculans*	4 (4)
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	41 (19)
Broad-tailed (Inland) Thornbill	*Acanthiza apicalis*	57 (12)
Brown Falcon	*Falco berigora*	1 (1)
Brown Honeyeater	*Lichmera indistincta*	7 (4)
Brown-headed Honeyeater	*Melithreptus brevirostris*	59 (10)
Chestnut Quail-thrush	*Cinclosoma castanotum*	4 (2)
Chestnut-rumped Thornbill	*Acanthiza uropygialis*	41 (17)
Collared Sparrowhawk	*Accipter cirrhocephalus*	2 (2)
Common Bronzewing	*Phaps chalcoptera*	3 (2)
Crested Bellbird	*Oreoica gutturalis*	12 (9)
Crested Pigeon	*Ocyphaps lophotes*	4 (3)
Dusky Woodswallow	*Artamus cyanopterus*	28 (8)
Emu	*Dromaius novaehollandiae*	4 (3)
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	1 (1)
Galah	*Eolophus roseicapillus*	24 (9)
Gilbert's Whistler	*Pachycephala inornata*	9 (5)
Golden Whistler	*Pachycephala pectoralis*	1 (1)
Grey Butcherbird	*Craticus torquatus*	12 (9)
Grey Currawong	*Strepera versicolor*	11 (8)
Grey Fantail	*Rhipidura fuliginosa*	4 (4)
Grey Shrike-thrush	*Colluricincla harmonica*	27 (15)
Horsfield's Bronze Cuckoo	*Chrysococcyx basalis*	11 (11)
Jacky Winter	*Microeca fascinans*	9 (6)
Little Eagle	*Hieraaetus morphnoides*	2 (1)
Little Falcon	*Falco longipennis*	3 (2)
Major Mitchell Cockatoo	*Cacatua leadbeateri*	6 (4)
Mistletoebird	*Dicaeum hirundinaceum*	3 (3)
Nankeen Kestrel	*Falco cenchroides*	2 (2)
Pallid Cuckoo	*Cuculus pallidus*	9 (8)
Magpie Lark	*Grallina cyanoleuca*	1 (1)
Pied Butcherbird	*Cracticus nigrogularis*	16 (11)
Port Lincoln Parrot	*Barnardius zonarius*	37 (15)
Purple-crowned Lorikeet	*Glossopsitta porphyrocephala*	123 (15)
Red-backed Kingfisher	*Todiramphus pyrrhopygia*	2 (2)
Red-capped Robin	*Petroica goodenovii*	20 (11)
Red Wattlebird	*Anthochaera carunculata*	155 (23)
Redthroat	*Pyrrholaemus brunneus*	16 (5)
Regent Parrot	*Polytelis anthopeplus*	8 (4)
Rufous Treecreeper	*Climacteris rufa*	30 (15)
Rufous Whistler	*Pachycephala rufiventris*	6 (4)
Sacred Kingfisher	*Todiramphus sanctus*	1 (1)
Southern Scrubrobin	*Drymodes brunneopygia*	4 (2)
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*	78 (11)
Spotted Harrier	*Circus assimilis*	2 (2)
Striated Pardalote	*Pardalotus striatus*	155 (21)
Tree Martin	*Hirundo nigricans*	18 (6)
Weebill	*Smicrornis brevirostris*	171 (19)
Wedge-tailed Eagle	*Aquila audax*	2 (2)
White-browed Babbler	*Pomatostomus supercilliosus*	7 (2)
White-eared Honeyeater	*Lichenostomus leucotis*	23 (8)
White-fronted Honeyeater	*Phylidonyris albifrons*	21 (8)
White-winged Triller	*Lalage sueurii*	2 (2)
Willie Wagtail	*Rhipidura leucophrys*	33 (16)
Yellow-plumed Honeyeater	*Lichenostomus ornatus*	237 (20)
Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	28 (11)
Yellow-throated Miner	*Manorina flavigula*	17 (4)

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Opening of the workshop on terrestrial fauna surveys databases

B Bowen

Chairman, Environmental Protection Authority, Westralia Square, 141 St Georges Terrace, Perth WA 6000

This workshop is about the possibility of a coordinated and integrated database for terrestrial fauna survey data for Western Australia. In 1984, the then Department of Conservation and Environment produced a publication entitled 'A Bibliography and Research Inventory of Vertebrate Fauna in WA'. The introduction set out that 'this Bulletin is primarily aimed at providing assistance for persons and organisations involved in environmental planning, impact assessment and management.' The need for an integrated database is not new, but the urgency to progress the subject increases every year.

Western Australia has a unique assemblage of animals in a fragile environment, and their habitats are continually being eroded. The pressure on those habitats will not diminish, but to an increasing extent the public want to be assured that those pressures do not lead to further reductions in fauna populations. This is a real dilemma for those with management responsibility; there is increasing development pressure but with increasing expectations by the community to know about and protect the fauna being impacted. All of this is in a climate of reduced funding for field surveys by those with specialised knowledge to do so.

Much of the potential for data collection now is by way of fauna surveys as a result of the environmental assessment process. Many of the consultants are responsible in their desire to undertake good work, but for this to really add to our knowledge in an organised and efficient manner there needs to be a partnership between industry and government.

Government should be providing ready access to an integrated database, but it should also be setting the standards for biological surveys. Some of this is set out in a Position Paper released today by the Environmental Protection Authority entitled 'Terrestrial Biological Surveys as an Element of Biodiversity Protection'.*

One of the passages from that Position Statement reads ' The EPA intends to encourage the coordinated development of a state-wide database for EPA-related biological surveys in consultation with environmental practitioners and Western Australian natural resource management agencies and authorities.

I am delighted that the Royal Society of Western Australia has arranged for this workshop to be held as part of its function of promoting science. I congratulate the Society on its initiative.

I have pleasure in opening this workshop and wish participants well in their discussions.

* Terrestrial Biological Surveys as an Element of Biodiversity Protection. Position Statement No 3. March 2002. Environmental Protection Authority, Perth. ISBN 0 7307 6674 8, ISSN 1441 1741.

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Do we need a terrestrial fauna survey database in Western Australia?

G G Thompson

Edith Cowan University
Joondalup Drive, Joondalup WA 6027
email: g.thompson@ecu.edu.au

Introduction

Early in 2000 I started exploring the use of Microsoft Access® to record and organise data from a pit-trapping program that was being undertaken in the vicinity of Ora Banda, Western Australia. A database was developed that met our initial needs, but it soon became evident that it would be much more useful if it could include pit-trapping data for other study sites. In addition, I started to explore a range of additional questions for which the database could not effectively generate the appropriate data. This change in my requirements and focus meant that the Access® database needed to be significantly altered. Instead of going through the process all over again, I investigated how other researchers stored and accessed their data, hoping that I might learn from their experiences. It quickly became evident that a standard protocol for recording pit-trapping data, and perhaps data collected using other search strategies would be useful, as it would enable the sharing and comparing of data for a range of habitats. My enquiries indicated the issue of a Western Australian terrestrial fauna survey database had been discussed among the relevant State government agencies for a number of years, but nothing tangible had occurred. It was my assessment that a couple of the State government agencies saw it as their prerogative to develop and manage the database, but because agreement among agencies could not be reached and the issue was not given sufficient priority in any one agency, nothing had happened.

In May 2000 the Environmental Protection Authority (EPA) released Preliminary Position Paper No 3, *General Requirements for Terrestrial Biological Surveys* (EPA, 2000) that indicated it was concerned about the lack of appropriate, targeted information that would allow the Authority to properly assess potential impacts of disturbance at both a local and regional scale. The Preliminary Position Paper indicated the following key issues contributed to the difficulty of assessing the impact of a disturbance on the biodiversity:

- a lack of appropriate scale baseline information for most areas of the State;
- replication of databases;
- site-specific data not being interpreted/analysed for biodiversity value or in a regional context; and
- a lack of a consolidate database on fauna captures.

In the subsequent EPA Position Paper No 3, *Terrestrial Biological Surveys as an Element of Biodiversity Protection* (EPA 2002), the Authority as an overarching principle indicates it 'expects that terrestrial biological surveys will be made publicly available and will contribute to the bank of data available for the particular region, to aid the overall biodiversity understanding and assessment by facilitating transfer into State biological databases'. The Position Paper goes on to indicate that the EPA intends to encourage the coordinated development of a state-wide database for EIA-related biological surveys in consultation with environmental practitioners and Western Australian natural resource management agencies and authorities.

My investigations also indicated that a number of government agencies already had their own databases for fauna, but there was little coordination among agencies or even within agencies. The Wildlife Branch of the Department of Conservation and Land Management (CALM) has developed a database of threatened fauna, and a database, *Fauna File*, to support its fauna recovery plans. Staff in CALM *Science* (Woodvale) had an alternative method of recording pit-trapping data. Staff in some of the regional offices of CALM also had pit-trapping data files, again recorded in locally-designed systems. Access to some of this information by researchers and environmental consultants was often difficult.

CALM, as part of its licence requirements to catch and take fauna, requires researchers and environmental consultants to submit an annual return of their fauna captures. The format in which consultants and researchers present data, and the recording of these data by CALM, is such that this information does not currently constitute a useful database of fauna records.

The Western Australian Museum (WAM) has a very substantial computerised record of mammals, reptiles and amphibians lodged with WAM since early last century. This is a very important database as it provides a description of known taxa in time and space. However, as pointed out by Ponder *et al.* (2001), there are significant problems with museum collections when used for biodiversity assessment. The most notable is the 'gaps' in species distributions because of the *ad hoc* nature of the collecting effort. Museum records are not a reliable source of data on abundance, and at a local scale are unable to provide accurate records of species richness unless the area was a specific study site for Museum staff or researchers that routinely provide voucher specimens. It is regrettable that many Australian museums are now charging researchers for access to records that were often provided by researchers. The selling of what should be publicly available information discourages the sharing of data and may inhibit the development of a State database for terrestrial fauna survey data.

This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

Many of the well-established environmental consultants that regularly undertake terrestrial fauna surveys maintain their own databases, but in almost every case access to this information is restricted to the owners of the information. A small number of researchers (academics and postgraduate students) in Western Australia who have undertaken pit-trapping programs for small terrestrial fauna have significant fauna records for specific sites. Academic ownership of these records means that these data are generally not publicly available.

EPA (2002) stressed the need for quality field survey data inputs into the preparation of Environmental Impact Assessments (EIA) and comprehensive analyses of these data in the context of biodiversity conservation and ecological function. However, Fraser (2001) reported that during the preparation of 15 recent EIA statements for mining developments in the Goldfields region;

- 3 of 15 consultants searched the CALM or WAM databases;
- 12 of 15 consultants analysed field data in a regional context;
- 2 of 15 lodged voucher specimens with WAM, where there was a doubt about the specimens identity;
- 3 of 15 evaluated community assemblages and field data in an ecological context; and
- none of the field surveys were adequate for the preparation of an inventory of species in the area.

There appears ample evidence to suggest that an integrated database for terrestrial fauna survey data is required. For this to proceed, four general questions need to be addressed:

- what information should be recorded and stored, and how do we ensure its accuracy?
- who owns the data and how should it be accessed?
- who will manage the database? and
- who should develop the database and what should be its format?

These four broad questions can be further divided into a more detailed list of specific questions that need to be addressed before an integrated database of terrestrial fauna records can be established (Appendix 1). It was the task of this workshop to address those questions it considered appropriate.

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Appendix 1

Issues to be considered in the development and management of a Western Australian terrestrial fauna survey database.

Information base:

What taxa are recorded?

- Reptiles
- Amphibians
- Mammals
- Birds
- Fishes
- Invertebrates
- Rare species
- Only terrestrial, aquatic, marine, stygofauna, vertebrate or invertebrate
- Metadata catalogues – are there general elements with wide applicability?

Specimen data

- Locality
- Geographic site registration conventions/protocols
- Habitat
- Date
- Collector
- Land tenure
- Morphometrics (size and mass; should we standardise measurements), do we need these data?
- Method of capture / observation
- Non-Western Australian specimens
- Past information or only new information

Accuracy of data

- Data standards, what are they and who is responsible for managing and publishing them?
- Data quality tags/standards
- Who checks the data
- Who changes the data
- Nomenclature – which authors and versions?
- Mis-identification
- Voucher specimens
- Submissions, additions and corrections to data
- Strategies for protecting indefeasible raw data

Integration with other databases

- Soils, pre-European vegetation (*Aust. Soils Atlas*, Bureau of Rural Sciences)
- Vegetation, (Beard's maps, available from Agriculture WA), remnant vegetation (AgWA)
- Climatic
- GIS friendly
    - o Arcview, Arcinfo
    - o ER Mapper
- Platypus – http://www.environment.gov.au/abrs/abif-fauna/intro.htm
- WAM database
- CALM rare and endangered, priority taxa

Proprietary issues

Ownership of data

- Copyright
- People just looking – interested
- Use by researchers but not for commercial gain
- Use by others for commercial gain

Access to data

- Discriminating between the roles and responsibilities of data producers and data publishers
- Who
    - Collector
    - Depositor
    - Researchers
    - Consultants
    - Students
    - Government departments
    - Restrictions placed on access (read only access)
- How, via
    - Internet
    - Email
    - Hardcopy

Who can change the database?

Management issues

Management

- Managing changes
- Who, which agency, people and costs
- Legal agreements
- Assessing the probability of use of data
- Identifying likely information retrieval requirements
- Strategies for managing derived data

Costs

- Establishment
- Maintenance
- Access

Should the database be linked to CALM licence returns?

Technical issues:

Storage of data

- Where
    - Physical location
    - Hardware
- Format
    - Software
- Internet

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Importance of accuracy in co-ordination and integration of terrestrial vertebrate fauna survey databases in Western Australia

R Teale

Biota Environmental Sciences, Suite 2 First Floor, 186 Scarborough Beach Road,
Mt Hawthorn WA 6016
email: biota@biota.net.au

Abstract

Fauna data collected at present typically comprise species identity, abundance, morphometric and meristic measurements, and some basic information on life history. Any database incorporating such data must be designed with its end use in mind. End uses may include determining species distributions, abundances, average weights, *etc.* In the context of this workshop, a key outcome is to facilitate the documentation of Western Australia's biodiversity. Accurate species identifications are imperative in a database designed to document biodiversity, and the only clear mechanism to ensure this is vouchering. The obvious repository for this information is thus FaunaBase, which is held by the Western Australian Museum. It is after all the responsibility of the WA Museum to review and update the taxonomy of the fauna of Western Australia, which surely is the first step in documenting biodiversity.

On a parity with accuracy is precision of data, particularly in relation to morphometrics and meristics. There are clear examples of where differences between observers in measuring techniques, *etc* have generated different interpretations. Similarly, abundance values are contingent on the methodologies used to collect the data and the experience of field practitioners, particularly in relation to opportunistic collecting techniques such as head-torching, raking, *etc.*

There is clearly a "need for better coordination and integration of terrestrial fauna survey data" from surveys across the State. However, there are numerous issues inherent with an observational database, including differing data collection methodologies and experience of field practitioners, which reduce its scientific value. I would argue that much of the underlying infrastructure required to achieve the necessary coordination and integration is already in place in the WA Museum FaunaBase, but that it is currently under-utilised and perhaps under-resourced.

Keywords: database, fauna survey, voucher specimen

Introduction

The intention of this workshop is to investigate the development of a database to house all relevant data from all fauna surveys across the state. The rationale behind the development is "If data from surveys were coordinated and integrated it would provide an enhanced opportunity to understand and interpret the biodiversity and ecosystems of WA." In this case the definition of biodiversity follows that of the Environmental Protection Authority (EPA):

> *It is the variety and variability of all life forms, all plants, animals and micro-organisms, the genes they contain and the ecosystems they form.*

It is worth noting at this stage that the proposed database would largely be an observational database, in contrast to say the Western Australian Museum FaunaBase that only stores information on vouchered specimens. A key advantage of the latter is that through the vouchered specimen we can be more confident of the accuracy of the dataset. If there are any questions or taxonomic revisions, then we can go back to the original specimens and check the records again.

Stimulus for workshop

The stimulus for this workshop seems to have been recommendations made within the Environmental Protection Authority Position Statement No. 3 "General Requirements for Terrestrial Biological Surveys for Environmental Impact Assessment in WA". This Position Statement highlights, with respect to databases:

> "The need for both a consolidated database and for data to be collected by the proponent or their consultants in a format to allow ease of assessment at the local, regional and national levels, and to facilitate transfer to State biological databases"

The above EPA recommendation covers a broad range of topics. It first mentions a need for a consolidated database, secondly that data be collected in a format to allow ease of assessment, and thirdly that it can be transferred into State biological databases.

Compatibility with State databases

I think that the issue of compatibility is a key component of the EPA's statement and leads us to ask ourselves some fundamental questions:

- can existing databases give us insights into understanding and interpreting biodiversity in WA?
- recognising the cost associated with maintaining databases, can we use those resources to improve on existing databases in preference to embarking

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This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

on the development of the proposed new observational database?

- would any such improvement negate or partially offset the need to develop a new database?

In my role as a consultant, I use on a regular basis a number of State databases and some private ones including our own. One of the most useful resources is provided by the Western Australian Museum (WAM) collection, which is essentially the foundation of their database FaunaBase. The value of the collection is that it gives us an assurance of accuracy, provides us with a means to review taxonomy and is readily updateable in response to taxonomic review. Interestingly, the WAM is looking towards coordinating data storage/retrieval not only at a State level but also at a National level with other museums across Australia (P Berry, WAM, personal communication).

Fundamentally, the checks and balances required to ensure the highest accuracy of data in any new, largely observational database would also enhance the value of FaunaBase. Experience indicates that databases are costly to establish, populate and maintain. Therefore any resources we might have to put towards developing integrated data management would perhaps be better channelled into existing databases to further enhance their functionality and value, particularly those databases that underpin our understanding of biodiversity.

Accuracy and vouchering

So what are the 'checks and balances' alluded to above? Basically they are the process of ensuring accuracy through vouchering. In a sense vouchering could be considered as peer review of field identifications, which are otherwise often carried out in isolation, in an analogous way to peer review of the resulting papers. This is particularly important where the work is carried out by inexperienced field practitioners or where experienced practitioners are working in new regions. Where the focus of a paper is a species inventory or where species identification is critical to the conclusions of the study, then it is crucial that the field identifications are correct.

Similarly, the worth of a database lies in the accuracy of data that it contains *i.e.* "put rubbish in, get rubbish out". Accuracy of data is acknowledged as one of the key issues requiring discussion at this workshop and encompasses the following sub-topics in relation to development a new observational database:

- Mis-identification
- Who checks
- Who changes
- Nomenclature
- Voucher specimens
- Submissions, additions and corrections to data

Observational databases already exist for avifauna records and provide a template to address the above subtopics. For example, in the Bird Atlas program (Birds Australia) records can come from any registered individual. These records are vetted by a panel of experts and questioned if the records are of species at the edge of, or beyond, their known range of habitat preferences or distribution, or involve uncommon or rare species. However, these unusual records are often exactly the types of records that the scientific community is interested in, particularly many ornithologists. Observational datasets are largely unavoidable for birds because vouchering of this group is impossible for the typical amateur bird observer. In addition, very few bird studies, particularly those carried out during inventory surveys, use mist netting or other trapping techniques to record birds, as it is much simpler to observe and record. However, inexperienced bird watchers do make mistakes and often only record the common species (Saffer 2002), and as such these sorts of datasets are limited in their use.

Are similar identification errors made when identifying non-avian fauna? Clearly the answer is yes. Species within the *Neobatrachus*, *Heleioporus*, *Ctenotus*, *Pseudomys* and *Sminthopsis* genera often provide challenges for experienced field biologists, let alone inexperienced ones. Indeed, experienced field biologists working in one region of WA may not necessarily be familiar with species in a different region. Furthermore, and perhaps more importantly, the taxonomy of many of Western Australia's herpetofauna and mammalian fauna (unlike our birds) is incomplete (*e.g. Gehyra* spp, *Cryptoblepharus plagiocephalus/carnabyi*, *Lerista muelleri* complex, *Menetia greyii* complex, Aplin & Smith 2001; B Maryan, WAM, personal communication; G Harold, personal communication), *Planigale* spp, *Sminthopsis macroura* complex (N Cooper, WAM, personal communication). Quite the opposite of birds, reptiles and mammals are largely recorded from trapping and rarely through observational data (with the exception of large macropods, possums, varanids, *etc*) and this gives us the opportunity to confirm preliminary field identifications through subsequent vouchering.

This is not to say that every record obtained during inventory and survey needs to be supported by an accession number, nor that vouchering should be indiscriminate. Rather, each taxon needs to be supported by at least one vouchered specimen (qualified below) and possibly more, depending on the geographical spread of the study sites and the taxonomic status of the species. Vouchering also needs to take into consideration the fragmentation and size of habitat, historical collections from the locality, and the conservation status and distribution of the species.

However, it is not just a question of getting the identification right; it is also a matter of resolving taxonomy, being able to describe new taxa and enhancing the States biodiversity knowledge base. Taxonomy is constantly under revision and without voucher specimens we cannot describe new taxa. Surely taxonomy is a first step to documenting biodiversity, a key aim of this workshop.

Crucially, without vouchers we may not be certain of the identity of records for recently resolved taxa identified from within large species complexes (*e.g. Lerista muelleri*). LA Smith (WAM, personal communication) has recognised approximately 17 species in the *L. muelleri* complex, all of which were previously registered as *Lerista muelleri*. Such a process of revision for a large and well collected species complex, with constituent taxa demonstrating some sympatry, renders universal changes in observational databases nearly impossible and may in fact invalidate large amounts of data *e.g.* nearly all *L. muelleri* records will need to be eliminated. There are many other examples of such species complexes in WA (Aplin & Smith 2001).

Whilst the resources are not yet available to undertake every required taxonomic review, a database supported by voucher specimens will not suffer from problems associated with invalidated data. Taxonomists can undertake reviews at a later stage and then make the changes to records of the vouchered specimens.

Once voucher specimens are lodged with the WAM, the responsibility of the tasks identified in the above bullet points becomes obvious:

- Mis-identification / Who checks — The WAM staff, using the extensive collection and their specialist knowledge, can compare newly vouchered specimens against the collection to check field identifications.
- Who changes — If necessary, WAM staff can then make the changes, or alternatively the vouchered specimens remain in the WAM until relevant experts undertake a revision.
- Nomenclature — The WAM is responsible for determining which nomenclature practitioners in WA should be using, *e.g.* 'Checklists of the vertebrates of Western Australia' published in 2001 in Records of the Western Australian Museum, Supplement 63.
- Submissions — WAM staff enter the information for vouchered specimens into FaunaBase, so there is no need to duplicate this information in another database.

Vouchering of specimens in WA seems to be limited to a handful of individuals (N Cooper, WAM, personal communication). This lack of vouchering seems to be central to the issue of the perceived need to develop a new database infrastructure.

If as a group, field biologists are interested in gaining a better understanding of biodiversity (as defined by the EPA), then we first need to ensure accuracy. It is my belief that the best mechanism for ensuring accuracy is through vouchering. Furthermore, this provision of specimens also enables taxonomists to carry out taxonomic revisions and identify new taxa, another key component to understanding biodiversity. In addition if field biologists voucher more diligently, then FaunaBase itself becomes a much more useful tool for other types of data interrogation.

Ramifications of an increase in vouchering

If as a first step to integrating our data, we need to ensure that accuracy is assured through vouchering, then we will obviously need to consider the significant resource/funding constraints that this will place on the WAM. By way of example, a total of 1300 herpetofauna records encompassing 79 taxa were made, and approximately 330 specimens were vouchered, from a recent survey (Biota Environmental Sciences 2002 Proposed Hope Downs Rail Corridor from Weeli Wolli Siding to Port Hedland – Vertebrate Fauna Survey; unpublished report for Hope Downs Management Services) involving over 5000 trap nights spread along a 330 km transect. From the same survey, there were 480 records of non-volant mammals, with 109 individuals vouchered.

What are the approximate resource demands on the Western Australian Museum from this level of vouchering? If the animal is alive, the process of euthenasing, extracting tissue for DNA, preserving, databasing, labelling and putting in the collection takes at least 45 mins per specimen, longer for mammals (1.5 hours) if the skull has to be prepared. So, 330 herpetofauna would take 245.7 person hours or 31 person days, whilst 109 mammals would take 163.5 person hours or 21 person days (N Cooper, WAM, personal communication).

If we have time and energy/resources to assist with developing a new database, I think that these would be more appropriately channelled (at least initially) into ensuring that the foundations of the database (*i.e.* accuracy and taxonomy) are adequately addressed. The feedback mechanism to the field biologists also provides important training.

Misplaced conservation

Misplaced conservation (after M Craig, personal communication) refers to the focus of biologists and others at the level of individual animals, rather than at the population level, when considering species conservation. In large intact areas of vegetation, considered vouchering would not in all likelihood cause a detectable impact to population levels. In the above example, the 330 vouchered individuals from in excess of 70 taxa were from 33 sites, each spread on average 10 km apart. This equates to ten individuals per site. The Biota (2002) survey recorded on average 7.8 ± 5.2 species per site, thus in most cases only one or two individuals of any one species were taken from each site. Clearly this level of collecting would not have a detectable impact on local populations. In contrast, in highly fragmented and small remnants, vouchering of some species may hasten the demise of local populations. As stressed above, vouchering should not be indiscriminate.

In the above example, vouchered specimens included one species possibly new to science (*Ctenotus* aff *uber johnstonei*), a recently "re-discovered" species that is poorly collected (*Ctenotus* aff *robustus*), and another poorly collected taxon, *Vermicella snelli*. Other specimens that were vouchered included taxa (*Diplodactylus stenodactylus*, *Lerista bipes*, *Lerista muelleri* and *Menetia greyii*) that are known to belong to species complexes, and some that are just extremely difficult to accurately key out in the field (*e.g.* members of the genus *Ramphotyphlops*).

Limitations of observational data

What about the remaining observational data that were collected in the above example (*i.e.* the other 1000 herpetofauna records) — what are their value? My response to this question is, what is the intended end use of the data? Fauna data collected typically comprises species identity, abundance, morphometrics and meristics, and some basic information on life history. End uses may include determining species distribution, abundances and average lengths, weights, *etc.*

If the end use is species distributions, then the Western Australian Museum FaunaBase is already established and can incorporate representative vouchers from the study site. For rare species, where observational data is important due to restrictions on collecting threatened taxa, the Department of Conservation and Land Management Rare Fauna Data Base is already established.

Abundance data are contingent upon the methodologies used for collection, for example, Elliott trapping, pit fall trapping (buckets or PVC tubes), head torching, raking, *etc*, seasonal timing, and survey duration. Undoubtedly the experience of the practitioner also markedly affects abundance values, especially from opportunistic collections and in selecting trapping sites.

Morphometric data are highly variable between different observers; even within observers some characters cannot be scored reliably (Humphreys 1990). Clearly the amalgamation of meristic and/or morphometric datasets from a large number of different observers is of little value for any detailed descriptions.

Exceptions

There are some extremely good practitioners whose observational datasets would be of huge value if used correctly. For example, Greg Harold (a very experienced field biologist) has recorded every single herpetofauna he has seen since the mid 1970s. This would be a fantastic dataset and one that would probably have no more errors in it than FaunaBase. These data could thus reliably be used to obtain a better idea of species distributions. Similarly, where datasets are supported by adequate vouchering, location details from non-vouchered records can add to our knowledge of species distribution.

Conclusions

Any new database would largely store observational data. An observational database would not meet the primary objective of the rationale behind its development, that is:

"If data from surveys were coordinated and integrated it would provide an enhanced opportunity to understand and interpret the biodiversity and ecosystems of WA."

Clearly there are many limitations on collective data placed into an observational database by many observers, which end users may not always be aware of or may not consider. These include different methodologies, experience of the field biologists, weather, fire history, *etc*. When combined with questions of accuracy and precision, these can significantly undermine the value of an observational dataset.

We cannot understand nor interpret the States biodiversity (as defined by the EPA) without ensuring accuracy of our field identifications. The need to voucher to ensure accuracy means that FaunaBase will support more records and become a more useful tool for interrogation.

To summarise, we should initially examine existing databases before embarking on the development of a new database. FaunaBase is an obvious choice as it resides with the Western Australian Museum, whose staff can confirm initial field identifications, are responsible for nomenclature in the State and regularly undertake taxonomic reviews. FaunaBase is already operational, has the necessary IT infrastructure in place, has a clearly identified custodian and is widely accessible to the scientific and general community. This addresses many of the issues that would undoubtedly arise in the delivery of any new database.

Implications are that the increased level of vouchering that would be required to ensure the accuracy of any data that we would place into a proposed observational database would place considerable strains on the resources at the Western Australian Museum. However at the same time the value of FaunaBase would be enhanced so that it may offset the need to develop a new database. Rather than investing in a new database, what I believe is required - at least initially - is better support, funding, resourcing and in particular USE of existing databases such as FaunaBase. If through this process we became more confident in the accuracy of our data, then we could re-examine an integrated observational database. As indicated above, there are also other databases available that we need to consider, for example the CALM Rare Fauna Database and the Pilbara Biological Reporting Database (see Biota 2001).

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Should we have a co-ordinated and integrated database for terrestrial fauna survey data for Western Australia? Government researchers view

N L McKenzie & K D Morris

Science Division, Department of Conservation and Land Management
PO Box 51, Wanneroo WA 6065
email: normm@calm.wa.gov.au, keithm@calm.wa.gov.au

Introduction

In Western Australia (WA), a variety of private environmental consultants carry out fauna surveys for industry and government. Their focus is usually local, *e.g.* mine-site surveys. The State Government, through the Department of Conservation and Land Management (CALM) employs four full-time survey zoologists and four technical staff variously specialising in aquatic invertebrates, spiders, birds, reptiles and mammals. The government focus is on regional surveys that are often undertaken in collaboration with the Western Australian Museum, universities, CSIRO and consultants.

How is fauna data currently used in land-use planning?

Most land-use planning at regional and local scales have been based on 1:250 000 soft-geology, land-unit or vegetation maps in the hope that they provide adequate surrogates for patterns of biodiversity. Usually, these map-units are 'enhanced' with relevant fauna data held in museums, field guides or threatened species atlases. Typically, threatened fauna (and flora) atlases are based on 'presence-only' data, with a high proportion of records collected opportunistically next to roads. Their value in understanding the species distribution, habitat and status is impaired by the inherent sampling biases. If resources are available, specific fauna surveys are also commissioned. In WA, these local fauna surveys are probably the first substantial ecological reconnaissance within 200 km of the area. Most of the fauna records obtained during these surveys are treated as an end in themselves rather than as the first step towards developing an understanding of regional biodiversity.

Fauna data for land-use planning, but in the right form

A one-to-one relationship between species composition and physical attributes at sites provides data with an 'open architecture' and permits cost-efficient analyses. Open architecture is important because it allows different data sets to be combined, so that biodiversity models can be upgraded as new data are collected. Site-based data are amenable to interpolation procedures that predict the species composition at locations between the sampled sites, as we are unable to sample every point on a landscape.

To minimise their impact, land-use planning decisions need to be based on explicit biodiversity models that link "what" to "where". To build realistic models of patterns of biodiversity, we need to collect data for a variety of taxa because levels of cross-taxon congruence are generally low at both local and regional scales (Fig 1). The more taxa we sample, the more realistic our biodiversity models become.

Fauna data are expensive to collect, even at local scales, and it takes even more time to collect reliable site-species lists, which adds to delays. Even then, sub-optimum land-use decisions are inevitable unless the data can be interpreted in a regional context.

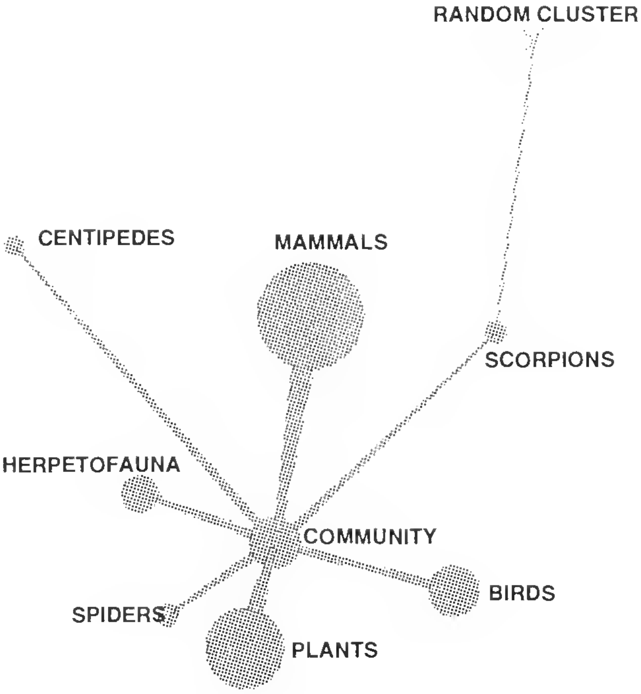

Figure 1. Three-dimensional scatter plot showing the low level of cross-taxon congruence among the seven biodiversity subsets sampled in the Carnarvon Basin, Western Australia (modified from McKenzie *et al.* 2000). 'Community' indicates the position of the combined data set. Standard error bars for the random cluster were calculated from 1000 matrices generated using a uniform random distribution. Minimum spanning tree linkages are shown. The radius of the biodiversity cluster was 80% of the distance from 'community' to the centre of the random cluster.

This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

Regional surveys

Problems of associated with costs and delay are exacerbated for regional surveys because they need sufficient resolution to represent biodiversity patterns accurately at this scale. Considering the size and diversity of WA, building this 'context' for even one of the State's 26 bioregions is an enormous task. Twelve person-years of effort goes into one of CALM's regional surveys; about 70% of this effort is on the faunal components.

Land-use decisions in most parts of WA will have to continue to be made using whatever fauna data are available, so we need to establish standardised protocols for future fauna surveys, and optimise access to existing data.

Standardising protocols for future surveys so that fauna data is effective

The challenge is to design fauna surveys so that they provide the maximum return of useful information for a particular input of resources and can add as much value as possible to existing knowledge. In the context of survey design, we recommend a publication by Margules & Austin (1991). As far as possible, future surveys should be site-based to retain the advantages of 'open architecture', sites should be exhaustively sampled, and surveys should cover a range of taxa with different physiologies and life-history strategies.

Future surveys should have a standard reporting format that includes detailed explanations of how the sample sites were stratified, the sampling methods that were used for each of the taxa, the sampling effort employed, the sampling periods/seasons, and a listing of specimens vouchered with the Western Australian Museum. Fauna survey designs should also include representative sampling based on environmental stratification, ensuring appropriate scale and number of replicates is used, ground-truthing data from desktop studies, and ensuring the dynamics in faunal composition (seasonal abundance) are addressed. Inevitably there will be a compromise between statistical sampling requirements and the practical logistical problems and costs.

Optimising access to existing data

Existing fauna data take a variety of formats, such as specimen-based natural history collections; unpublished reports in the files of private consultants, resource industries, government (Agriculture WA, CALM) and academics; government data-bases on threatened species (CALM, Environment Australia) and the published literature.

Stability and validity issues associated with any database can be difficult to manage. These include species identifications (failure to include the taxonomic authority), failure to update the database after a taxonomic change, recording presence-only data (absence data are seldom recorded) and failure to record sampling effort.

It is unlikely there will ever be a 'one-stop-shop'; you have to know who to ask, and the data may still need "interpretation" (reliability of identification, a cross-reference to locality data) before it can be appropriately used as records often lack an environmental context and their locality can be vague.

Conclusions

We need a single, co-ordinated and integrated data-base for fauna survey data that allows ecologists to quickly locate and list what is known. It needs to be layered, separating incompatible types of data (site-species data, land-unit lists, opportunistic records etc) so that it is useful to all. Given the incompatibility in the various types of data available, we need a filter as well as a custodian. We also need to review similar systems operating in other places such as Canada, Britain, and South Australia.

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Co-ordination and integration of terrestrial vertebrate fauna survey databases for Western Australia: The mining industry perspective

M Robertson

Executive Officer, Environment, Chamber of Minerals and Energy of Western Australia,
12 St Georges Tce, Perth, Western Australia, 6000
email: m.robertson@cmewa.com

Abstract

The mining industry understands the need to protect environmental values, and supports the establishment of a fauna database. The database should include vertebrates, and possibility some invertebrates, particularly stygofauna. Locality, habitat, age, sex and where appropriate deformity information should be recorded with data ranked according to reliability of source, with specimens vouchered with the Western Australian Museum ranked highest. Access to the database should vary in a similar fashion to that for the *Florabase* that is managed by the Western Australian Herbarium, and cost of access should take into account the purpose for which data are to be used. Long-term options should be considered when deciding who should establish, manage and maintain the database.

Keywords: database, fauna, mining

Introduction

The environmental impacts of mining operations have come under increased scrutiny as awareness of environmental issues and an understanding of the implications of environmental impacts has grown. As this community awareness has grown over recent years there has been a change in attitude from the community that can be categorised as a progression; *Leave me alone ? tell me ? consult me ? involve me* (Morgan 2000). That is, the community has become more and more interested in the operations of industry.

Highly publicised events such as the Romanian tailings spill have increased the community's distrust of the mining industry. This has come despite the fact that the mining industry, in general, is operating in an environmentally acceptable manner and in many cases has (arguably) been at the forefront of developing best practise in environmental management.

With the development of community awareness has come increased pressure on regulatory authorities to give consideration to issues and concerns on environmental grounds. Additionally, the scientific understanding of environmental impacts has increased and regulatory authorities are increasingly better able to assess the likely impacts of projects provided the appropriate data are available. To ensure that the correct decisions are made, project proponents are required to supply ever more data on the environment in which the project will operate. Given that these data requirements are going to continue to increase, there are two particular aspects that are important to the industry in relation to the establishment of databases to coordinate the data collected:

1. A database will establish a consistent framework for the collection and presentation of the data. Results should enable comparison among collected data from different projects and also on how these data were utilised in assessment by the Environmental Protection Authority (EPA). While this is an advantage to project proponents in establishing the views of the EPA (and other agencies) it also provides a benchmarking opportunity that will drive continual improvement in the quality of proposals that are submitted.
2. Over time it could be expected that information from a wide variety of sources and studies will be available to provide a much more detailed and rigorous assessment of the distribution of vertebrate fauna.

The presence or absence of species from project areas can then be predicted with greater certainty and efforts to mitigate environmental effects on vertebrate fauna for an area can be more effectively targeted. The possibility of impacting upon threatened species can also be more confidently predicted and steps taken to ensure their protection. As the database develops a greater understanding of the status of species should result. It is possible that this will lead to the removal of some species from the priority species lists. Conversely, some species may be reclassified into a higher priority conservation status. The overall result from a mining company perspective is that a reliable indication of the conservation status of species will be available allowing more effective environmental planning. This also has potential environmental benefits as resources can be directed in the most appropriate fashion for a given area.

What taxa should be covered?

If a fauna database is established, it must cover all vertebrate groups and consideration should also be given to covering invertebrates. Stygofauna is looming as an important issue that has the potential to affect resource development, largely due to a lack of knowledge about such organisms (Playford 2001). In this issue a co-

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This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

ordinated approach to the establishment of a database could develop as the knowledge stygofauna is progressed. That is, we have a unique opportunity to start from scratch and get the collation of data right from the outset.

Which data are important?

Depending on the purpose of the survey, the type of data required is extremely variable and covers a wide range of possibilities. It would seem that as much data as possible should be collected and recorded to allow for the variety of uses to which the database may be put. For the mining industry the database should record;

- Locality; is this species likely to be found in the project area, and if so, is it also found in other areas?
- Habitat; where to look for it, and are there comparable areas outside of the project area. This is particularly important in terms of the regional significance of specific habitats.
- Age classification and sex; these would be useful data to help understand the population dynamics for an area. While these data change, it may allow the status of a population to be assessed over a period of time, particularly in regard to the effects of the introduction of industry.
- Deformities; for data kept on frogs, for example, it would be useful to include details of deformities. This can help to establish background deformity rates allowing the potential effects of industry to be assessed over time (Read & Niejalke 1996).
- Past information; this should be incorporated into the database. The value of such a database is directly linked to the amount of data it contains. That the collection of vertebrate fauna data is not starting from a zero base should be recognised.

What accuracy is appropriate for the data?

The accuracy of data is an important issue if the database is to be useful. However, it is unlikely that a significant body of data will be built up in a reasonable space of time if only data supported by voucher specimens and collected by a select group of ecologists is used. Data collected on an *ad hoc* (or organised) basis by people such as pastoralists and mining industry personnel need to be incorporated where feasible, as in some areas this may represent a significant body of information. To allow for this without impacting upon the accuracy of the database, it may be possible to introduce a rating system that ranks the reliability of each record according to specific criteria.

Is GIS capability necessary?

The database must have a capacity to be utilised by GIS systems. A system that does not have this capability will be outdated before it is even established. Mining industry, land planners, researchers and many others are increasingly turning to GIS systems as important tools of trade. To ensure the proposed database has long term value it must be in step with the technology that is in widespread use. It is also important to recognise that this type of technology is evolving rapidly and a commitment to continual development should aim to keep pace with advance in GIS capabilities.

Should there be linkages with other databases?

As our knowledge of environmental protection and restoration increases there is shift to considering not just individual aspects of an ecosystem but the interaction of all aspects and to ensure that a functioning ecosystem is maintained or restored (G Thompson, Edith Cowan University, personal communication). In this context the database should be linked as much as possible to other relevant databases, provided the information in these databases is consistent with current regions or interpretations.

How can we resolve issues of ownership, funding and access?

Finally, the issues that I believe will require the most thought and planning are those relating to ownership, access and funding. Who takes responsibility for the administration and maintenance of the database? Who is allowed to use it? Who pays for its upkeep?

The maintenance of the database will require a considerable commitment of resources over a long period of time. The value of this database is likely to increase over time as more and more data are included, therefore it is important that a long term view is taken when considering the funding aspect. It is possible that a pay-for-use system will recover some of the funds; for this reason it is important that usage for commercial gain is not ruled out. I would classify commercial gain as including the use of the data for the development of environmental impact assessments for commercial activities such as mining projects, particularly where this is conducted by a third party on a contract basis. It is difficult, however, to envisage that the demand for such use will enable the costs to be covered while maintaining an acceptable cost for access.

An option for consideration may be to have the database held by a tertiary institution with maintenance of the database incorporated into the program of an appropriate computer science course providing practical experience for students and a long term administrator for the database. This does not resolve the issue of who actually owns the data; the specific institution that administers the database may have some right to claim ownership of the data. To avoid conflicts the owner of the data should be an independent government body such as the Environmental Protection Authority or the Conservation Commission with a *Memorandum of Understanding* (MOU) established with the database administrator.

The usefulness of the database for any group or individual will relate to access and it is important to consider what level of understanding of Australian native fauna is desirable. Personally, I would like to think that eventually there will be a high level of interest and knowledge of the fauna within even the general public. For this reason access to basic levels of the database should be made available to anyone who has an interest in native fauna.

The *Florabase* project developed by CALM provides a useful example of how the database could have various levels of access. In the *Florabase* example, the information available depends largely on the access level that is purchased but other restrictions could be implemented as appropriate (*e.g.* rare species). In the *Florabase* example (Table 1), a number of levels are applied:

Table 1

Cost of accessing various levels of the *Florabase* database. (*WA Herbarium Schedule of Fees, November 2002*) .

		Access Type			
Features	Standard	2	3	4	5
Price (AU$ per annum)	Free	$200	$500	$1000	$2000
Search Names & Library	✓	✓	✓	✓	✓
View Images	✓	✓	✓	✓	✓
View Maps		✓	✓	✓	✓
View Descriptions		✓	✓	✓	✓
Search Descriptions		✓	✓	✓	✓
View Specimens			✓	✓	✓
Search Specimens				✓	✓
View & Search Specimens of Declared and Priority taxa					✓

Exemptions to this schedule are provided for:

- community groups participating in the Regional Herbarium network;
- students;
- CALM staff, where projects are not the subjects of external grants;
- academics and researchers, where projects are not the subjects of external grants;
- developers of biological information systems in other institutions, scientists and other members of the community can ensure that money is not requested by collaborating in a variety of ways;
- specimen curation;
- providing vouchered plant photographs for use in *FloraBase*;
- inclusion of Herbarium specimen processing costs in grant applications;
- providing descriptions of taxonomic groups for inclusion in *FloraBase* in DELTA format, and
- using *Max* to provide databased information on disk, which saves considerable processing time.

The mining industry understands the need to protect environmental values; therefore, the establishment of a vertebrate (and potentially other) fauna database for Western Australia would be viewed favourably by the mining industry. It is also important that the database can be used for environmental impact assessments. To achieve this access for industry personnel and consultants information derived from the database will need to be approved by the Environmental Protection Department as acceptable for the purposes of project referrals.

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Cost effectiveness and data-yield of biodiversity surveys

L Bisevac & J Majer

Department of Environmental Biology,
Curtin University of Technology,
GPO Box U 1987, Perth WA 6845
email: bisevac@webace.com.au

Abstract

The most common approach to general biological surveys is based on various measures of plant communities in the investigated area. Fauna are not usually considered, and if animals are included the emphasis is generally on the more "charismatic" vertebrates. Invertebrates are ideally suited for conveying information about the environmental status of an area. This paper makes a comparison of the logistics of performing plant, vertebrate and invertebrate samples in a biological survey. Evidence is presented which indicates that the inclusion of invertebrates in surveys can contribute to data on physical factors, as well as on plant and vertebrate communities. Some invertebrate taxa are richer in species than the corresponding vertebrate fauna. In terms of trends in species richness across sites, and also in terms of changes in community composition, certain invertebrates portray a better interpretation of changes in habitat than do the vertebrates. It is suggested that invertebrates can provide a cost-effective means of generating information on the environmental status of an area.

Keywords: biological survey, community composition, cost-effectiveness, invertebrates

Introduction

Biological surveys are carried out to prepare environmental impact statements, as part of general biological surveys to assess the impact of disturbance or, conversely, to assess the effectiveness of rehabilitation programmes. There has been a repeated tendency to concentrate on plants and, if fauna are considered, the vertebrate fauna. There are compelling reasons why invertebrates should be included in these biological surveys (Abbott 1989; Hutson 1989; Majer 1990).

In this paper, the possibility of using selected invertebrate taxa in biological surveys, along with plants and vertebrates, is evaluated. Specifically, this study evaluated the value of sampling this diverse range of organisms as part of Completion Criteria schedules using a Western Australian mineral sand mine as a case study (Eneabba; Iluka Resources). The results nevertheless have applicability to other types of biological surveys.

A chronosequence of 10 restored areas and four heath controls was selected and sampled by plant, invertebrate and vertebrate sampling protocols. Invertebrate samples were sorted in the laboratory to broad taxonomic (ordinal) levels and, for a selection of groups representing different trophic levels, to species. Plants and vertebrates were surveyed in the same plots by independent consultants. The entire procedure was timed, and the period of time allocated to sampling, ordinal level sorting, sorting of each individual taxonomic groups and data processing, were recorded. The ultimate aim of the study was to assess the time- and cost-effectiveness of sampling the various taxa and the data-yield that can be derived from them.

Material and methods

A 100 m transect was established in the centre of each rehabilitated plot and in controls. Three methods of collection were used; pitfall traps, suction, and litter sampling. Twenty one pitfall traps, consisting of 4 cm internal diameter plastic tubes containing 50 ml of alcohol/glycerol (70/30 v/v) were buried level to the ground at 5 m intervals along the transect. Traps were left open for 7 days and then taken out for sorting. Along each transect, 10 suction samples were taken, each covering an area of 50 m^2. Arthropods were vacuumed off the plants for 10 minutes per sample, using a modified garden leaf vacuum machine and then placed in containers of 70% alcohol for later sorting. Litter samples were collected along transects and placed in 3 kg polyethylene bags (the same amount of leaf litter was collected from each plot). After returning to Perth, the samples were placed in Tullgren funnels. Temperatures in funnels were gradually increased from 25 to 40 °C over a one week extraction period. All extracted invertebrates were placed in 70% alcohol until further sorting. All sampling methods were performed six times, between August 1997 until November 1998, at three monthly intervals.

Plants were surveyed by Mattiske Consulting Pty Ltd in October and November 1998 in a range of plots. Between 100 and 140 quadrats were set at each plot, and plants were mostly identified in the field; species that could not be identified in the field were collected for later identification. Data presented here are only for those rehabilitated and control plots that are the same as the ones used for invertebrate sampling; data for plants are not available for one of the control plots.

This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

Vertebrate animals were collected by Halpern Glick Maunsell Pty Ltd on two separate occasions, October 1997 and February 1998, as a part of a larger fauna monitoring programme. Fauna was surveyed at five of the rehabilitated and three of the control plots. Ground vertebrate fauna was collected at each plot using 10 pitfall traps, 10 bucket traps, 16 Elliott traps and four wire cage traps. The traps were arranged in two transects, one that ran north-south, and another that ran east-west, forming a T-configuration. Data on the presences of bird species were obtained by systematic censuses at each plot.

All parts of the work were timed and expressed as time (in hours) per plot required to perform each task. In this way, the time and ultimately the cost involved in performing surveys using each of these taxa can be estimated and the data-yield from each of these groups can be compared.

Data-sets were analysed using the PATN computer package (Belbin 1995). Hierarchical cluster analysis (UPGMA) was used to examine patterns of species composition in the data matrices of each taxon. The association measure Two Step (Belbin 1980) was used to determine the quantitative relationship between each pair of species, and the Czekanowski (1932) measure was used to compare the plots according to their similarity. An ordination of the plots for each taxon was created using results from these analyses. Cross-taxon analysis involved the estimation of the influence of each taxon on the overall community composition (McKenzie *et al.* 2000). Databases of all taxa were used as sub-sets and were combined to create the community matrix. The community matrix was based on four invertebrate taxa (springtails, spiders, beetles and ants), plants, birds and terrestrial vertebrates (amphibians, reptiles and mammals) from a total of eight plots (five rehabilitated and three control plots). Using Pearson product-moment correlation, the relationship between each pair of taxa was calculated. By doing this it was possible to derive similarity matrices for each data sub-set, as well as for the combined dataset. These matrices were represented as linear similarity vectors. This correlation matrix was converted to a dissimilarity matrix and Semi-strong Hybrid Scaling was used to reduce dimensionality of this matrix, so that relationships between different taxa datasets could be displayed in three dimensions. Here, the Minimum Spanning Tree was superimposed to indicate the nearest-neighbour linkages in the ordination space. In order to provide some extrinsic measure of distance across the ordination space, 1000 uniform random matrices were generated and plotted in the same ordination space. The resulting diagram provided a measure of how much each taxon reflected the composition of another taxonomic group, and also of the congruence of each taxonomic group to the combined data-set, which itself is our best estimate of the overall community composition.

Results and Discussion

The times taken to conduct the various invertebrate components of the Eneabba invertebrate survey, as well as to sort and tabulate the material, are shown in Table 1. The mean time required to sample the entire invertebrate material at Eneabba was 2.3 h per plot, comprising; 1.1 h for pitfall traps, 1 h for suction samples, and 0.2 h for litter samples. The time needed to identify material to ordinal level was 3.5 h per plot, comprising; 2.5 h for pitfall traps, 0.4 h for suction samples, and 0.6 h for litter samples. The ratio of time spent in collecting material to time spent in the laboratory identifying and tabulating material to ordinal level was 1:1.5. The highest ratio was for litter samples (1:3), since much of the material was microscopic. The ratio for pitfall traps was 1:2.3. But, because relatively few animals were obtained in suction samples, the time spent in the laboratory processing this material was less than the time in the field (1:0.4).

Table 1 shows the number of species of plants, selected invertebrates and vertebrates obtained in the

Table 1

Numbers of species or orders sampled during five seasons in 10 restored plots and four heathland control plots at the Iluka mineral sand mine, near Eneabba, Western Australia. Also shown is the mean time to sort/identify each group to morpho-species or species level.

Taxon	Total morpho-species or orders	Time to sample one plot (hr)[a]	Time to sort one plot (hr)[b]	Total time (hr)	Species or orders per hr
Plants	194	3.0	2.4	5.4	35.9
Arthropoda – Orders	27	2.3	3.5	5.8	4.7
Crustacea – Isopoda	3	2.3	0.2	2.5	1.2
Chilopoda	3	2.3	0.2	2.5	1.2
Collembola	22	2.3	11.1	13.4	1.6
Chelicerata – Araneae	96	2.3	4.3	6.6	14.6
Insecta – Coleoptera	172	2.3	6.3	8.6	20.0
Insecta – Formicidae	86	2.3	7.1	9.4	9.1
Vertebrata – Amphibia	9	7.0	1.0	8.0	1.1
Vertebrata – Reptilia	15	7.0	2.5	9.5	1.6
Vertebrata – Aves	47	4.0	0.0	4.0	11.8
Vertebrata – Mammalia	4	7.0	1.0	8.0	0.5

[a] within the invertebrate and vertebrate groups, the field times collectively cover all groups, rather than being cumulative times.
[b] times to sort invertebrate groups to species assumes that they have already been sorted to order

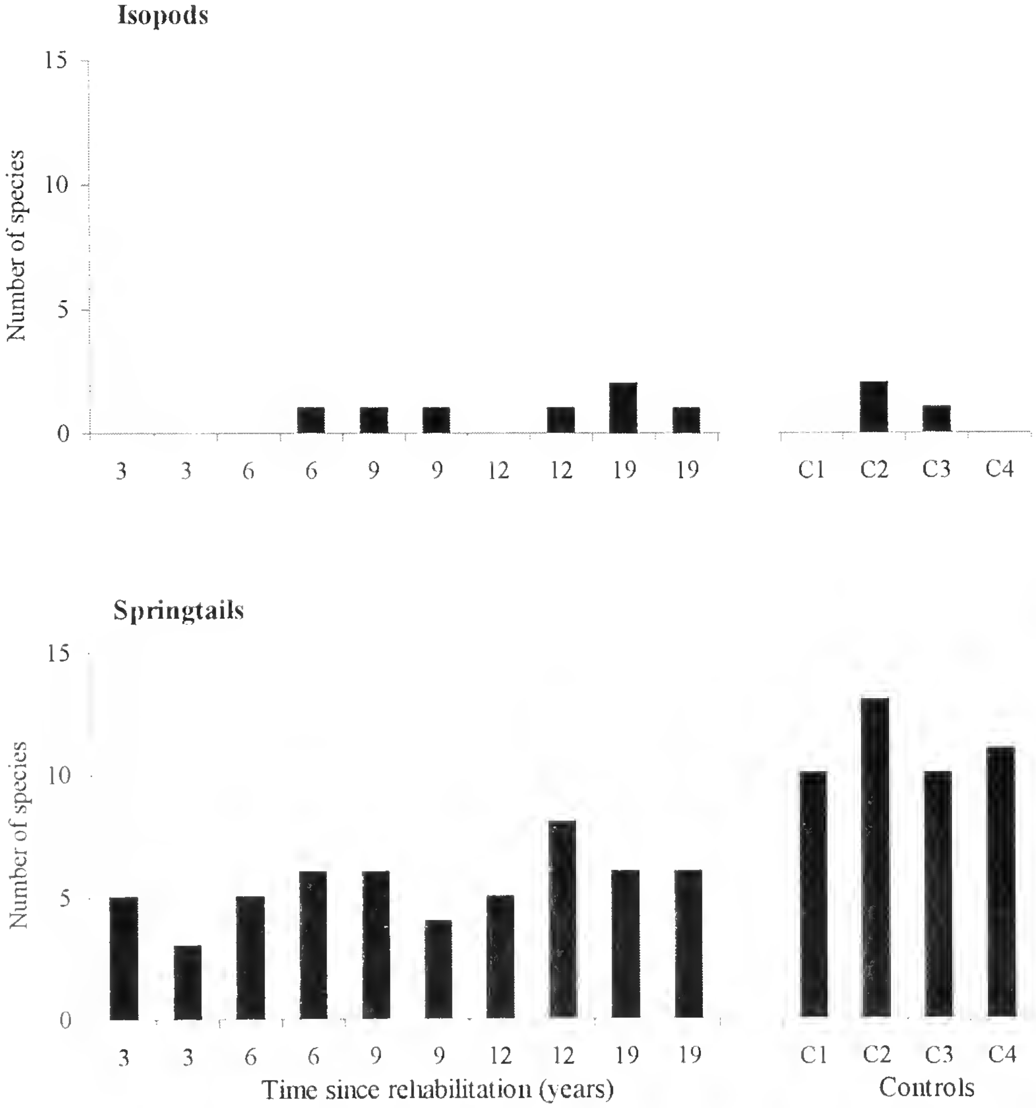

Figure 1. Comparisons between species richness of isopods and springtails on rehabilitated plots of different age with control plots.

investigations. It also shows the mean field time taken to sample and sort/identify these taxa from a plot. Although plants were the most diverse group, beetles, spiders and ants were almost as species rich. Birds were reasonably diverse, but reptiles, amphibians and mammals were represented by few species. These trends were also represented in the number of species obtained per hour of effort.

The data-yield in terms of numbers of species sampled per unit effort is of importance, because diverse samples are likely to yield more information about restoration success than less diverse taxa; taxa with low numbers of species can produce spurious results. This is well illustrated by the chronosequence data in Fig 1, which indicates that although a discernable trend is evident for a species-rich group such as the springtails (Collembola), it is impossible to detect any consistent trends with a group where few species were found, such as the slaters (Isopoda).

Relationships and correlation coefficients between examined taxa and "overall community composition" are shown in Fig 2. Plants, ants and beetles were the taxa with the highest correlation with the overall community composition. Terrestrial vertebrates (amphibians, reptiles and mammals), although not represented by a very high number of species, proved to be relatively close to the overall community composition, with a high correlation coefficient. For birds and spiders, the closest neighbour in ordination space was not overall community; birds showed highest correlation to springtails, and spiders to ants. This suggests that, despite high numbers of species in these taxa, birds do not appear to be reliable indicators of the community in which they occur. Alternatively, their pattern of occurrence across the plots may be different from that of some of the other taxa that we considered.

The high invertebrate diversity has implications for the types of statistical analyses that may be performed on the data. Collections that contain high numbers of species lend themselves to robust data analyses by such techniques as classification, ordination and other multivariate analyses. Trends in diversity indices also

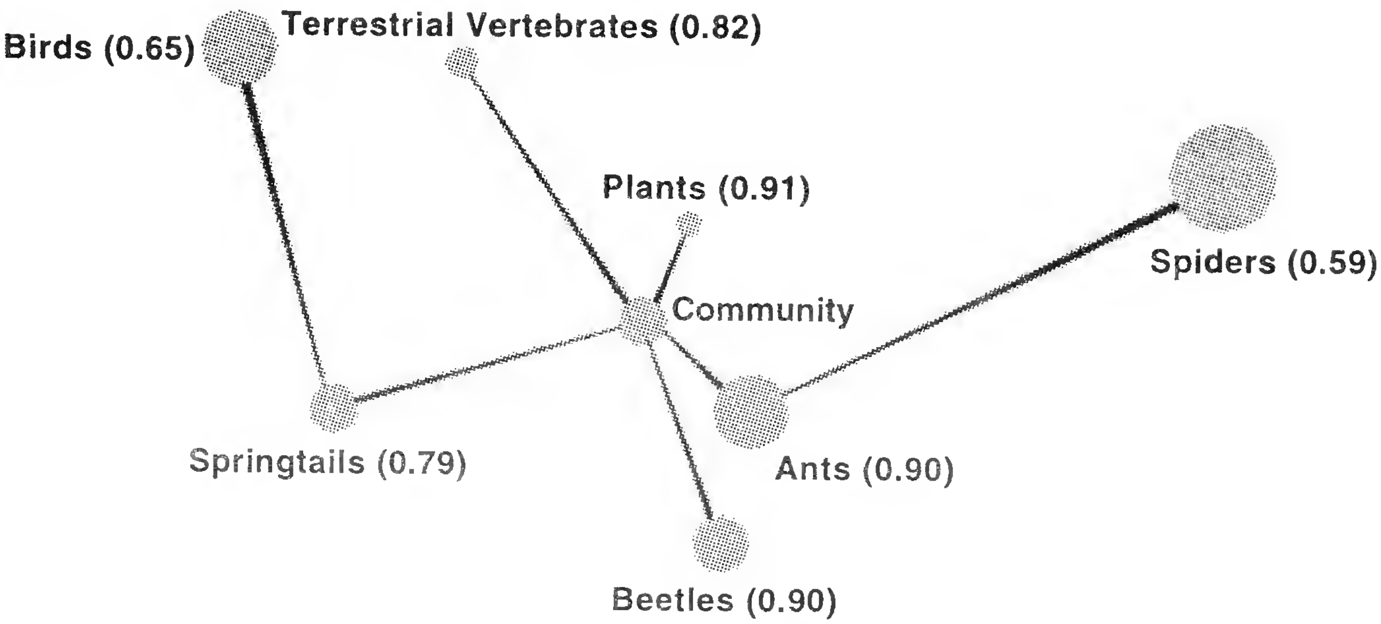

Figure 2. Comparison of the community patterns derived from seven taxa sub-sets, and from the total data-set. A matrix of correlation coefficients was compiled from a pairwise comparison of the relevant transect similarity matrices. Results are displayed in three-dimensions using Semi-strong Hybrid Scaling (stress = 0.07). Minimum Spanning Tree linkages are superimposed to indicate nearest neighbours in community space. The correlations of each taxon with the community are shown in brackets.

tend to be more meaningful in cases where high numbers of species are involved; variations in low-diversity taxa between sites can yield serendipitous results.

There is also the issue of how well each taxon represents differences, or changes, in community composition between plots. The invertebrate data reported here prove themselves to be cost-effective to gather and potentially high in information content. Being the most diverse members of the animal kingdom, their inclusion in surveys can contribute to data on physical factors and plant and vertebrate communities in habitats. As well as strengthening the conclusions reached from a study of these aspects alone, invertebrate data can provide an indication of the degree of re-establishment of ecosystem functioning.

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Flat and relational structures for a terrestrial vertebrate database

P C Withers

Department of Zoology, University of Western Australia, Crawley WA 6009
email: philip.withers@uwa.edu.au

Abstract

A cooperative effort among a number of governmental agencies, industry including private environmental consultancies, and other interested parties such as university academics and the Royal Society of Western Australia, could enable the establishment of a regional terrestrial vertebrate database for Western Australia. The form of such a fauna database is not obvious because of conflicts between ease of data entry for those individuals collecting the raw data, optimal strategies for storing and accessing a large amount of data by database managers, and expeditious and aesthetic accessing of the data by end-users. A spreadsheet is a powerful tool for data entry, manipulation and summary, and is widely available and used by biologists. Such a simple flat database structure (*e.g.* a pre-formatted Microsoft Excel spreadsheet) has advantages in ease of data entry, widespread availability of software, and minimal training requirements for data-entry operators. Limitations of spreadsheets include redundancy of repeated cells, the opportunity for mistakes in redundant data entry, and the potential for many empty cells. For data storage and access, a more complex relational database with pre-designed relational tables (*e.g.* Microsoft Access database) has advantages of optimal data structuring and sophisticated search capabilities compared to spreadsheets. I suggest that the optimal strategy for a regional terrestrial vertebrate database is a combination of a flat spreadsheet structure for data entry and submission, then conversion to a relational database for storage, management, and end-user access.

Keywords: flat database, spreadsheet, relational database, terrestrial vertebrates, regional fauna

Introduction

Currently, many fauna surveys are undertaken each year in Western Australia for a variety of reasons, including government-sponsored regional surveys (*e.g.* Department of Conservation and Land Management, Western Australian Museum), private industry surveys (*e.g.* as part of Environmental Impact Assessment submissions for the Environmental Protection Authority), and as independent scientific studies (*e.g.* university-based research). As more fauna survey data are collected every year, it is becoming increasing obvious and imperative that some structure needs to be established to centralise, store, manage and provide future access to these data. Hence the increasing local interest in the establishment of a terrestrial fauna database (*e.g.* Regional Fauna Database Workshop organised by the Royal Society of Western Australia, 5th April 2002 and this issue of the Journal of the Royal Society of Western Australia.

What I address here is the possible structure for such a regional terrestrial vertebrate database. This requires a very general overview of various structures of databases from a functional viewpoint to bridge the gap from simple data entry via spreadsheets to the structure of complex "relational" databases. Most biologists are familiar with "flat" spreadsheets, and routinely use such programs (*e.g.* Microsoft Excel®) for data entry, structuring, and statistical and graphical analyses. A relational database (*e.g.* Microsoft Access®) can more economically and efficiently arrange large amounts of data, but at the cost of increased complexity in design and management. Few biologists need to use a relational database, and therefore generally do not have the required knowledge or skills.

I describe here in general terms how a flat spreadsheet works and why it may be the method of choice for entry of data, and how relational databases are much more powerful and complex and why they may be the method of choice for storage of a centralised database for fauna data. The general principles of spreadsheet and relational database programs are similar regardless of the computer platform (*i.e.* PC, MAC, Linux) and the particular spreadsheet or relational database program. I will use Microsoft Excel® as an example of a spreadsheet program, and Microsoft Access® as an example of a relational database program, as these are generally available to biologists. Microsoft's user's guides for Excel (Anon 1994a) and Access (Anon 1994b) provide more detail on use of these programs, and examples.

"Flat" Spreadsheet Databases

Most biologists are familiar with and use "flat" spreadsheets (*e.g.* programs such as Excel, Lotus 123, Quattro Pro, StarOffice) for routine data entry, manipulation and analyses, and as a simple database. A spreadsheet is a "flat" database (Fig 1) because its data are arranged as a 2-dimensional table, with columns (A, B, C, *etc*) and rows (1, 2, 3, *etc*). Each cell of the table is uniquely identified by its column and row (*e.g.* C11), as well as the worksheet name (*e.g.* trapdata) and file name (*e.g.* Trapping Data.xls). Each column can be given a

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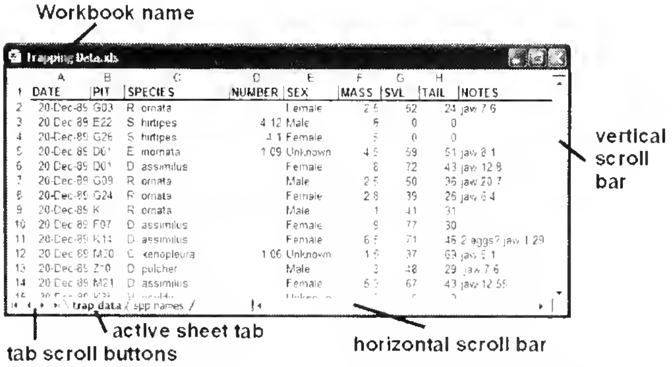
This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia



	A	B	C	D	E	F	G	H	
1	DATE	PIT	SPECIES	NUMBER	SEX	MASS	SVL	TAIL	NOTES
2	20-Dec-89	G03	R ornata		Female	2 5	52	24	jaw 7 6
3	20 Dec 89	E22	S hirtipes	4 12	Male	6	0	0	
4	20-Dec-89	G26	S hirtipes	4 1	Female	5	0	0	
5	20-Dec 89	D01	E inornata	1 09	Unknown	4 5	59	51	jaw 8 1
6	20 Dec-89	D01	D assimilus		Female	8	72	43	jaw 12 8
7	20-Dec-89	G09	R ornata		Male	2 5	50	36	jaw 20 7
8	20-Dec-89	G24	R ornata		Female	2 8	39	26	jaw 6 4
9	20-Dec-89	K	R ornata		Male	1	41	31	
10	20 Dec 89	F07	D assimilus		Female	9	77	30	
11	20-Dec-89	K14	D assimilus		Female	6 5	71	46	2 eggs? jaw 1 29
12	20 Dec 89	M30	C xenopleura	1 06	Unknown	1 5	37	69	jaw 5 1
13	20-Dec-89	Z10	D pulcher		Male	3	48	29	jaw 7 6
14	20 Dec 89	M21	D assimilus		Female	5 5	67	43	jaw 12 55

Figure 1. General 2-dimensional structure of a spreadsheet, showing columns (A, B, *etc*), rows (1, 2, *etc*), the workbook name, active sheet tab, tab scroll button, and horizontal and vertical scroll bars, illustrated by an example of pit-trapping data in a Microsoft Excel spreadsheet.

header name (in row 1), and that column is called a field; each row is a record entry. Each file, or "workbook", can contain a number of different tables ("worksheets"). Information can be linked between worksheets (and even between different workbooks). For example, a list of species names can be used as a drop-down list (see below) for data entry, thus facilitating entry of species names and avoiding errors. Nevertheless, the essential structure of a worksheet table is a simple 2-dimensional grid of values. A spreadsheet approach for summary of fauna sampling data from pit-trapping (*e.g.* Fig 1) could include fields such as dates for trapping, a pit identification number, identity of specimens captured, sex of individual, mass, *etc*. Additional information for use in a wider regional context could include a study site identification, GPS locality, and vegetation, soil, geographical and geological information.

In a flat spreadsheet, each record (row of information) usually needs to contain a cell entry for each field. Any information that is the same between rows, such as locality, GPS reading, or pit trap grid identity, needs to be entered individually in each row. This repetition is redundant, it requires computer memory for storage, and even more seriously it is prone to data entry errors since misspelling of names or incorrect entry of values leads to confusion. For example, if a data-entry operator occasionally misspells the species name *Diplodactylus assimilis* as *Diplodactylus assimilus*, then this species would appear as two separate species in any sorted list, pivot table, query or report. Such an error might be fairly obvious to a biologically-experienced database user, but many input errors would not be so obvious. For example, entering a UTM coordinate of 11 4 23 818 E as 11 4 32 818 E is not an obvious error, and might never be identified as an error once it was miss-entered. Such data miss-entry can be avoided by copying to fill a series of redundant cells, or using a drop-down list for entry of fixed values in a specific field. For example, a list of species names in one worksheet (or even in another workbook) can be used to define a list, which can then be used to select names from the dropdown list, avoiding any possibility of typing errors.

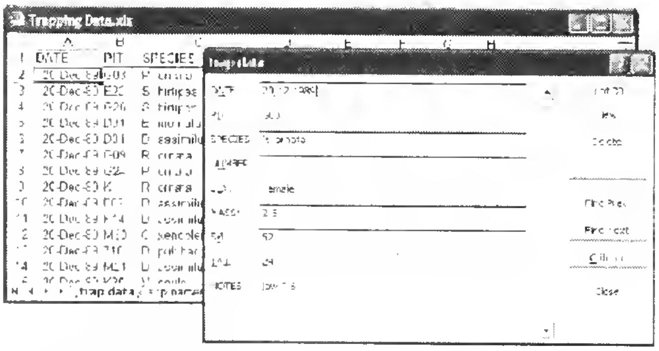


Figure 2. Example of a form used for data entry in a Microsoft Excel spreadsheet.

Another limitation of a flat spreadsheet is that often some fields don't relate to all records. For example, a field for entry of tail break occurrence might be useful for some lizards but is not applicable to other lizards, frogs, birds or mammals. A field for observation of lactation might be relevant for female mammals but not males or other vertebrates. To minimise empty cells, different worksheets might be used for different types of animals (*e.g.* separate worksheet for amphibians, reptiles, birds and mammals).

Simple forms are available in Excel for data entry, but these forms (Fig 2) are not customisable and are relative primitive compared to more sophisticated forms that can be designed in a relational database (such as Access) for data entry. A spreadsheet data form is a dialog box that provides a convenient form for entry or display of one complete row of information, or record, at one time. A form can be used to add a new row of data, delete a row of data, move to previous or subsequent records, and set criteria for data entry, but a form does not provide access to dropdown lists. Quite sophisticated data entry coding and programming with macros can be accomplished in spreadsheets. A macro is a series of commands that can be run in a spreadsheet whenever a repetitive task needs to be performed.

Using a simple flat spreadsheet approach for fauna survey results would involve considerable redundancy and many empty cells, but hopefully potential for miss-entry of data could be minimised by use of drop-down lists and careful checking by the data-entry operator. Provision of appropriate drop-down lists and templates for organisation of data would facilitate preparation of spreadsheets in a standardised format. However, storage and retrieval of information from a flat spreadsheet is not optimal; even a simple relational database is better for this. Nevertheless, I suggest that despite its limitations (redundancy, empty cells), a spreadsheet would be the best format for routine data entry by individuals, and transfer to a centralised database manager.

Relational Databases

There are a variety of more complex designs for databases than spreadsheets, which allow relationships between entities (Kroenke & Dolan 1988; Robinson 1989; Date 1990; Gault 1994; Viescas 1993). The hierarchical database model provides limited relationality, the network database model provides more relationality, and the relational database model provides the most powerful description of relationships between entities. In a hierarchical database model, a set of records can have links to other record types, but these links can only be "one-to-many" (*e.g.* a pit trapping grid may contain a number of different pit traps, but each pit trap is only found in one particular grid). A network model can have "many-to-many" relationships (*e.g.* a pit trap may capture a number of different species, and each species can be captured in a number of different pits). A relational model replaces the structural complexity of hierarchical and network models by using flat files (that have been normalised) and providing operations for manipulating these flat files.

A relational database has a number of different tables that store related information. The arrangement of data amongst tables should minimise redundancy, likelihood of data entry errors, and numbers of empty cells. It does not necessarily reflect the structure of the data as collected, or as used (*e.g.* as reports). A relation is a 2-dimensional table that differs from a general flat file in that;

- each column has a distinct name;
- all data items in a single column are of the same type;
- all rows are distinct — there can be no identical, duplicate rows; and
- the order of rows and columns doesn't affect the information content of the file.

Three kinds of relationships can occur in a relational database, and it is important that the correct relationship is used. A one-to-many relationship is common. Here, a record key in a table can match more than one record in another table, but a record in the second table can only match a single record in the first table. For example, a pit trap grid (*e.g.* grid A) might have a number of separate pit traps (pits A1 to A36), but an individual pit trap (*e.g.* A1) occurs only in a single grid. A many-to-many relationship is also fairly common in relational databases. Here, a record in one table can have more than one matching record in a different table, and a record in the second table can have more than one match in the first table. A one-to-one relationship is less common; here a record in one table has only one matching record in another table, which only has one matching record in the first table. Thus, a relational database can contain a number of tables linked by various relationships.

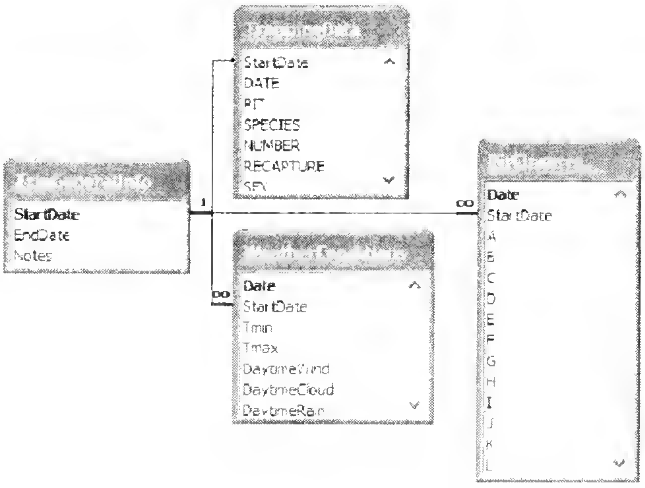


Figure 3. Example of links between relations (normalized tables).

For a regional terrestrial vertebrate database, a number of data tables would be required, and relationships between them could be one-to-many, many-to-many and even one-to-one if necessary. A simple example of relationships for a pit-trapping database has a number of one-to-many relationships (Fig 3). This simple example illustrates the basic differences between using a flat spreadsheet and a relational database, and the relative advantages of the relational approach. An Access database could contain different tables for general field trip information, trapping data, and pit trap grid data. Establishment of relationships between the various tables allows efficient storage of information and retrieval of information by queries or as reports.

Entry of data in a relational database program, such as Access, can be facilitated by the use of forms (Fig 4). This is a major advantage of Access over forms in

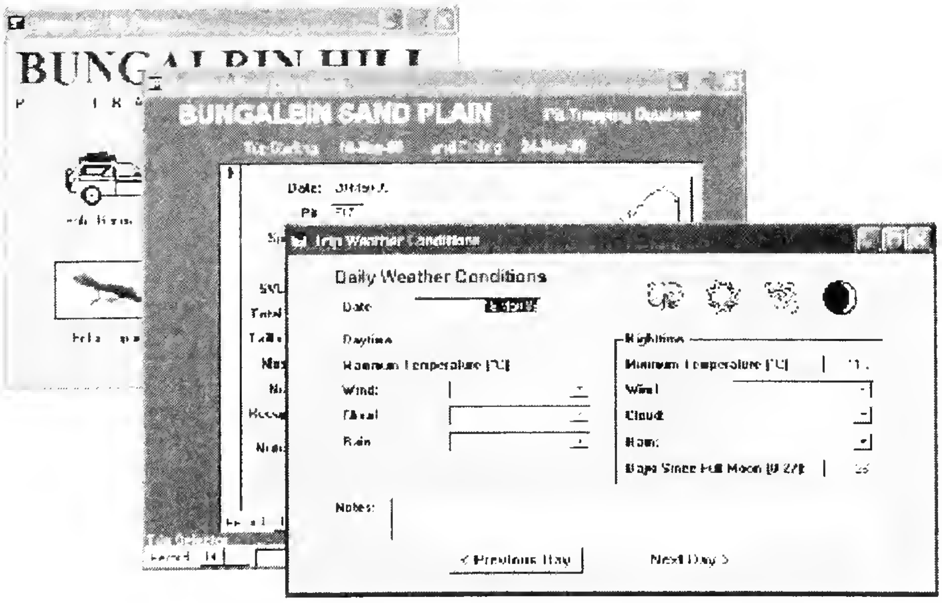


Figure 4. Examples of forms used for data entry in a relational database program (Microsoft Access).

Excel, where data entry via a form is possible but the form is much less flexible than in Access. Forms in Access can be quite complex, with fields in particular arrangements with graphics to optimise the data entry process.

Data can be readily retrieved from a relational database using queries and reports. A query is a question about data stored in a relational database. A select query (Fig 5) allows viewing and analysis of data from one or more tables. Other types of query include crosstab, action, union, pass-through and data-defining queries. There is considerable flexibility in the design of particular queries and they can be quite powerful. Reports are information selected, retrieved and organised to fit specific requirements. They allow presentation of subsets of the data in a meaningful organisation, often for presentation. Forms allow graphical viewing of all of the information for a record at a time, queries allow selection, analysis and viewing of specific sets of data, and reports organise and print data for formal summary and presentation.

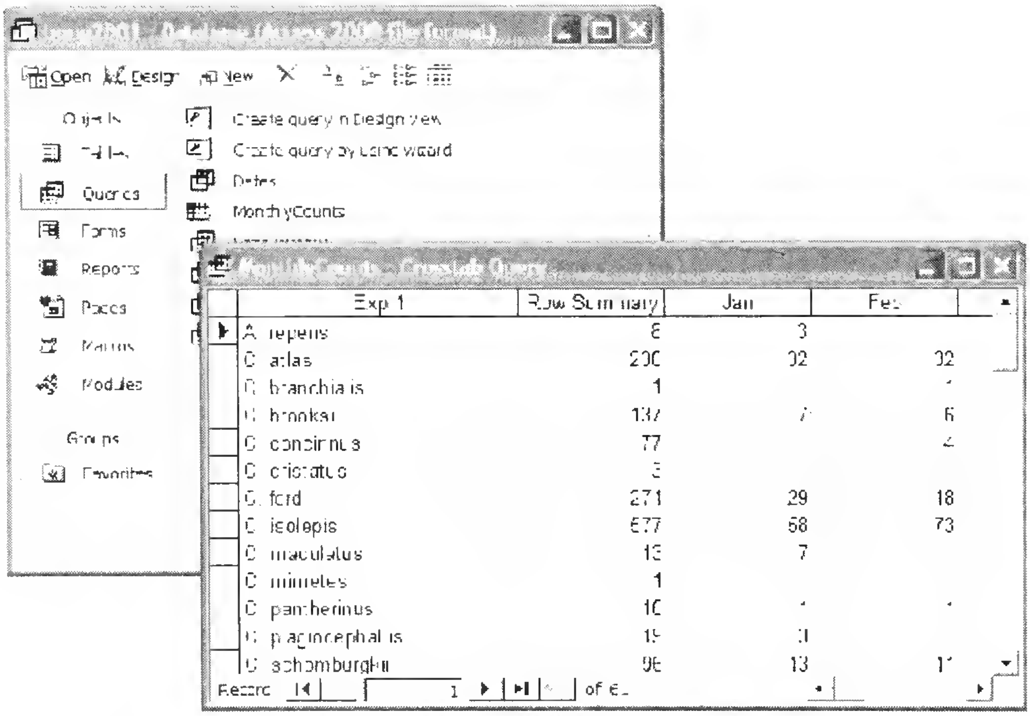
Clearly, relational databases can be a very powerful tool for data entry, manipulation and summary but they are more complex and less widely used by scientists than flat spreadsheets. They require considerable skill in designing the relations for optimal functioning, and can be difficult to modify during the inevitable long-term development that would take place for a large, sophisticated database. Nevertheless, I suggest that any large regional faunal database would have to be organised as a relational database, even though the best format for routine data entry by individuals would be a spreadsheet format despite its limitations (redundancy, empty cells).

Strategy for a Terrestrial Vertebrate Database

I suggest that any large regional terrestrial vertebrate database should be organised as a relational database. Then there would be three technical challenges;

1. Providing suitable flat spreadsheets with standardised drop-down lists, templates and structures, for routine data entry (*e.g.* using Microsoft Excel). This simple and widely available spreadsheet technology would be a suitable method for submission of data to be deposited automatically into a centralised database. From the perspective of a contributor to the database, data entry must be simple enough that it will not deter individuals un- or semi-skilled in database operation from contributing data. A simple spreadsheet data entry system could even be required for CALM licensing returns, thus making all regional data potentially available to a centralised database.
2. Designing an optimal relational database for storage of information and subsequent access to information through queries and reports (*e.g.* using Microsoft Access); this more complex relational approach would require centralisation, staff with the appropriate database skills, and access to sophisticated technology for internet accessibility.
3. As seamlessly as possible facilitate transfer of information from spreadsheets to the relational database; this may well be the biggest technical challenge of the three.

From the perspective of a paying end-user, a high quality database and access service would have to be



	Expr1	Row Summary	Jan	Feb
▶	A. repens	8	3	
	C. atlas	200	32	32
	C. branchialis	1		[illegible]
	C. brooksi	137	7	6
	C. concinnus	77		4
	C. cristatus	3		
	C. fordi	271	29	18
	C. isolepis	577	58	73
	C. maculatus	13	7	
	C. mimetes	1		
	C. pantherinus	10	[illegible]	[illegible]
	C. plagiocephalus	19	[illegible]	
	C. schomburgkii	96	13	[illegible]

Figure 5. Example of use of queries in Microsoft Access, to extract information from a database. Here, a query for monthly counts provides a summary of the total numbers of each species captured in each month, during the multi-year trapping program.

provided, to justify a cost for database access. Data retrieval by queries must be simple enough that it will not deter use, and provide a sufficiently attractive service to justify the costs that would be required to maintain the regional database.

Establishment of a terrestrial vertebrate database raises the issue of data verification. It is essential that some consideration be given to the extent of data verification (especially species identification) from the perspective of data contributors, database managers and end-users. Even checking of data entry files by data contributors for errors would be time-consuming and tedious, but necessary. The highest level of verification for species identification would be voucher specimens lodged in the Western Australian Museum for confirmation of identity by recognised experts in the field. An intermediate level of verification could be consistency of identification with species range distributions. Some level of data verification would be essential to providing a justification for a cost to end-users for accessing the database.

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Operational fauna databases within the Western Australian Department of Conservation and Land Management: Tools for managing rare and threatened species

PR Mawson & P Orell

Department of Conservation and Land Management, Locked Bag 104,
Bentley Delivery Centre, Perth
WA 6983
email: peterm@calm.wa.gov.au, petero@calm.wa.gov.au

Keywords: database, fauna survey, threatened species

Introduction

The Western Australian Department of Conservation and Land Management operates and maintains two fauna databases to assist in its statutory role as conservator of native fauna. One was originally established in the early 1990s on an ORACLE mainframe system. This database, the Threatened Fauna Database (TFdB), was later transferred to a stand-alone Microsoft Access system and is upgraded regularly. The second database was established in April 1996 to support the Department's fauna recovery program, *Western Shield*. This database, *Fauna File*, is also established on a Microsoft Access system.

The two databases share common features and there is potential to readily transfer data from *Fauna File* to the Threatened Fauna Database as required. Both systems are geo-spatial and can be interfaced with GIS software packages such as Arcview® and ArcInfo®. Both databases are housed in the Department's Wildlife Branch and two senior staff act as custodians of the datasets. Software maintenance and upgrades are provided from within the Wildlife Branch.

Threatened Fauna Database

The Threatened Fauna Database is used to store geo-spatial records on all species of native fauna that are gazetted as being 'rare or likely to become extinct' under the provisions of section 14(2)(ba) of the *Wildlife Conservation Act 1950*. The database also contains records on those species of native fauna on the Department's Priority Fauna List. The data set includes historical records, some dating back to the 19th century.

The minimum information requirements necessary to establish a record in the database are; species, observer's name, date of observation, and location (Lat/Long or AMG). There are a number of additional fields that can be completed for each record, and the more that can be completed the more useful the record can be (see Appendix 1).

When the database custodian receives each new record, it is vetted to determine veracity (is the species correctly identified) and accuracy (does the geo-spatial data match the location description). Based on the information provided in the record submission, the quality of the record is coded from 1-3, 1 being very certain, 2 moderately certain, and 3 uncertain. The value of such data vetting becomes obvious when considering records that constitute range extensions, new, extra-limital and disjunct populations, or records of species that were presumed to be extinct (*e.g.* Gilbert's Potoroo).

The data that form the basis of new records are obtained from a variety of sources. Some are derived from Departmental staff activities, in particular fauna inventory and fauna monitoring such as with *Western Shield* (see below). The general public provides other records, along with researchers affiliated with tertiary institutions, staff from other government departments, and professional biological consultants. Most of the latter sources of data reach the department via reports submitted as part of Scientific Purposes (Regulation 17) licence returns.

The TFdB currently contains more than 4500 records, up from 500 in 1994. At present only a small proportion of the data on threatened fauna and rare fauna species available in the Western Australian Museum (WAM) database are incorporated in the Department's TFdB. Negotiations are underway to reach an agreement on a data exchange. It is worth noting that the WAM data set includes all fauna species and is largely based on vouchered specimens, while the Department's data set is largely based on sightings, documented records from the literature, and catch-release records from various surveys and monitoring programs.

The data record sheets also contain a number of other fields such as land tenure, landform, vegetation association and datum type. The completion of these fields becomes very important when considering rare or threatened species that are poorly represented in museum collections, or for which there is very little biological information. It is almost impossible to interpret the presence of rare or threatened species in a variable landscape when insufficient data have been recorded on exactly which part of the landscape the species was using when it was observed or trapped. The situation becomes even more important if the species is cryptic or known to have little or no capacity for movement or dispersal (*e.g.* mygalomorph spiders and *Geocrinia* frogs).

This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

Fauna File

The Department's fauna recovery program *Western Shield* was launched in April 1996 with the aim of restoring a suite of native species, primarily small–medium sized mammals, to a range of sites within the south-west of the state. The most obvious aspects of this program have been the broad scale fox baiting on conservation estate and the well-publicised species re-introductions and translocations. What is less well known is that the Department has established 66 fauna monitoring sites throughout the south-west from Kalbarri south to Albany and east to Cape Arid. A range of census techniques is used to either monitor the response of extant fauna populations following the implementation of fox baiting, or the re-establishment of re-introduced or translocated populations.

The Department has developed an in-house training course to ensure that those staff involved in the fauna monitoring program are competent and can carry out the work efficiently and humanely. To date nearly 160 staff have completed the course and a high percentage of those remain within the Department.

The fauna monitoring carried out under the *Western Shield* banner results in a wide range of mammal, reptile and amphibian species being captured, along with a small range of birds. *Fauna File* was established to store all of the records derived from the monitoring program and also caters for common and widespread species as well as threatened and priority species. The success of *Western Shield* is measured by the recovery and maintenance of selected species at pre-determined levels.

As with the TFdB, *Fauna File* records geo-spatial information on species, along with specific details on the monitoring sites, the location of trap lines or survey routes, and survey effort. The data entered into *Fauna File* are predominantly generated via departmental activities but there is provision for the collection and storage of incidental sightings by members of the public.

Fauna File is a far more complex relational database than TFdB but with a 'user friendly' interface designed to enable some basic data manipulations. For example, it can calculate 'trap success' or 'known to be alive' (KTBA) statistics for individual species on a transect or groups of transects. These data manipulations are easily achieved by the user selecting the appropriate parameters and values from a simple menu and clicking on a button to generate the results. The user can therefore get useful information from survey and monitoring data with a minimum of effort. This encourages more effective use of the database by Departmental staff and the *Fauna File* has become a very valuable tool for storing and analyzing fauna data on an operational scale within the Department.

What makes a good database?

The old adage "if you put rubbish in you get rubbish out" sums up the most important aspect of databasing. It is vital that the custodian of any database vets and verifies records prior to incorporating them into the master data set. A number of factors influence the quality of potential records including:

- the quality of the observation (was it an animal in the hand or a fleeting glimpse of an animal crossing a road at night?);
- the skill of the observer (a seasoned field ecologist or a new graduate?);
- the record being founded on good field notes rather than a half remembered recollection;
- the taxonomic identity assigned to the record being correct and current;
- the geo-spatial system used in the field being accurate (AGM datums have changed several times in the last 40 years); and
- accurate reconciliation of Museum accession numbers with field notes.

Good databases work both ways – data in and out

There is little value in accumulating data if there is no subsequent analysis of the data and no capacity to share some or all of the information with other potential users. The Department uses the data in its two databases to help it manage threatened and priority fauna, since it is responsible for conserving those species whether they reside in conservation estate or lands and water vested in other agencies, or private freehold land. The Department offers a fee-for-data service on threatened and priority fauna to consultants and researchers, with the information generally provided in a presence/absence format based on a search of particular areas defined by co-ordinates provided by the consultant or researcher. The reason the client is seldom given direct access to the geo-spatial information is that it is sometimes necessary to protect the precise location of highly valued species (such as nest location of black cockatoos) or cryptic and sedentary species (such as some frogs). The other reason is that without expert interpretation some data can by misleading, and experience has shown that not all clients have the necessary knowledge of less well-known species to make best use of the data without some assistance.

Not surprisingly, the Department pays particular attention to the results from its own fauna monitoring activities in areas subject to fox control programs. Regular analysis of trapping data can provide early warning of sub-optimal baiting effort, or the early achievement of target levels in fauna recovery programs that may then lead to formal changes in the conservation status of threatened species (*e.g.* downgrading from EN to VU, or even de-listing from the threatened fauna list) or allow the option of redirecting limited resources to other projects ahead of schedule.

This workshop provides a unique opportunity to discuss what we would like, what we really need, and what we can actually create, so look, ask questions, and think about what you need and can contribute.

APPENDIX 1

DEPARTMENT OF CONSERVATION AND LAND MANAGEMENT
THREATENED FAUNA REPORT FORM

FILE# ______ PRECISION: ______ DATABASE RECORD# ______

SPECIES ______ NO. SEEN: ______

DISTINGUISHING FEATURES OBSERVED: ______

CERTAINTY OF IDENTIFICATION: ☐ Very certain ☐ Moderately certain ☐ Not sure

AGE AND SEX:

No. of Adults: ______ Male ______ Female ______ Sex unknown

No. of Juveniles: ______ Male ______ Female ______ Sex unknown

COLLECTOR/OBSERVER: ______ PHONE NO: ______ SURVEY DATE: ______ TIME: ______

SHIRE: ______ CALM REGION: ______

LOCALITY: ______

MAP REF: CALM MAP NAME: ______ Grid Reference ______

(Complete one line ONLY) Latitude ☐☐° ☐☐ ☐☐ S Longitude ☐☐☐° ☐☐ ☐☐ E

AMG Zone ☐ 49 ☐ 50 ☐ 51 Northing ☐☐☐☐☐☐☐☐ Easting ☐☐☐☐☐☐

LAND STATUS:

☐ Nature Reserve ☐ State forest ☐ Private Property ☐ Road Verge Shire ☐ National Park

☐ Vacant Crown Land ☐ Road Verge MRD ☐ Pastoral Lease ☐ Other reserve ______ ☐ Unknown

LANDFORM TYPE:

☐ Flat ☐ Gully ☐ Lake ☐ Cliff ☐ Rocky outcrop ☐ Other ______

☐ Slope ☐ Swamp ☐ River ☐ Ridge ☐ Sand dune

VEGETATION TYPE:

☐ Forest Significant species ______ ☐ Grassland

☐ Woodland Significant species ______ ☐ Sedgeland

☐ Mallee Significant species ______ ☐ Rock communities

☐ Tall Shrubland Significant species ______ ☐ Wetland

☐ Heathland Significant species ______ ☐ Other ______

OBSERVATION/COLLECTION METHOD:

☐ Daylight sighting ☐ Night sighting ☐ Heard ☐ Caught or trapped ☐ Diggings

☐ Droppings ☐ Feathers ☐ Bones ☐ Dead ☐ Other

BEHAVIOUR:

What was the animal doing? ______

BREEDING:

☐ Pregnant ☐ Lactating ☐ Mating ☐ Male in breeding colours ☐ Eggs/young in nest ☐ Other ______

FIRE HISTORY:

☐ Not known Year burnt ______ Month (approx) ______

☐ Next prescribed burn: Year ______ Month ______

CURRENT LAND USE:

☐ Nature Conservation ☐ Agriculture ☐ Pastoralism ☐ Mining ☐ Forestry/Multiple purpose ☐ Recreation ☐ Other ______

FERAL ANIMALS:

Habitat damaged by feral animals ☐ Yes ☐ No ☐ Unknown

Feral species and damage type ______

SPECIMEN: ☐ Retained by collector ☐ WA Museum ☐ Other ______ ☐ Not retained

ATTACHED: ☐ Map ☐ Mud map ☐ Photo ☐ Notes

ACTION, TAKEN/REQUIRED: ______

OTHER COMMENTS: ______

COPY SENT TO: ☐ Regional Office ☐ District Office ☐ Head Office

Signed: ______ Date: ______

PLEASE SEND COMPLETED FORM TO SENIOR ZOOLOGIST, WILDLIFE BRANCH

DEPARTMENT OF CONSERVATION AND LAND MANAGEMENT, LOCKED BAG 104 BENTLEY DELIVERY CENTRE W.A. 6983

[RECORD NO.]

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Fauna collections databases in the Western Australian Museum

P F Berry & G Christie

Western Australian Museum
Francis Street, Perth WA 6000
email: paddy.berry@museum.wa.gov.au

Abstract

The history of computerisation of the Western Australian Museum's modern fauna collections is outlined (it was initiated in the late 1970's on the Treasury mainframe computer). The Museum is custodian of approximately 1.5 million specimens and specimen lots of modern fauna. The majority of specimens in its collections are from Western Australia, but the collections also include specimens from Indonesia and New Guinea. Currently only the vertebrates are comprehensively databased. The Museum's current primary collections database system is briefly described as well as its recently released on-line version – *FaunaBase.*

Keywords: Database, museum, Faunalist, FaunaBase

Historical background

The first faunal specimens with associated data were accessioned into the Western Australian Museum collection in the 1890's. As was traditional with natural history museums, specimens were (and still are) arranged in collections corresponding to phylogenetic groupings (mammals, birds, arachnids, *etc*). The practice of assigning each specimen within a collection a unique registration number, recording associated data on a label, and entering duplicate and additional data into a hand written catalogue was started in the early 1900's. However, different curators adopted somewhat different methods of assigning registration numbers. In some collections the specimens were numbered sequentially, whereas in others they were numbered sequentially by year. Also, data accompanying many of the earliest records are often imprecise, particularly the collection locality (*e.g.* "Western Australia").

The first attempt to produce an electronic listing (but not a database in the modern sense) was in the late 1970's when a catalogue of the modern mammal collection was produced using the Treasury mainframe computer and involving punch cards and special programming. In 1983, as a foundation member of the Western Australia Land Information System, the Museum received funding for an in-house UNIX server through the Government Computing Committee and the Museum employed a contract programmer (with a background in biology) to develop customised database software for the mammal, herptile, fish, arachnid and crustacean collections. This in-house system ran very successfully until the late 1980's when the Museum's inability to continue to support it prompted a switch to a commercial multi-user database system (INGRES), developed and supported externally. The Museum's collections databases were temporarily transferred to FOXPRO in about 1995, pending availability of BIOLINK, a multi-user database designed for biological collections management and research under development by CSIRO.

BIOLINK was not designed with registration number as a key field. For this and other reasons the Museum decided in 2000 to adapt the collections management system developed in Microsoft Access® by the Department of Agriculture for its entomology collection. This was done by Dr Graeme Christie and is the system currently in use and described below.

The Museum's primary collections databases

The approach taken was to develop a generic database system that accommodated the collections management requirements of all the Museum's fauna collections. This necessitated considerable effort to standardise fields and existing differences in data standards before all collections could be successfully migrated to the new system. Post migration required extensive validation of data.

Currently there are eleven faunal collections databases operating on this generic Microsoft Access® system. The

Table 1

List of modern fauna collections in the Western Australian Museum, numbers of records databased and proportion of each collection databased.

Collections	Numbers of databased records	Approximate percentages of collections databased
Mammals	49,734	100
Sub-fossil Mammals	10,000	15
Birds	33,822	100
Reptiles/Amphibians	131,847	100
Fishes	47,748	100
Arachnids	46,666	<10
Insects	34,183	<10
Molluscs	22,400	<10
Crustaceans	31,056	30
Worms	4,277	<10
Other Marine Invertebrates	12,062	<10

This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

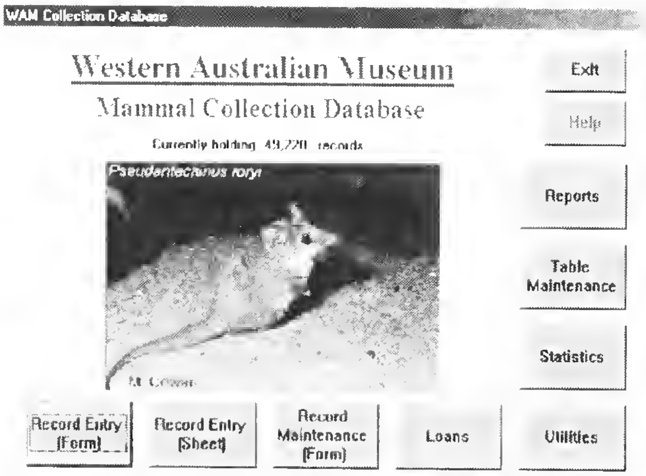
size of each, and degree to which data capture of each collection is complete varies and is summarised in Table 1. The vertebrate collections are the most comprehensively databased, the invertebrate groups are the least (because of the larger numbers of taxa and poorer knowledge of the taxonomies).

The Museum's primary collections databases were designed with ease-of-use being the primary aim without losing the potential to expand or accommodate new technology as it became available. Being based on Microsoft Access®, the database technology follows what has become an industry standard and as such is well understood and supported; an important consideration for ongoing development and maintenance. This technology also allows for immediate integration to a wide spectrum of other existing or newly developed computer technologies, in particular the Internet.

The ability to rapidly and accurately enter large quantities of information into the primary databases has been addressed in the database design. Predefined forms are used to enter the data for one record at a time: each record is uniquely identified by its Registration Number, which doubles as the collection Lot number. Wherever feasible, for example, in the selection of taxonomic names, country, state, etc, look-up lists are provided for ease of data entry and integrity. Data validation is enforced at field level to avoid the entry of invalid or inaccurate data. Automated processes, such as the ability to automatically derive higher taxa from genus, or the selection of default values, have been implemented. An interface to an external gazetteer database provides the ability to rapidly obtain latitudes and longitudes from selected place names and/or offsets from these places, or *vice versa*. Automatic conversion from latitude to decimal is also implemented.

An interface to a 'Tissues' database is provided in order to cater for the increasing need to use molecular technology to support taxonomy. Similarly, an interface to an Images database links specimen records to digitised images.

A suite of utilities has been developed for rapid database maintenance. In order to ensure that collections database records align with taxonomic changes a program has been developed using Visual Basic. This program allows global changes to the database records whenever changes to taxonomic names are required or if taxa are incorrectly positioned within the taxonomic hierarchy. A taxonomic tree is generated based on the taxa within the database and any taxon can be moved to its correct location in the hierarchy using a "drag-and-drop" method. All SQL statements required to implement these global changes are automatically generated by the program. This utility can also generate a distribution map for any taxon. Each specimen is represented by a single dot on the map indicating its collection location. Underlying records for that taxon can then be interrogated and edited, if required, by selecting the dot or dots. A related program provides a read-only taxonomic tree/mapping interface. Another utility allows up to 20 related or unrelated taxa to be plotted superimposed on the same map for comparison. This program is useful for rapidly finding and editing records with incorrect geographical coordinates.



Western Australian Museum

Mammal Collection Database

Currently holding 49,220 records

Figure 1. Example of primary collection database entry page (for mammals) showing the main menu options.

Additional utilities have been developed to support the ongoing curation of collection specimens, such as a label generator, loans management, report production, and search facilities. The database design also handles interfaces to third party products, such as ArcView.

The primary collections databases have been designed to accommodate observation records by standardising on table structure. This approach allows existing interfaces and utilities to work seamlessly over collections records and/or observations records (see Fig 1 for example of an entry page to one of the primary databases).

The Museum's Secondary On-line Databases – *FaunaList* and *FaunaBase* (www.museum.wa.gov.au/faunabase)

FaunaList is an on-line phylogenetically arranged checklist of the scientific names for each vertebrate group (amphibians, birds, mammals, reptiles and fishes) recorded from Western Australia and the surrounding seas. Based on a recently published checklist (Aplin *et al.* 2001) it contains literature references, flags gazetted "threatened" fauna, and provides information on numbers of taxa and lists of type specimens in the Museum's collections. It is easily updated and it is the Museum's intention to keep it current.

FaunaBase, which is a derivative of the primary fauna collections databases, has been developed as an on-line product tailored to meet the needs of the majority of users. Currently it provides access to records of more than 170,000 terrestrial vertebrate specimen records and 32,965 bird observational records of Western Australian taxa [*i.e.* it excludes records from overseas (the Museum holds extensive collections from south east Asia and New Guinea) and from the rest of Australia if the taxa do not occur in this State]. Recently *FaunaBase* has added terrestrial vertebrate records of the Queensland Museum, and Museum and Art Gallery of the Northern Territory. However, *FaunaBase* has the potential to deliver all data contained in all the primary databases

Users of *FaunaBase* may access specimen records via a number of entry modes: common names, thumbnail images, a taxonomic tree, Family or a search on scientific name. It is also possible to define and search a specified area to produce a listing of taxa recorded within it. All methods produce for each taxon a map showing the distribution of all Western Australian Museum specimen records in Australia, an image (if available) and a written description of its total distribution. Restricted access is possible to specimen records underlying mapped distribution points.

FaunaBase provides 'snapshots' of integrated information taken regularly from the Museum's primary collections databases. Meanwhile, the digital distribution maps for each species are not predefined but dynamically generated by the system's GIS. One of its strengths is its simplicity. The system draws on the nomenclature contained in the *FaunaList* database, a flat structure akin to spreadsheets. During searches of *FaunaBase*, the GIS superimposes geographic information on a base map of Australia using ASP and Java technology. The Museum's server uses ASP technology to extract information from the databases for three corresponding values: latitudinal coordinates, longitudinal coordinates and date category. These values are passed to a Java applet, which generates maps in the client's browser. Geographical coordinates are assigned simplified corresponding x/y decimal values, which are then identified and extracted by the applet. The date categories (50 year intervals) simply provide a breakdown of when the specimen was collected. To conduct an area search, users can either type in specific coordinates or click the mouse twice to define the top left and bottom right corners of the area to be searched; JavaScript is used to enable this function. It is recommended that *FaunaBase* be viewed using Internet Explorer version 4 or above with Cookies, JavaScript and Java enabled.

Discussion

Containing more than 1.5 million specimen records, the Museum's primary fauna collections databases are by far the largest taxonomically verifiable databases of the Western Australian fauna (they are taxonomically verifiable because each record is underpinned by a voucher specimen). Other strengths include their long temporal coverage, extensive (rather than intensive) geographical coverage of the State and the high degree of reliability of identification of taxa. Weaknesses include the mainly low spatial resolution (particularly of older records), they consist of point data reflecting presence only (not absence) and they are inadequately resourced, with the result that backlogs of data capture remain substantial for invertebrates. Very large observational databases, particularly for birds, also remain to be captured electronically.

Development of *FaunaBase* has been a significant step towards on-line delivery of specimen and observational data contained in the Museum's primary databases. The quantity of fauna data potentially available should significantly increase in the near future through access to Western Australian fauna records currently held in the collections of other state museums and CSIRO. OZCAM (On-line Zoological Collections of Australian Museums) is a joint Commonwealth and State funded project that will enable distribution of fauna data held by these institutions.

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Database ownership and access issues: A discussion paper

P Gioia

Department of Conservation and Land Management,
Herbarium, Kensington WA 6151
email: paulg@calm.wa.gov.au

Keywords: fauna survey, database, ownership, access

Introduction

The need to coordinate fauna survey databases across a range of private and public agencies has resulted in a proposal to house survey data in a single repository. This repository would be accessible to data contributors, such as environmental consultants, mining companies or conservation agencies undertaking fauna survey, and data users such as the Environmental Protection Authority (EPA) for the purpose of environmental impact assessment (EPA 2000), or other researchers.

The advantages of such a repository include increased consistency in survey design and consequent data capture and storage, a reduction in replication, increased collaboration between consultants and State government agencies, and an improved basis from which to understand Western Australia's ecosystems and biodiversity.

A number of important issues need to be addressed in the development of this database. Should the project be owned solely by government or a consortium of private and public participants? What access would non-contributors have? What protection or copyright issues are involved? Who would own the data and what rights would this confer? What data licensing arrangements would be required, if any? What security system should be established?

From an implementation perspective there are other important questions. What kind of model would best suit the repository – a data editing environment, a read-only warehouse or some other model? What level of ongoing data maintenance would be required and who would pay? What relationship would there be with the Western Australian Museum's specimen database, the Department of Conservation and Land Management's historical survey databases, or other related databases?

This paper canvasses some of these questions, albeit at a superficial level, for discussion purposes. It does not attempt to provided definitive statements on areas involving copyright or IP law, nor detailed specifications for a computing infrastructure. However, some recommendations are made, based on previous experience, on important requisites for an effective repository.

Implementing a common repository

Where

A repository as described above would involve contributors from both the private and public sectors. Where should the repository be best housed – within a specific agency (be it private or public) or in a commercial facilities management situation? Factors that should be considered in this choice include longevity of the project, primary users, cost and ease of implementation and maintenance.

Data arising from fauna surveys are largely publicly funded. A common repository would include data from environmental impact assessments, biodiversity inventories and research, and research activities generally by the public arena. By its nature, a fauna survey data repository would become increasingly useful in the longer term as data are added. This would provide a broader base for data analyses and a wider scope of data to prevent the possibility of data duplication.

These arguments lend support to housing the data within a public agency having a significant legal obligation to deal with or manage conservation-related information. Agencies that fit these criteria include the Department of Conservation and Land Management, the Environmental Protection Authority and the WA Museum. The Department of Conservation and Land Management might be better suited to housing the repository because of its status as a public instrumentality and its legal obligation to manage fauna data at an operational level. Hosting by a public agency may also have lower costs than a commercial company, depending on the situation (*e.g.* where a Department is already providing a similar function). Given the public interest nature of the repository, it might be possible for a cost-effective arrangement to be worked out with the agency. That would be much less likely for a commercial company.

How

As a prerequisite, a repository needs a hosting agency with adequate existing infrastructure and commensurate biological data management skills, or the resources to provide those requirements. That infrastructure should support not only database management, but also online delivery capabilities (*i.e.* the web), and appropriate security capabilities. With respect to biological data management skills, particular regard needs to be given to the ongoing management of species-based data. The basic unit of a fauna survey is a species at a location. Depending on the fauna group, different and conflicting species classifications may exist. Within the context of

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This paper was presented in similar form at the Workshop on the Co-ordination and Integration of Terrestrial Vertebrate Fauna Survey Database for Western Australia, held on April 5, 2002, at the University of Western Australia

Western Australian fauna names, it is highly desirable that a single taxonomy be adopted and the custodianship of the WA Museum prevails. Furthermore, an effective fauna repository would be dependant on access to current, authoritative names from the WA Museum, provided on a regular basis.

There are also issues associated with data ageing that must be considered. Changes to species names occur as the result of taxonomic research and revision. This can be a problem in particular groups, such as invertebrates. It can be argued that tracking of names and synonymies is an essential task of any species database if it is to be of ongoing value to a broad range of users (for flora, this function is provided by the WACensus database at the WA Herbarium).

For non specimen-backed records, as is often the case with fauna survey data, name changes represent a major problem, and the integrity and usefulness of survey data will diminish over time. However, it can also be argued that any data are better than no data at all. Historical records can still be of great value to science despite problems with identification.

Ultimately, it is a decision for those implementing the repository as to what resource is applied to this problem, and what reasonable expectations users might have of the database to contain accurate, useful information for scientific research.

Consider now two approaches for how a repository could operate: implement a repository as a read-only warehouse containing a merged copy of datasets maintained elsewhere; or alternatively, develop a more traditional data-editing environment. There are pros and cons to both models, each with significant impacts on ongoing maintenance.

Read-only Warehouse

In this model, data would be maintained externally by contributors. They would be responsible for all aspects of integrity relating their own datasets. Data would be delivered in a prescribed format, adhering to specified standards as called for in EPA Position Paper 3 (EPA, 2000). Updating of species nomenclature would be the responsibility of contributors. Any changes to names would require all contributors to update their relevant datasets where required.

Those data would then be merged into the repository. If data standards have been adhered to, then the merging process should not be problematic. In this model, the repository is refreshed as often as desired and made available on a read-only basis in an agreed manner. "Home" for data resides with the contributors and corrections to data must be applied by the contributor and the repository refreshed with the new data.

The warehouse model is simple, and places the least burden on the hosting agency. Because data editing and maintenance largely occur elsewhere, a much simpler data delivery environment is required and data uploading is relatively straightforward. However, experience has shown that despite the existence of standards, there are invariably different interpretations of those standards and some data 'massaging' will be required. This arrangement places the responsibility for data maintenance on the original contributor, and because of the reality of name changes in some groups, contributors will need to provide an ongoing resource for maintaining the data. On the other hand, the contributor is like to have the greatest knowledge of the data set concerned and is therefore better placed for its ongoing maintenance.

Traditional Database Model

This model describes the way many databases are implemented; a set of data entry, validation and maintenance tools integrated with various delivery methods such as reports, online queries, *etc.* Data should, in theory, be delivered in adherence to the set standards described above. In this model, editing capabilities can be used to correct errors *in situ*, as well as enhance existing data. 'Home' for the data would become the repository. Any subsequent corrections made by contributors to source data sets would have to be carefully merged into the repository without deleting changes made therein. Alternatively, contributors would need direct editing access to the repository.

While the notion of contributor responsibility would remain intact, experience often dictates otherwise. Contributors with limited resources are more likely to provide the data as is, leaving the burden of data validation and integrity with the hosting agency. This would place greater responsibility upon the hosting agency, both in terms of increased system complexity and increased data maintenance. On the other hand, it represents an opportunity to establish a greater degree of integrity in the data.

Security

A repository as described above would have data contributed from a number of sources, both private and public sector. In some cases the data might be freely contributed; in other cases it might come as the result of conditions attached to an EIA. In some cases the data might require restricted access by virtue of confidential information on threatened species or the like, in other cases data may have access limitations imposed by custodians. Furthermore, distributed data editing access might be required, depending on which implementation approach was adopted. Thus, security mechanisms would need to be implemented which enabled arbitrary portions of the data to be screened from unauthorised access or alteration.

Custodianship and maintenance

From the above discussion, it is clear that dataset maintenance and custodianship are key issues defining the implementation of a common repository. Survey datasets are generally funded by one-off funding situations. Resources for ongoing maintenance of datasets are rarely factored into grant applications, and when they are, rarely granted. Furthermore, researchers generally do not have the resources to be encumbered by an increasing array of legacy datasets. Thus, the tendency is to relinquish responsibility for a dataset once its sponsoring project is complete and data are published. It should not be surprising, therefore, to have the idea of a common repository greeted with ambivalence by many researchers, unless it minimises their responsibility for ongoing data maintenance.

Of course, an approach could be taken whereby data are accepted as is, without further encumbrance or liability, either to the contributor or the host of the repository. This may be the only realistic approach. Users would query and interpret data on that basis. Users generally are also quick to notice inconsistencies in data. If those inconsistencies remain without any attempt at error correction, there may be less willingness to use the data meaningfully and the value of the repository may be undermined to some extent.

How much?

The initial costs of designing and implementing a repository are generally straightforward to calculate and will not be dealt with further here. It is the maintenance of the repository that that is of greater concern. If a warehouse model is adopted, data maintenance costs will be spread across contributors as the onus of data validation and integrity would fall largely on the contributor. If a data editing/value adding model is chosen, ongoing resource will be required to reconcile disparate datasets, either because of inconsistent species nomenclature or other data validation problems. In fact, both models will require a minimum level of maintenance, neither will run on their own after implementation with ongoing assistance to the hosting agency and data custodians.

Data ownership issues

The above situation might understandably create concerns for contributors regarding ownership and access issues. It is important to understand what protections are available under Federal or State law, what is capable of being owned, and what arrangements can be made to protect ownership whilst at the same time supporting the original notion of a common repository for fauna survey data.

Data in itself is not capable of being owned. The physical manifestation of the data can be owned, for example, in paper or electronic form, the manner in which data are displayed or a compilation of data may be protected as a copyright work under the Copyright Act 1968 (Commonwealth) and may also be owned. However, the most significant 'protection' which is afforded to data is the ability of the data custodian to control access to the data and through placing contractual limitations upon the use of data that is accessed.

Copyright

The following notes on copyright are by no means authoritative or exhaustive. Further information can easily be obtained from the Copyright Council website at *http://www.copyright.org.au*.

At this point in time, the only relevant form of protection for data in Australia comes from the Copyright Act 1968 (Commonwealth). Copyright law does not protect ideas or information, and raw data is in itself *not* protected by copyright. However, the expression of that data can be, including compilations of data, so long as it meets certain criteria. A compilation may be protected by copyright if "there has been sufficient intellectual effort in the selection or arrangement of the information; or if the author has engaged in sufficient work or incurred sufficient expense in gathering the information, even if there is no creativity involved in the selection or arrangement" (ACC, 2001a). The definition of what constitutes "sufficient" is obviously open to argument. Thus, so long as there is sufficient effort incurred in a particular database by its author, the database is protected by copyright. However, there is nothing to prevent someone using the same source data to produce another compilation, so long as they meet the above criteria. According to copyright law, even forms and tables can be copyright, so long as tests of originality are met.

Copyright in databases or compilations will only be infringed if the alleged infringer copies a substantial portion of the work. Extraction of a single or a small number of pieces of data will not infringe the copyright, neither will the extract of a large amount of data if it is reproduced in a different form which is not a substantial reproduction of the original database or compilation.

Normally, the author is the copyright owner, with certain exceptions. These exceptions include employees where the work is undertaken as part of normal duties for an employer. A State, Territory or Federal Government is normally the first owner of copyright for data assembled by, or for, public servants. In the case of a consultant it depends on the terms of the consultancy. Furthermore, copyright can be both assigned or licensed via written agreement (ACC, 2001c). Interestingly, under the Copyright Act, governments, including State Governments and qualifying agencies, can copy any copyright material without infringing copyright, so long as the copying of material is for government purposes having a demonstrable public interest component. Use of copyright material may require notification of the copyright owner and possibly a written agreement. A fee may be required to be paid to the copyright owner.

Government departments have no independent legal status. The copyright of material created by, or for, government departments and agencies is owned by the relevant State or Commonwealth Crown. Thus, issues of access to data between and internal to Government agencies are not determined by ownership, but administrative policy. More general details on government and copyright can be obtained from the Australian Copyright Council (ACC, 2001b).

Implications for a common fauna survey data repository and data licensing

If, as is suggested above, a repository is implemented and/or hosted by a State agency, access to the data compiled therein would be controlled by the hosting agency on behalf of the State. This would be the case irrespective of who provided the raw data. The terms of access could be modified by a data licensing agreement.

For a common fauna repository to work effectively, a suitable data licensing agreement would be required. A key issue the license should define is identification of parties to the licence (*ie* who's in the "club"). The license should anticipate the kinds of contributors to, or users of the repository, and purposes for which the data may be used, particularly in prospective commercial environments. In other words the license should define who a participant in the repository is.

Other areas the license should deal with include:

- acceptable purposes for use of data,
- responsibilities of the hosting agency in maintaining database infrastructure and ensuring access to license partners,
- responsibilities of contributors in providing data to an agreed standard with agreed levels of ongoing maintenance,
- determination of costs associated with the maintenance and provision of data,
- indemnity issues,
- termination,
- data transfer to non-participants, and
- other specific conditions.

Examples of licensing agreements are available on the web (*e.g.* WALIS, 2000) or on request from agencies such as the Department of Conservation and Land Management, any of which could be used as a starting point. It is likely that there would be a number of different licenses to cover specific situations, including both commercial and non-commercial situations.

Furthermore, by developing a *Memorandum of Understanding* (MOU) between all parties, the licensing agreement could be substantially simplified.

Conclusions

The implementation of a fauna survey repository accessible by a wide variety of users for the purposes of environmental impact assessment or further research is feasible. However, such a repository would be best implemented within a State agency having an ongoing responsibility in the management of fauna data. That agency should also have adequate resources, not just for hosting the repository, but its implementation phase and ongoing maintenance.

There would need to be clear lines of responsibility for the ongoing maintenance of data, particularly with regard to species names, and a clear data standard to adhere to.

A suitable data licensing agreement and/or MOU is essential, to which all contributors or users would be party to, so that future terms of access are clearly understood and agreed to.

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Summary of the Workshop

The Royal Society of Western Australia, with sponsorship from the Department of Conservation and Land Management, Environmental Protection Authority, Chamber of Minerals and Energy, Centre for Ecosystem Management (Edith Cowan University) and The University of Western Australia, held an open workshop on the 'Co-ordination and Integration of Terrestrial Vertebrate Survey Data Bases for Western Australia', on 5 April 2002. The intention of the workshop was to address an important State-wide issue which has been a concept for many years but has never achieved any practical progress in establishing a database of surveyed terrestrial vertebrate fauna for Western Australia. More information about the Workshop and the issues are available from the Royal Society's website at http://www.ecu.edu.au/pa/rswa/workshop/.

The workshop was well attended by about 50 representatives of government departments, academic institutions, and business (including private environmental consultants). A number of papers were presented at the Workshop. This was then followed by considerable discussion amongst the participants on wide-ranging topics related to the establishment of a survey fauna database.

There was universal agreement amongst the participants that the need was now greater than ever for the establishment of a coordinated database of the terrestrial vertebrates surveyed in Western Australia. The timeliness of this workshop and the topic of a regional fauna database were highlighted by the release at the workshop of Position Statement No. 3 of the Environmental Protection Authority on 'Terrestrial Biological Surveys as an Element of Biodiversity Protection'. This document states emphatically (among other topics) that —

> *The EPA expects that terrestrial biological surveys will be made publicly available and will contribute to the bank of data available for the particular region, to aid the overall biodiversity understanding and assessment by facilitating transfer into State biological databases*

and that —

> *The EPA intends to encourage the coordinated development of a state-wide database for EIA-related biological surveys ....*

After widespread discussion at the Workshop, it was clear that there were two general (and not exclusive) approaches to establishing a fauna survey database for Western Australia —

- the Western Australian Museum fauna database be used as the basis for a coordinated survey database; this is a current, accurate and large database which is based on vouchered specimens lodged in the Western Australian Museum, and
- fauna survey data that are provided annually to CALM as part of their licensing system be used as the basis of a fauna database; such a database would consist of observational and unsubstantiated identifications of fauna, and therefore be prone to inaccuracies, so that some linkage with a verified identification by voucher specimens in the Western Australian Museum would be required to "value-add" to such a general database.

There was general agreement that the Western Australian Museum was the appropriate body to provide the correct nomenclatural classification (*i.e.* names) of all animals for any coordinated regional database – an appropriate system of animal names is an essential prerequisite for a fauna survey database.

It was considered essential that entries into the survey fauna database are checked for accuracy. The identification of specimens is often not an easy or unequivocal exercise. There needs to be some level of verification for records in a database, varying from just conformity to the presumed geographic distribution of species to the highest level of accuracy which is the vouchering of specimens in the Western Australian Museum. It was considered essential that specimens continue to be lodged with the Western Australian Museum for identification by experts in their taxonomic field, and for reexamination/reinterpretation of specimens, for example after taxonomic revision of animal groups or description of new species.

Although the scope and time constraints of a one-day workshop precluded the formulation of more specific plans for the implementation of a survey fauna database, it was clear that future progress required the participation and cooperation of at least three Government agencies (the Department of Conservation and Land Management, the Western Australian Museum, and the Environmental Protection Authority), and the participation of private environmental consultants and university academics and researchers. The Royal Society of Western Australia was seen as an appropriate body to be involved as a facilitator, for example by holding the initial workshop, by publishing its results, and by sponsoring future workshops.

The Royal Society of Western Australia encourages the establishment of a terrestrial fauna database. The Society wrote to the relevant Minister encouraging her to develop a terrestrial survey fauna database in cooperation with the various government departments, private consultants, and academic researchers in establishing a regional fauna database. The Royal Society of Western Australia, as an independent Society whose aim is to promote science in Western Australia, indicated its willingness to continue its role as a facilitator in the process.

Graham Thompson and Philip Withers
Convenors

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The oldest rocks:
The Western Australian connection

J R de Laeter & A F Trendall

Department of Applied Physics, Curtin University of Technology, GPO Box
U1987, Perth WA 6845
e-mail: rdelaete@cc.curtin.edu.au

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Abstract

The discovery of ancient fragments of the Earth's crust has provided new evidence to our understanding of the early history of the Earth. One of the earliest measurements of the age of terrestrial materials using the newly discovered radioactive decay of U to Pb was carried out by a Western Australian scientist, E S Simpson, in the first decade of the 20th century. Probably motivated by a visit to Perth by F Soddy in 1904, Simpson measured the age of a Western Australian U-rich mineral by the U-He method. Simpson's work largely went unnoticed until L R Cotton calculated the U-Pb ages from four U-rich samples analysed by Simpson. One of these ages was subsequently published by A Holmes, and this led to the belief that Western Australia was the location of the world's oldest rocks. In 1950, M Oliphant encouraged physicists at the University of Western Australia to build a mass spectrometer to measure the age of these old rocks. Subsequently P M Jeffery established a geochronological laboratory in which the U-Pb, Rb-Sr and K-Ar methods were developed, and the discovery of the "whole rock" Rb-Sr technique earned the laboratory an international reputation. In 1981, evidence of old banded gneisses (3550 Ma) was found at Mount Narryer, in Western Australia, and subsequently zircons of approximate age 4200 Ma were found at Jack Hills in the N-W corner of the Yilgarn Craton, 70 km north of Mount Narryer. In 2001, zircons up to 4400 Ma in age were discovered in the Jack Hills region, and this has led to a re-examination of our understanding of the early history of the Earth. These discoveries would not have been possible without the development of the Sensitive High Resolution Ion Micro Probe mass spectrometer (SHRIMP). This instrument revolutionised the science of geochronology by permitting the *in situ* microanalysis of U-Pb ages in zircons and other U- and/or Th- bearing minerals.

Keywords: geochronology, Jack Hills, Mount Narryer, rubidium-strontium, SHRIMP, uranium-lead, zircon

About this time, Rutherford, walking in the Campus with a small black rock in his hand, met the Professor of Geology: "Adams," he said, "how old is the Earth supposed to be?" The answer was that the various methods led to an estimate of 100 million years. "I know," said Rutherford quietly, "that this piece of pitchblende is 700 million years old." This was the first occasion when so large a value was given, based too on evidence of a reliable character: for Rutherford had determined the amount of uranium and radium in the rock, calculated the annual output of alpha particles, was confident that these were helium, measured the amount of helium in the rock and by division found the period during which the rock had existed in a compacted form. He was the pioneer in this method and his large value surprised and delighted both geologists and biologists (Eve 1939).

Introduction

The recent discovery in the Yilgarn Craton (Fig 1) of zircon grains which crystallised within the Earth's crust more than 4 Ga ago (Mojzsis *et al.* 2001; Wilde *et al.* 2001), may appear to reflect the simple confirmation of a belief, widely held through much of the 20th century, that the Earth's oldest rocks occur in Western Australia (Jeffery 1976). However, the connection between these recent papers and that long-standing belief is neither direct nor simple. The ages of the >4 Ga zircons from the Yilgarn Craton were determined using an advanced mass spectrometer (SHRIMP) designed and built in Australia (Compston 1996). The idea that the oldest rocks on Earth occurred in Western Australia had its origin in chemical analyses made by E S Simpson (Simpson 1910, 1911, 1912, 1919) of radioactive minerals from the Pilbara Craton, some 700 km to the north of the Yilgarn Craton location (Fig 1), and of uncertain geological relationship to it. A stimulus for Simpson's initiative was probably a visit to Perth in 1904 by F Soddy, an English chemist who had worked closely with E Rutherford in Canada on developments in radioactive decay, and was therefore aware of Rutherford's seminal realisation (Rutherford 1906) that the ages of radioactive minerals could be measured by determining the relative amounts of parent element and daughter product within them. Simpson's results made little impact at first, but Cotton (1926) and later Holmes (1927) and Holmes & Lawson (1927) revived interest in them. In particular the publications by Holmes brought the age and significance of the Pilbara minerals to the attention of the international geological

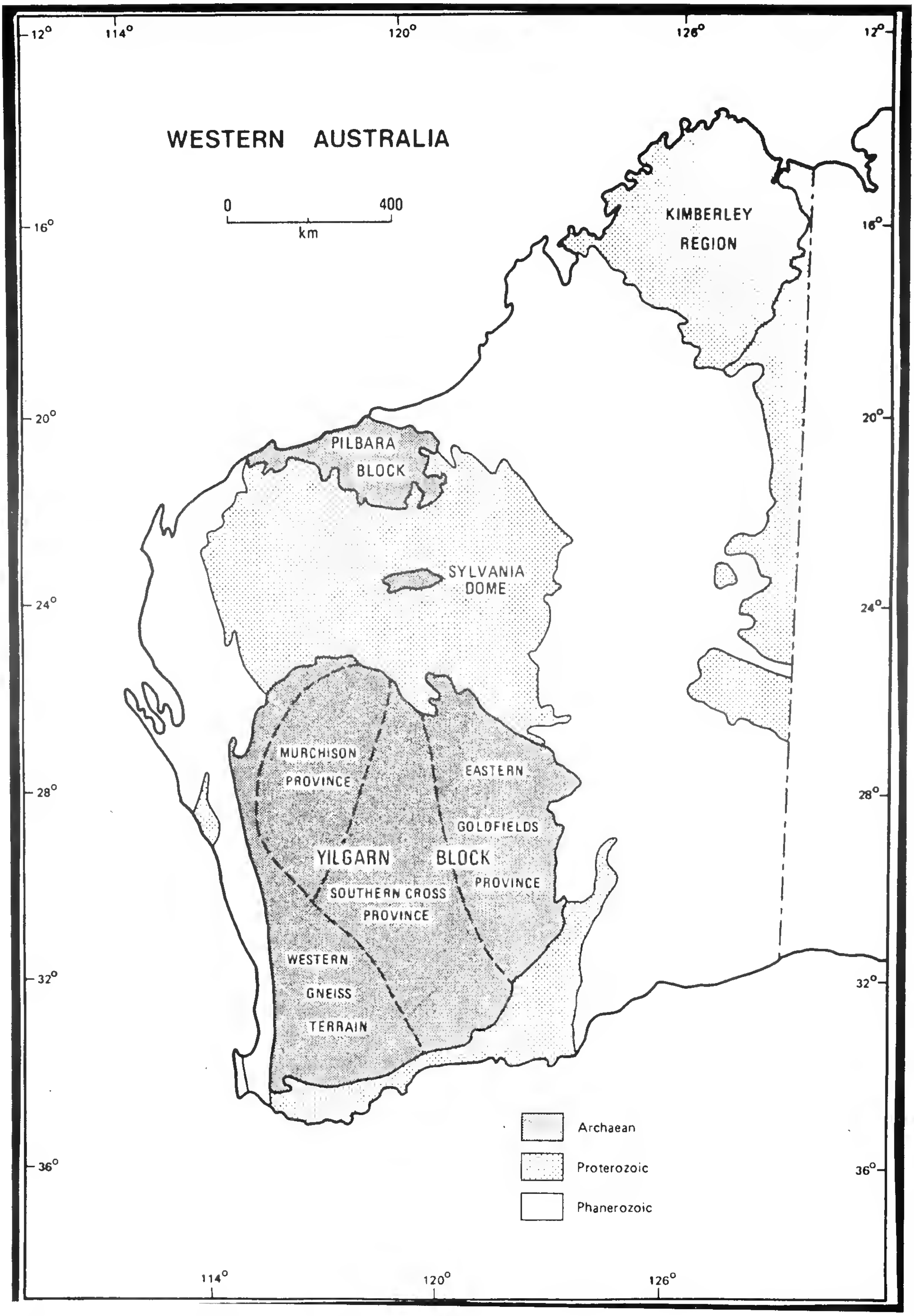

Figure 1. Map showing the Archaean areas in Western Australia.

community, and established Western Australia as the place where the oldest minerals occurred.

Other events flowing from that early work, and particularly from worldwide awareness of it, later led to a strong interest within Western Australia in the determination of rock and mineral ages using physical methods based on mass spectrometry, including SHRIMP. We believe that these events, and the serendipitous way in which they interacted to provide both the material and conceptual infrastructure for the recent Yilgarn Craton discoveries, provide a microcosm of scientific progress of sufficient interest to be worth recording. Our purpose in this paper is to provide such a record by summarizing the relevant events in greater detail.

Frederick Soddy's visit to Western Australia

The concept of time has never ceased to intrigue those who have thought about it. In particular, the age of the Earth has been studied by scientists over the centuries. Lord Kelvin estimated the age of the Earth by heat flow, George Darwin by tidal interactions, Edmund Halley from the saltiness of the oceans, and Charles Walcott by the accumulation of sediments. However, none of these "clocks" was particularly accurate and the physicist, Kelvin, fell into disrepute with geologists because his estimated age of 10 Ma, which he obtained by examining the cooling of the Earth from a molten body, was far too short as compared to geological estimates. Unfortunately for Kelvin, radioactivity was unknown at that time.

The discovery of radioactivity by H Becquerel in 1896, coupled with M & P Curie's demonstration that radioactive atoms transmute into atoms at predetermined and essentially immutable rates, provided the basis for a new clock to measure geological time. In 1902, two scientists at McGill University in Canada, the New Zealand physicist Rutherford, and Soddy, investigated the radioactive decay of U and showed that it decayed to the end-product Pb and also produced He from the alpha particles emitted in the decay scheme. In 1905, in the Silliman lectures at Yale University, Rutherford suggested the possibility of using radioactivity as a geological timekeeper on the basis that if one could measure either of the decay products He or Pb, then one could measure geological time by this nuclear clock (Rutherford 1906).

The Western Australian connection with the Earth's oldest rocks began in most unusual circumstances. In 1904, Soddy, a leader in this new field of radioactivity, visited Western Australia to give a series of lectures on recent developments in science. Soddy had left McGill University in 1903 to join W Ramsay at University College, London, and had demonstrated that radon and He were produced in radioactive decay. In the English summer of 1904, Soddy was persuaded to make the long sea voyage to Australia by a group of Western Australians, under the chairmanship of J W Hackett, who was trying to arouse public interest in the need to establish a University in Western Australia. At that time secondary school students in Western Australia sat for the South Australian Public Examination, and a few Perth Technical College students sat science degree examinations at the University of Adelaide under an arrangement established by W H Bragg, who was Head of the Department of Physics at that University.

Soddy gave a number of lectures in Perth (6), Fremantle (3), Kalgoorlie (2) and in five other country towns (1 each). His lectures covered "electricity, x-rays, radioactivity, the structure of matter and the evolution of the universe" (Jenkin 1985). Soddy was in great demand as a public lecturer in London, in part because of the demonstrations he used to illustrate his lectures. He brought an extensive array of equipment to Perth and his lectures were well attended and much appreciated. In fact, Soddy's first lecture in Perth was booked out, and hundreds of people were unable to gain admission. It is of interest to note that Soddy sold his equipment to Perth Technical College at the end of his lecture tour and some of that equipment is now on display in the Department of Applied Physics at Curtin University. Jenkin (1985) reports that Soddy's visit helped to hasten the establishment of the University of Western Australia.

The work of E S Simpson

An interesting but almost completely unknown aspect of the geochronology of Western Australian geological specimens emerged in 1910 when E S Simpson, then Chemist and Assayer of the Geological Survey of Western Australia, measured the age of a U-rich mineral, which he named pilbarite, from a pegmatite at Wodgina in the Pilbara Craton. One might assume that Simpson was influenced in this endeavour by Soddy's visit, as he measured the amount of He released from the pilbarite as well as the U content, using chemical techniques, and thereby calculated an age of 13 Ma (Simpson 1910, 1911).

The only means available at that time for measuring He and Pb were chemical techniques, and both suffered serious shortcomings. Helium, which is a gas, leaked out of U-rich ores because of radiation damage and weathering effects. Thus, calculated ages were underestimates. On the other hand, the measurement of the quantity of Pb could not distinguish radiogenic Pb from primordial Pb, and could not identify the source of the radiogenic Pb. Simpson understood the limitations of the U-He methodology he had adopted, because he pointed out that the mineral he had used was a secondary weathering product and had probably lost radiogenic He (Simpson 1910, 1911). At about the same time, Simpson also fully analysed two associated U minerals from the same pegmatite, which he identified as mackintoshite and thorogummite, parental to the pilbarite. An intriguing question then presents itself as to why Simpson failed to calculate the ages of all three minerals from the amount of Pb present. He had determined this, and had specifically commented on its derivation by radioactive decay. Simpson was also familiar with the work of Boltwood, who had calculated radiometric ages based on chemically-determined Pb/U ratios, for he mentions him by name (Simpson 1912).

Whatever the reason for this puzzling omission, fifteen years went by before Cotton, Professor of Geology at the University of Sydney, used Simpson's analytical results to calculate chemical U-Pb ages for these minerals and also for fergusonite from another Pilbara pegmatite at Cooglegong, an analysis of which had by then been published by Simpson (1919). Cotton (1926) calculated ages of 620, 1475, 1460 and 3840 Ma respectively for fergusonite, mackintoshite, thorogummite, and pilbarite, and took account of the Pb contribution by Th. Holmes & Lawson (1927) independently revised Cotton's calculations, and the inclusion of the age of "mackintoshite, etc" as 1260 Ma in Holmes' (1927) popular book "The Age of the Earth", in which it was the oldest age recorded, placed the significance of Simpson's analytical work before a wide audience. It now appears that this age is too low by a factor of at least two, and this makes it even more ironic that it was probably largely due to Holmes' book that a widespread belief arose that the Precambrian of Western Australia contained the most ancient rocks of the Earth's crust (de Laeter & Trendall 1979).

Isotopic method of geochronology

The "chemical" method of age determinations, beset as it was with fundamental flaws, was of short-lived duration, since in 1912 J J Thomson at the Cavendish Laboratory in Cambridge University laid the foundation of "physical" geochronology by his discovery of isotopes. F W Aston, using a mass spectrometer of his own design, was able to show that a U-rich sample of bröggerite had at least three isotopes of Pb and that the sample was enriched in ^{206}Pb, a decay product of ^{238}U. This enabled an age of 909 Ma to be calculated for the bröggerite sample (Aston 1929). A companion paper by Rutherford gave an estimate of the age of the Earth as 3.4 Ga (Rutherford 1929).

This experiment by Aston (1929) heralded a new era in geochronology, an era based on isotopic rather than elemental measurements. Since that time the mass spectrometer has been an indispensable tool for every geochronologist, a veritable "time machine" that enables us to explore the past with a variety of radioactive decay systems with ever-increasing accuracy. A significant step in validating the isotopic method of age determinations was provided by A O Nier, who demonstrated that the isotopic abundances of Pb samples varied considerably, depending on the chemical composition and age of the ores (Nier 1938). Nier showed that U-rich ores gave Pb enriched in ^{206}Pb and ^{207}Pb, whereas Pb derived from Th-rich ores were enriched in ^{208}Pb. The only Pb isotope that is unaffected by radioactive decay is ^{204}Pb, because it is not the end-product of a radioactive parent and therefore represents primordial Pb that was inherited by the ore at its time of formation. ^{204}Pb can, therefore, be used to correct for primordial or "common" Pb contamination for the isotopes $^{206, 207, 208}$Pb. Using this technique, Nier *et al.* (1941) calculated a U-Pb age for a sample of monazite from Manitoba, Canada, of 2570 ± 70 Ma.

At the end of World War II, when non-military scientific research began its phenomenal growth, geochronology was poised to revolutionise our knowledge of geological events. One ingredient, however, was missing. Although the theoretical concepts of radioactive dating had been developed, no instrument existed outside physics research laboratories that would enable geologists to exploit the powerful new geochronological tools available to them. However, this situation was soon to be changed.

Until 1940, mass spectrometers were either sophisticated double focusing machines used primarily for measuring the atomic masses of nuclides, or large, complicated 180° machines that were difficult to build and operate successfully. However, in 1940 Nier described a distinctively different type of mass spectrometer that was destined to be the tool whereby geochronology could be exploited (Nier 1940). In 1947, using the extensive experience of building and using these mass spectrometers in the Manhattan Project during World War 11, and incorporating technological improvements that had occurred since 1940, Nier described a modified version of the 60° sector field instrument (Nier 1947). The importance of the 60° sector field instrument was that the elegance of its simple design enabled scientists other than physicists to utilise the power of isotopes in biology, chemistry, and geology, and this development was achieved against the prevailing opinion of the day, as expressed by Aston who believed that mass spectrometry would die away as an active research field (Svec 1985).

Geochronology in Perth

A number of geochronology laboratories were established in the 1950's based on the sector field mass spectrometer. These laboratories were often a cooperative arrangement between geologists and physicists, because mass spectrometers of that era were primitive instruments as compared to modern mass spectrometers and required much care and maintenance to keep them in an operating condition. This was certainly the case in Western Australia. In 1950, on his way to take up an appointment at the Australian National University (ANU), Professor (later Sir) Marcus Oliphant visited the Physics Department of the University of Western Australia (UWA) and spoke of the need for an Australian research program in geochronology, particularly in view of the widespread belief that this continent contained the Earth's oldest rocks (Jeffery 1976). Oliphant had worked with Rutherford in Cambridge, and was familiar with the physical techniques used in geochronology.

As a result, two staff members of the Physics Department at UWA, P M Jeffery and A H Morton, terminated the construction of a small accelerator and began instead to build a mass spectrometer, intended ultimately for a continuing geochronological program. Jeffery (1976) has given a graphic account of the difficulties involved. The instrument was first operated in late 1952, but its performance was unsatisfactory, and during 1953 it was decided to abandon the project unless more financial support could be found (Fig 2). Fortunately, a grant became available from the Carnegie Institute of Washington, sufficient not only to bring the home-made instrument into effective operation but also to provide a second, new, Nier-type mass spectrometer. It was with this second instrument that the first isotopic U-Pb age was obtained from a Western Australian mineral. The tanteuxenite analysed came from a pegmatite at Woodstock, again in the Pilbara Craton, and yielded a maximum age of 2790 ± 25 Ma (Greenhalgh & Jeffery 1959).

Figure 2. The original mass spectrometer flight tube used by P M Jeffery at UWA in the early 1950s. Shown in the photograph are three individuals who were involved with this equipment (left to right): J Budge (technician), W Compston and J R de Laeter (research students).

Jeffery and his team also established the K-Ar and Rb-Sr methods at Perth in the 1950s, and a seminal paper by Wilson *et al.* (1960) listed 36 Rb-Sr ages, 16 K-Ar ages and 21 U-Pb ages that resulted from this geochronological research. The first systematic attempt to relate this age data to the tectonic evolution of Western Australia was given in this paper (Wilson *et al.* 1960).

It is worth noting that Jeffery, in collaboration with W Compston who had been a doctoral student with Jeffery but now a staff member of the Physics Department at the UWA, proposed a "whole rock" Rb-Sr model. This represented an important advance in the interpretation of discordant Rb-Sr ages and established the Rb-Sr technique as a powerful geochronological tool (Compston & Jeffery 1959).

Unfortunately, by the end of the 1950s geochronological research had ended in Perth, but was established in the Department of Geophysics at the Australian National University (ANU). Compston was invited to lead the geochronology program and moved to the ANU in 1961. Geochronology was re-established in Perth in 1968, when another of Jeffery's former physics students (de Laeter) was appointed to the Department of Applied Physics at the Western Australian Institute of Technology (WAIT). With encouragement from Compston, a pilot-scale program of Rb-Sr geochronology was established in conjunction with the Geological Survey of Western Australia (GSWA). The Director of GSWA, J H Lord, accepted a recommendation from its petrologist (Trendall), that this cooperative work had considerable significant potential to advance the geological understanding of the Western Australian Precambrian.

The success of the early Rb-Sr work led to the extension of the geochronological program to include the Sm-Nd and U-Pb techniques, and the 60° sector field mass spectrometer used was progressively modified as technological advances in vacuum equipment, electronics and data handling facilities occurred. The cooperative program finally led to the appointment of a specialist geochronologist (D R Nelson), within the GSWA. In the mid-1970s, staff from UWA joined in the existing geochronology program, and clean-room facilities for U-Pb analyses were commissioned at that institution.

SHRIMP

As geochronology developed in many laboratories around the world, using an increasing number of radioactive decay schemes, the demand for improved mass spectrometric instrumentation led to a succession of technological advances in mass spectrometry. These advances enabled geochronology to reach a level of scientific sophistication of impressive dimensions. De Laeter (1998) has traced the development of geochronology in a mutually cooperative way with the development of mass spectrometry. Over the past 50 years or so technological advances have enabled the sector field instrument to meet most of the requirements of the various geochronological techniques that have been developed over this period of time.

During the past 25 years or so, however, radically new spectrometers have been developed. In terms of the Western Australian connection with the search for old terrestrial material, the most significant by far has been Secondary Ionisation Mass Spectrometry (SIMS). The ability to isotopically analyse minerals *in situ*, without the need of laborious chemical processing, in a mass spectrometer with high sensitivity and good resolution, has long been a goal for geochronologists. Furthermore, the ability to selectively analyse minerals without the inherent problems associated with whole rock analysis offers the opportunity of a quantum jump in the quality of geochronological information, thus opening up new frontiers of geological knowledge.

Compston and his colleagues at the ANU realised that a SIMS-type mass spectrometer would be required to achieve these geochronological objectives, incorporating an efficient ionisation source to provide the high sensitivity required for U-Pb analysis. This implied the need for a double focusing mass spectrometer with energy focusing to compensate for the large spread in energy possessed by the ions sputtered from a sample by

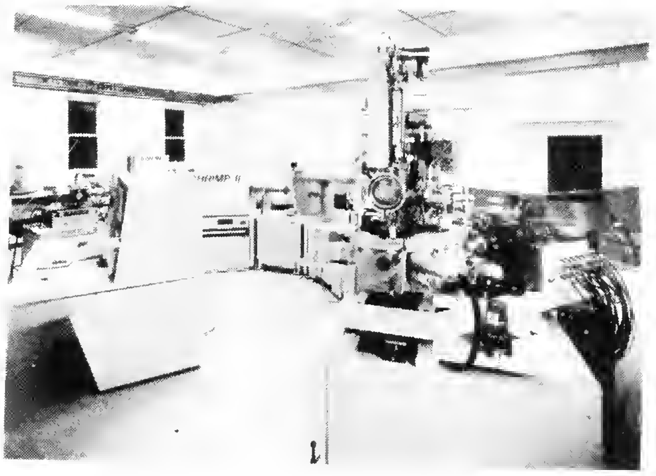

Figure 3. A photograph of SHRIMP II, located at Curtin University.

an ion bombardment source operated at a high accelerating voltage. The mass spectrometer would also need to possess high resolution to resolve interfering isobars in the vicinity of Pb and U, if effective U-Pb geochronology was to be carried out.

Compston (1996) has described the design, fabrication and operation of SHRIMP at the ANU. The success of SHRIMP I in the early 1980s led to the construction of a commercial version (SHRIMP II) in the late 1980s, and a consortium from Perth comprising Curtin University of Technology (formerly WAIT), the GSWA and UWA acquired a SHRIMP II in 1993 (Fig 3). The SHRIMP mass spectrometers at Canberra and Perth have been used extensively in analysing zircons and other U- or Th-bearing minerals in age determinations of rocks and minerals in Western Australia.

The Mount Narryer – Jack Hills Discoveries

The availability of a number of geochronological techniques was a crucial element in the search for the oldest rocks in the north-west portion of the Yilgarn Craton. The Yilgarn Craton is an ancient crustal block, one of the largest segments of Archaean crust in the world, and therefore of importance to studies of early crustal evolution. In 1981, a Rb-Sr age determination of banded gneisses near Mount Narryer yielded a whole rock isochron age of 3348 ± 43 Ma with an initial $^{87}Sr/^{86}Sr$ ratio of 0.7037 ± 0.0005 (de Laeter *et al.* 1981). These data indicated that the rocks had a prior crustal residence time of approximately 200 Ma to give a time of extraction of the granitic melts from the mantle of approximately 3550 Ma. The validity of this early Archaean age was supported by model Sm-Nd ages of 3510 Ma and 3630 Ma for two of the samples. These ages represented the oldest evolutionary sequence thus far identified in the Yilgarn Craton. The banded gneisses, (the Meeberrie Gneisses), were also subjected to U-Pb analysis to give a Pb-Pb age of 3357 ± 70 Ma, in close agreement with the original Rb-Sr age (de Laeter *et al.* 1985). This age was interpreted as resulting from metamorphic reworking of the primeval quartz-feldspathic material (de Laeter *et al.* 1981). Further Sm-Nd analysis of samples from the Meeberrie Gneiss gave T_{CHUR} ages of 3710 ± 30 Ma and 3620 ± 40 Ma confirming that the Western Gneiss Terrain is the oldest known major segment of sialic crust in the Yilgarn Craton.

Striking confirmation of the Mount Narryer results emerged from ion microprobe studies of the 3620 Ma Meeberrie gneiss sample carried out at the ANU (Compston *et al.* 1982). The analyses revealed that the youngest rims of several grains have a concordant U-Pb age of approximately 3300 Ma, whilst interior portions of zircons from the same suite give ages from 3690 Ma to 3560 Ma. These older ages have been interpreted as minimum estimates for the original magmatic ages of the xenocrystic cores.

U-Pb studies by the ion microprobe on detrital zircons from quartzite adjacent to the Meeberrie banded gneiss showed that most of them formed between 3500 and 3750 Ma ago, although some of them gave ages of about 3300 Ma (Froude *et al.* 1983). These ages suggest that the zircons may have been derived by erosion of the adjacent gneisses or their protoliths. In addition, Froude *et al.* (1983) reported the existence of four zircons from the same quartzite which have nearly concordant U-Pb ages between 4100 and 4200 Ma. These results suggest that pre-3800 Ma silica-saturated rocks were present in the Earth's crust.

The Jack Hills metasedimentary belt is a narrow curvilinear east to north-east trending belt approximately 70 km north-east of Mount Narryer. It is composed of minor metabasalts and substantial thicknesses of chert and banded iron formation interleaved with pelitic and psammitic metasediments. Detrital zircons from the Jack Hills metasedimentary belt analysed at the ANU using SHRIMP, revealed the oldest ages thus far determined. One zircon grain registered an age of 4276 ± 6 Ma, which is a minimum estimate for its original age (Compston & Pidgeon 1986). Sixteen other grains have similar ages to the zircon ages measured at Mount Narryer. One of the important features of the Jack Hills measurements has been that the frequency of occurrence of the old zircons (12 ± 5%), is some five times higher than at Mount Narryer.

Kober *et al.* (1989) reported the analyses of thirty zircon crystals from the Jack Hills metaconglomerate using the single zircon, direct evaporation, thermal ionization technique. Four of the thirty zircons gave ages in excess of 4000 Ma, confirming the microprobe analyses of Compston & Pidgeon (1986). Approximately 50% of the analysed zircons yielded an age of 3380 ± 20 Ma, whilst other crystals gave ages of 3300 Ma, 3440 Ma and 3570 Ma. As had been observed at Mount Narryer, some of the zircons demonstrated a more complex age structure with intergrowth of older mineral phases with younger domains.

However the exciting age determination of the 1980s is by no means the end of the investigation into the oldest rocks in Western Australia. Nelson *et al.* (2000) have described a zircon from a leucratic gneiss from the Narryer Terrane which records at least five high-grade thermal events at approximately 4186, 4140, 4005, 3978 and 3945 Ma, which may represent rapid tectonic reworking of siliceous fragments of the Earth's early crust by collision and amalgamation, or reworking by meteorite impacts. Later events are also recorded in this zircon, which can be related to known regional-scale tectonic events that affected the Narryer Terrane. This study demonstrates that the frontier of zircon geochronology is located within individual grains.

Then in 2001, two companion papers appeared (Wilde *et al.* 2001; Mojzsis *et al.* 2001), which have challenged our understanding of the early history of the Earth. A zircon crystal with an age of 4404 Ma was discovered at Jack Hills, Western Australia, making it the most ancient fragment of the Earth's crust ever identified (Wilde *et al.* 2001). The age determination was carried out with the SHRIMP at Curtin University. It is about 130 Ma older than any previously analysed material, and was formed approximately 150 Ma after the planet consolidated. Wilde *et al.* (2001) point out that the crystal has elevated oxygen isotope ratios suggesting a source rock that interacted with liquid water. This indicates that the Earth cooled much faster than previously thought and places constraints on the time that the Moon separated from the Earth. The crystal's chemistry is consistent with formation in a granitic rock whose precursor interacted with water, thus providing the earliest evidence of continents and oceans on Earth. In another study of zircons from Jack Hills (Mojzsis *et al.* 2001), a large range of oxygen isotope compositions (5.4-15.0 per mil) were measured in zircons older than 4000 Ma. Mojzsis *et al.* (2001) postulated that this large range in oxygen isotope ratios is evidence of re-working of the crust and the production of S-type granites, and for water near the earth's surface and the presence of a hydrosphere at 4300 Ma.

Conclusions

The evolution in geological thinking as a result of the discovery of ancient fragments of the Earth's crust is almost entirely due to developments in isotopic geochronology as an outcome of new and improved methods of mass spectrometric instrumentation. Although Western Australia is by no means the only geographic location where the search for old rocks has occurred, this State has nevertheless played an important role in this endeavour.

Probably as a result of the 1904 visit to Perth by Soddy, a Western Australian scientist measured the age of a U-rich ore by the U-He method in 1910 (Simpson 1910, 1911). Although Simpson's work was largely unnoticed, his age data were published in an international scientific journal by Cotton (1926), who recalculated Simpson's chemical analysis on four Western Australian minerals, using the U-Pb method. The republication of some of Simpson's age data in 1927 led to the widespread belief that the Precambrian of Western Australia contained the most ancient rocks in the Earth's crust (Holmes 1927).

It was this widely held belief that led Oliphant, in 1950, to suggest that a mass spectrometer be built in the Physics Department of the UWA to search for these ancient rocks. The geochronology laboratory established by Jeffery in the 1950s was an outstanding success, for it was not only the first mass spectrometry laboratory in Australia, but it provided the training ground for a number of young physicists, one of whom (Compston), was to play a unique role in isotope science research and in mass spectrometric innovation. The development of SHRIMP was the result of Compston's dedication and initiative and this instrument has revolutionised U-Pb geochronology using U- and /or Th-rich minerals.

Although the establishment of geochronology in Western Australia in the 1950s might appear to have been fortuitous, the infectious enthusiasm of Jeffery and the prior existence of instrumental skills within a Physics Department were basic ingredients for success. It was also significant that Precambrian granitic rocks with an age of about 2400 Ma which had been affected by a thermal overprint at about 520 Ma were available for study. It was the challenge of this situation that produced the Rb-Sr whole rock method, which in turn established the laboratory as an international leader in geochronology.

Furthermore, the presence of vast Archaean cratons in Western Australia virtually guaranteed that significant geochronological results would be forthcoming. Such results have emerged from the Mount Narryer – Jack Hills region over a period of some 20 years, commencing with the discovery of banded gneisses of approximate age 3550 Ma in 1981 (de Laeter *et al.* 1981), and culminating in the discovery of a 4404 Ma zircon in 2001 (Wilde *et al.* 2001).

The radioactive clocks, which are the key to our understanding of the chronology of the Earth, have progressively yielded their secrets as technological developments have enabled minute quantities of the radioactive elements and their daughter products to be measured with ever greater accuracy and precision. The development of SHRIMP has undoubtedly been of key importance in this work. There seems to be no reason to doubt that further refinements are possible as an ever-increasing number of chronometers are available singly or in combination to tackle the problems of Precambrian geology. The search for the oldest rocks in Western Australia continues after almost a century of effort built on the pioneering age determinations of Simpson.

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Occurrence of the eucalypt leaf beetle, *Cadmus excrementarius* Suffrian (Coleoptera: Chrysomelidae: Cryptocephalinae), in Western Australia

N dos Anjos[1], J D Majer[2] & A D Loch[3]

[1] Department of Animal Biology, Federal University of Viçosa, Av PH Rolfs, s/n, CEP: 36571-000, Viçosa MG Brazil
[2] Department of Environmental Biology, Curtin University of Technology, PO Box U1987, Perth WA 6845
[3] CSIRO Entomology, ℅ Department of Conservation, Brain Street, Manjimup WA 6258
email: nanjos@mail.ufv.br, J.Majer@curtin.edu.au, andrew.loch@csiro.au

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Abstract

The chrysomelid beetle *Cadmus excrementarius* has recently been observed as a pest in south-western Australian blue gum (*Eucalyptus globulus* ssp *globulus*) plantations. The insect was first recorded from Western Australia in 1904 and has since been found at over 30 different locations in the State. Seven host species from the genera *Eucalyptus* and *Corymbia* have been recorded in Western Australia. Most records of *C. excrementarius* adults were in the months of January to March. The insect mainly occurs on blue gums in the area bounded by the jarrah (*Eucalyptus marginata*) forest, where it may persist on flooded gum (*Eucalyptus rudis*) and to a lesser extent marri (*Corymbia calophylla*). *E. marginata* appears to be a less preferred host for *C. excrementarius* beetles, because its leaves were significantly less consumed than those of *E. rudis* and *C. calophylla*. Some observations on the natural history and predators of this beetle are presented.

Keywords: *Cadmus excrementarius*, beetle, Chrysomelidae, Cryptocephalinae, eucalypt, blue gum plantation, pest, jarrah forest

Introduction

Chrysomelid beetles are recognised as one of the most serious insect problems associated with fast-growing eucalypt plantations in several Australian states, due to the propensity of these insects to feed on newly expanded foliage (Elliott *et al.* 1998). Feeding damage to the new season's foliage often leads to the characteristic 'broom-topped' appearance of trees resulting from removal of the apical crown. Extreme levels of defoliation by chrysomelids have been shown to cause significant reductions in tree height, diameter and volume, and also potential growth malformation (Candy *et al.* 1992; Elliott *et al.* 1993; Elek 1997).

The cryptocephaline chrysomelid, *Cadmus excrementarius* Suffrian, was first reported in Tasmanian blue gum, *Eucalyptus globulus* ssp *globulus*, plantations in south-western Australia by Abbott *et al.* (1999), during their study of canopy arthropod faunas that was carried out between 1993 and 1994. It was not initially regarded as a serious pest, but it is now one of the major chrysomelid pests of Tasmanian blue gum plantations in south-western Australia (Loch & Floyd 2001). Only the adult stage of *Cadmus* species feeds on eucalypt leaves; the larval stage lives on the ground in an ovoid case made of faecal matter, and feeds on litter and recently fallen leaves (Reid 1999a, b). The congeneric beetles, *C. crucicollis* (Boisduval) and *C. nothus* Lea, occur in the jarrah forest (Abbott 1995) and have also been collected from Tasmanian blue gum plantations in south-western Australia, although they are much rarer than *C. excrementarius* (AD Loch, unpublished data).

An understanding of the ecology and behaviour of *C. excrementarius* is critical if this pest is to be managed effectively. The purpose of this paper is to report on the geographic and temporal distribution of this species in south-western Australia. Some observations on natural history, natural enemies and host range are also made. A further paper reports on its pest status in Tasmanian blue gum plantations (dos Anjos *et al.* 2002).

Materials and methods

Field trips throughout south-western Australia were conducted by NDA between January and November 2001, during which searches were undertaken for *C. excrementarius* adults and larvae in both blue gum plantations and native forests. Insect collections were also inspected in the Western Australian Museum, WA Department of Conservation and Land Management, WA Department of Agriculture, and Curtin University of Technology. Records of *C. excrementarius* were also supplied by C A M Reid (Australian Museum), and taken from scientific papers and from unpublished data provided by ADL. All records were geocoded and a map showing the species' geographic distribution throughout Western Australia was prepared using Range Mapper® V 2.0. In addition, the host, year and month of capture of all records were noted.

An experiment was conducted under field conditions in a blue gum plantation at Rocky Gully (34° 32' S, 117° 01' E) to examine whether there was any feeding preference between the three principal native tree species in the region and blue gum. A single, newly expanded, undamaged leaf of either blue gum, flooded gum, *Eucalyptus rudis*, marri, *Corymbia calophylla*, or jarrah, *Eucalyptus marginata*, was removed and inserted in a series of 150 ml vials filled with fresh water (n = 14 for each species). One female beetle was confined to the leaf by means of a plastic mesh sack that was clipped around the top of the vial. The leaves were exposed to the beetles for 48-hours from March 1 2001, and were then removed and stored in cool, moist conditions. The leaf shape was subsequently traced on green tissue paper and the shape of the undamaged leaf was recreated. The surface area of the paper model and the leaf remains were then measured using a Macintosh® computer scanner and the amount of leaf area eaten was determined by calculating the difference in the two areas. The leaf area of each tree species that was consumed by one female beetle was then compared by one-way ANOVA and differences between means were assessed using Duncan's multiple range test.

Morphological and behavioural aspects of each biological phase were noted, both under field conditions at Rocky Gully and in the glasshouse at Curtin University, Perth. Larvae were maintained in the glasshouse in an 80x40x40 cm glass tank filled with sandy soil, jarrah litter, and blue gum seedlings. Larvae collected from the field in April and June were also reared in petri dishes; they received fresh leaves three times a week. Field observations on larvae and observations on adult feeding, mating, oviposition and natural enemies were carried out throughout 2001. From 2-4 March 2001, ten wooden plates (10x10 cm) were placed on the ground at 10 m intervals inside both the Rocky Gully blue gum plantation and jarrah forest. Twenty egg scatoshells (eggs encased in faecal material) were then placed on each plate for 48 hours to observe predators. Plates were inspected every 2-3 hours during both day and the evening, and predators were collected.

Figure 1. Sites from which *Cadmus excrementarius* (•) has been collected in Western Australia. The thick line shows the boundary of the jarrah forest region (after Dell & Havel 1989).

Results

Geographic distribution in Western Australia

C. excrementarius was recorded at over 32 different sites in south-western Australia, ranging from latitudes 30° 22' S to 34° 58' S and from longitudes 115° 38' E to 123° 52' E (Fig 1). All but five of the sites were within the jarrah forest region. The exceptions were the Kalannie, Balladonia, Borden, Dumbleyung and Broomehill records, which were from eucalypt woodlands.

Temporal distribution in Western Australia

Adults of *C. excrementarius* were first collected in South Perth and Denmark at the beginning of last century, after which there were no records for about 60 years. Increasing numbers of records of this species started to appear in the early 1990s (Fig 2). More than 80% of the new records were made in 2000 and 2001, and more than half (53%) were in 2001. *C. excrementarius* adults have only been collected in Western Australia between December and June. Most adult records (87%) were for January, February and March, with more than half (57%) from February.

Host plants

C. excrementarius has been recorded from seven host species from the genera *Eucalyptus* and *Corymbia* in Western Australia. These include Tasmanian blue gum, jarrah, marri, WA flooded gum, tuart (*E. gomphocephala*), Dundas mahogany (*E. brockwayi*) and oil mallee (*E. kochi*). Host age was only known for *E. g.* ssp *globulus*, which varied from 6 months to 5 years, with more cases (71%) on trees in the first to fourth years of age. *C. excrementarius* has also been recorded from *E. largiflorens* near Swan Hill, NSW.

Feeding preference

The area of leaves consumed by *C. excrementarius* beetles differed significantly for *E. rudis*, *E. g.* ssp. *globulus*, *C. calophylla* and *E. marginata* ($F_{3,47} = 3.57$, $P = 0.02$). Mean area consumed was 318.67 mm² (n = 13) for *E. rudis*, 292.37 mm² (n = 14) for *E. g.* ssp *globulus*, 239.83

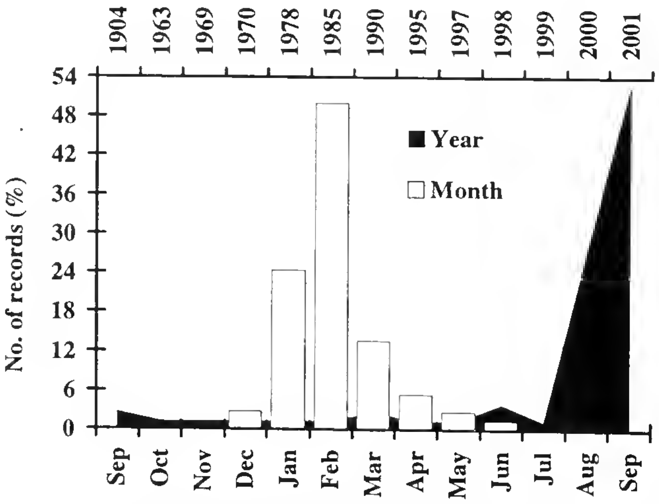

Figure 2. Collection records (months and years) of adult *Cadmus excrementarius* in Western Australia.

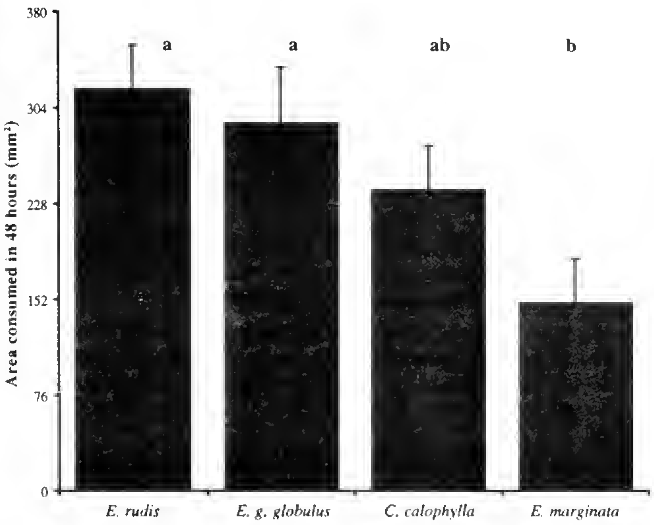

Figure 3. Mean (± se) leaf area consumed by single *Cadmus excrementarius* females on four different tree species. Means annotated with different letters are significantly different from each other ($P < 0.05$ by Duncan's multiple range test).

mm^2 (n = 14) for *C. calophylla*, and 150.30 mm^2 (n = 11) for *E. marginata*. Amounts of *E. rudis* and *E. g.* ssp *globulus* consumed were similar but significantly greater ($P < 0.05$) than that of *E. marginata*. *C. calophylla* was intermediate in this regard (Fig 3).

Natural history

C. excrementarius adults generally begin appearing in plantations during late December and January (ADL, unpublished observations), but under warmer greenhouse conditions in this study they started to emerge in November. Before emerging from its faecal case, the adult gnaws a circular opening to escape. They mostly exit the case in the morning, when day temperatures are increasing. Observations on larvae in petri dishes indicated that males started to emerge one day before females. One male can mate with more than one female, and females can copulate with two or more males during the same day. Duration of mating was 31.9 ± se 1.5 minutes (range 16-55 minutes, n = 17). Females started laying eggs the following day and produced 17.8 ± se 1.3 eggs female^{-1} day^{-1} (range 2-54, n = 24). Eggs were produced during day and night over several days, with a cumulative production of between 8 to 168 eggs per female (n = 6) over 9 days of laboratory observation.

Under field conditions, female beetles fed voraciously, stopping regularly to lay eggs and coat them with faecal residues; males tended to mate and then rest, spending little time feeding. The egg of *C. excrementarius* is yellow, oblong (1.1 ± 0.02 mm long and 0.4 ± 0.02 mm diameter; n = 24), has a soft chorion, and is encased in a rough brownish scatoshell. Newly built scatoshells are 1.7 ± 0.05 mm long and 1.1 ± 0.01 mm diameter (n = 35). Scatoshells are dropped on the ground beneath trees where the female feeds. Simulated rain in the glasshouse colony indicated that eggs hatch about 3 days after contact with moisture.

During the egg stage, scatoshells were frequently removed by ants, which took them to their nests. In the blue gum plantation, 47.5% (range 5-100%) of egg scatoshells were removed by ants, while in the jarrah forest only 6% (range 0-20%) were removed. Ants removing egg scatoshells in the blue gum plantation were *Rhytidoponera metallica* (F Smith) and *Pheidole ampla perthensis* Crawley, whereas those in the jarrah forest were *Rhytidoponera violacea* (Forel), *Monomorium sordidum* Forel, *M. sydneyense* Forel, and *Iridomyrmex chasei* Forel.

The egg scatoshell is retained as a case after the larva hatches, as in all Cryptocephalinae (Reid 1999a), and builds up with faecal residues as the larva grows. Full-grown cases may be 11.3 ± 0.2 mm long and 5.2 ± 0.1 mm wide (n = 32). Larvae feed gregariously on decaying leaves and other litter components, such as bark and twigs. Under glasshouse conditions, they will also feed on fresh leaves. Under moist conditions in the field, larvae were seen climbing on the basal part of saplings to feed on live leaves, but under dry soil conditions the larvae remained in groups (1-28, n = 46) under decaying leaves. In addition to being found in blue gum plantations, larvae were observed feeding on decaying leaves underneath *E. rudis*.

Before pupation, the larva inserts the opened side of the case into the ground and fixes part of the case inside the soil. It then blocks the case entrance with faecal residues and turns its head back to the upper side of the case before pupation. The exuvium is released on the bottom of the case. Under glasshouse conditions, larvae stopped feeding during 15-21 October 2001 and adults started emerging on November 22 2001. In petri dishes, they stopped feeding between 5-11 November 2001, and adults started emerging on December 6 2001. The pupal period is approximately 4 weeks in duration.

Under glasshouse conditions, pupae were attacked by fungus and mites (Pyemotidae), which sometimes killed the insects. Under field conditions, adult beetles were preyed upon by bugs (Reduviidae) and by a small spider (Theridiidae).

Discussion

C. excrementarius is extremely widespread in semiarid/arid southern Australia from Cunnamulla, Qld through NSW, VIC, SA to south-western WA (C A M Reid, Australian Museum, personal communication). However, in WA *C. excrementarius* appears to be generally distributed in forested areas under a Mediterranean climate. The records from Kalannie, Balladonia, Borden, Dumbleyung and Broomehill, indicate the presence of outlying populations of *C. excrementarius* in woodland or mallee areas. If this species is more widespread in WA than indicated by current records, it may be because of lower levels of collecting in other parts of Western Australia.

In south-western Australian blue gum plantations, *C. excrementarius* tends to be concentrated from Boyup Brook through to the east of Albany, where plantations are interspersed between fragments of jarrah forest. As all records of *C. excrementarius* in blue gum plantations were for sites inside jarrah forest, proximity of plantations to native forest could be a contributing factor to this problem, as suggested by Abbott *et al.* (1999) and discussed by Loch & Floyd (2001). The increased frequency of *C. excrementarius* collections in the last 2 years mainly reflects increased collecting intensity in blue gum plantations in south-western Australia. In addition, the rapid rise of the blue gum plantation industry has been associated with a corresponding increase in *C. excrementarius* occurrence, as it has with other insect problems (Loch & Floyd 2001).

E. marginata appears to be a less preferred host for *C. excrementarius* beetles, because its leaves were significantly less consumed than those of *E. rudis* and *C. calophylla* (see Fig 3). Similarly, Hall (1992) found distinct preferences of other chrysomelids for *E. rudis* and *C. calophylla*, rather than *E. marginata*. This is consistent with Majer & Recher's (1988) observation of significantly lower invertebrate populations on *E. marginata* than on other tree species. The jarrah forest is dominated by *E. marginata* and *C. calophylla*, with some areas of *E. rudis* and other species (Dell & Havel 1989). According to this study, *E. rudis*, whose leaves have higher concentrations of nitrogen, phosphorous and potassium (Abbott *et al.* 1993), appears to be the most favoured native host in the jarrah forest and could be the main source of *C. excrementarius*. To a lesser extent, *C. calophylla*, and other eucalypt species could also harbour populations of this beetle. Another important reason to expect pressure on blue gum plantations is the period of adult *C. excrementarius* activity (Fig 2), which coincides with the dry season in south-western Australia. At this time of the year, native eucalypts have few fresh or tender shoots but blue gum saplings, which grow vigorously at this time of year, are highly suitable as an alternative food source. This could be a further contributing factor to the incidence of this pest in south-western Australian blue gum plantations.

Eggs are typical of Cryptocephalinae beetles (Erber 1988) and are preyed upon by a group of ants, which are known seed collectors; possibly these ants are mistaking the eggs for seeds. Sites inside the plantation seem to exhibit more egg predation and by different species of ants than those inside the jarrah forest. Larvae of this species, and other Cryptocephalinae, may also be killed by fungi and mites (C A M Reid, Australian Museum, personal communication).

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Pollen limitation of fruit set in Western Australian terrestrial orchids

C P Elliott[1] & P G Ladd

School of Environmental Science, Murdoch University, Murdoch WA 6150
[1]Present address WA Herbarium, Department of Conservation and Land Management,
Locked Bag 104, Bentley Delivery Centre WA 6983
email: carolee@calm.wa.gov.au

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Abstract

Hand pollination was used to test whether fruiting success in six Western Australian terrestrial orchid species is limited by the availability of pollen. Open pollination controls all had a lower production of fruit than hand pollinated flowers. Species offering nectar had a higher open pollinated fruiting success (*Lyperanthus serratus*, *Prasophyllum elatum* and *Prasophyllum fimbria*) than those that did not (*Caladenia flava* and *Diuris brumalis*). One species (*Pterostylis recurva*) had almost equivalent fruit production for hand and open pollination, and may be resource limited as its habitat was the most heavily shaded. The results of this investigation confirm that similar processes seem to be operating in the environmentally similar, but widely separated, areas of the Cape of South Africa and the south-west of Western Australia.

Keywords: pollination, fruit limitation, necter reward, orchid, terrestrial, Western Australia

Introduction

Fruit set in many plants is considerably less than the number of flowers apparently available for fertilization. Many studies have examined this phenomenon and provided proximate and ultimate reasons for why this might occur (Bierzychudek 1981; Ayre & Whelan 1989). Two main areas were identified. The first is resource limitation, where the number of fruits is limited by the amount of nutrients or carbohydrates that can be supplied by the maternal plant. The second is pollen limitation where there is a lack of suitable pollen supplied to flowers to ensure fertilization (Burd 1994; Johnson & Bond 1997).

In some mediterranean ecosystems, pollinators seem to be very abundant (*e.g.* Whelan & Burbidge 1980; Coetze & Giliomee 1985; Horskins & Turner 1999) so that low soil nutrients may be limiting for species that heavily invest their seeds with scarce mineral nutrients (Pate *et al.* 1986). However there are also systems in which pollinators seem relatively rare, particularly at some times of the year, so that receipt of appropriate pollen may limit successful fruit set (Dafni 1984; Johnson & Bond 1997). Several studies on the pollination of eastern Australian orchids (both sexually and florally deceptive species, and those with rewards) have revealed that some are pollen limited (Bartareau 1995; Dafni & Calder 1987; Jones 1972; Neiland & Wilcocks 1998; Sydes & Calder 1993).

In Cape fynbos, pollen limitation is a very common cause of low seed set (Johnson & Bond 1997). Pollinators, at least for some groups, seem to be scarce. As an example, at least 15 red-flowered fynbos species rely for pollination on the butterfly *Meneris tulbaghia* (Cowling & Richardson 1995). In south-west Western Australia, the vegetation is very similar to that of the Cape, with many parallels in structure and function (Cowling *et al.* 1994). If pollen limitation in fynbos is prevalent, then is this also the case in the south-west of Western Australia? This study aimed to examine this question using a set of six orchid species of common occurrence in the Perth area of Western Australia.

Methods

Six species, from five genera with a range of pollination systems, were chosen from areas close to the Perth metropolitan region in Western Australia where orchid species were known to flower in reasonable numbers (Table 1). Orchid population density was determined by the T-square sampling procedure (Krebs 1989) or from quadrats. Canopy projective cover was determined from analysis of digital images taken vertically upwards with a camera 1 m from the ground, at ten randomly chosen points along a transect through the area where each species grew (Table 1).

Orchid pollen coheres to form a pollinium, generally found near the top of the column, attached to a small sticky button called the viscid disc (Hoffman & Brown 1998). The structure was easy to remove with tweezers and place on another flower's stigma. Xenogamous pollinations were between flowers on plants at least several metres apart to ensure outcrossing beyond clones.

Between 10 to 20 plants were tagged in a population, with 40 flowers being randomly assigned to a control or experimental group. As this study only aimed to test if pollen delivery was limiting fruit production, flowers were not bagged. None of the species spontaneously self-pollinated. Fruit set was recorded about 5 weeks after pollination. In some cases the flowers on the plant died, reducing the number of flowers available for assessment. Fruit set is the most efficient measure of female success in orchids, which have thousands of microscopic seeds (Johnson & Bond 1997).

Table 1

Location and attributes of the orchid populations.

	Caladenia flava	***Diuris brumalis***	***Diuris brumalis***	***Pterostylis recurva***	***Lyperanthus serratus***	***Prasophyllum elatum***	***Prasophyllum fimbria***
Location	32° 3′ 1.4″ 115° 56′ 4.0″ Canningvale, corner Nicholson Rd and High Rd	31° 53′ 17.0″ 116° 13′ 9.7″ Mt Helena, Dowie Rd	31° 53′ 14.0″ 116° 13′ 21.4″ Mt Helena, Dowie Rd	32° 5′ 23.7″ 116° 3′ 45.3″ Rolystone, Douglas Rd	32° 6′ 2.7″ 116° 3′ 23.5″ Rolystone, Robinson Rd	32° 5′ 46.3″ 116° 2′ 51.9″ Rolystone, Canning Mills Rd	32° 3′ 0.5″ 115° 56′ 1.9″ Canningvale, corner Nicholson Rd and High Rd
Habitat	Degraded open eucalypt woodland	Degraded semirural (mostly cleared)	Degraded open eucalypt woodland	Casuarina – eucalypt forest	Degraded eucalypt open forest	Eucalypt woodland	Recently burnt heathy swamp
Date of pollination	9 October	8 July	8 July	9 October	9 October	9 October	9 October
Time to fruit set	5 weeks	6 weeks	6 weeks	5 weeks	5 weeks	5 weeks	5 weeks
Canopy cover (%)	8.2 ± 4.4	7.8 ± 5.5	29.6 ± 10.5	57.4 ± 7.2	49.4 ±8.9	3.5 ± 2.3	0
Density (m^{-2})	1.5	3.6	3.0	0.1	0.3	Two colonies of 4 - 5	0.6
Range (m^{-2})	1.0 – 2.9	2.5 – 6.1	1.7 – 13.7	0.1 – 0.2	0.2 – 1.3	-	-
Number of plants used	17	40	40	40	24	10	10
Number of flowers used	34	40	40	44	40	40	40
Flower death (%)	0	10	0	36	10	55	0
Nectar	-	-	-	-	+	+	+
Perfume	-	-	-	-	+	+	+
Flower visitors*	beetles	Native bees	Native bees	Mosquitoes, flies	Weevils, bees, moths	Bees, flies, beetles, wasps	Bees, flies, beetles, wasps
Flower visitors (this study, [1] = pollinium adhereing)	-	-	-	Midge[1]	Brown weevils	Black beetles	Gnats, bupestrid beetle[1]

* (Bernhardt 1990; G Brockman, personal communication; A Brown, CALM, personal communication; Brown *et al.* 1997; Hoffman & Brown 1998).

Results

The orchid species had a range of pollination systems and pollinators, and grew in a number of vegetation types, from forest to wet heathland (Table 1). Three species (*Prasophyllum elatum, P. fimbria* and *Lyperanthus serratus*) offered a food reward (nectar) to pollinators whereas the other species did not (Bernhardt & Burns-Balogh 1986; Coleman 1933; Hoffman & Brown 1998; Jones 1972). In *Prasophyllum* and *Lyperanthus* the nectar collects at the base of the labellum (Bernhardt & Burns-Balogh 1986; Coleman 1933; Hoffman & Brown 1998; Jones 1972). As well as nectar, these species have a strong fragrance.

Caladenia flava has a general attraction to pollinators via colour, while *Diuris brumalis* is considered to mimic Fabaceae species (Adams & Lawson 1993; Beardsell *et al.* 1986; Dafni & Bernhardt 1988; Nilsson 1992). Nothing specifically is known about the method of attraction to *Pterostylis recurva*, except that it may exploit flies which are dependent on winter mushrooms, or may attract flies via its opaque colour (Bernhardt 1990; A Brown, CALM, personal communication)

Plant densities ranged from approximately three plants m^{-2} for colonial species to 0.1 plants m^{-2} for solitary species (Table 1). Most of the species do not have episodic flowering. However, *P. elatum* and *P. fimbria* are stimulated to flower after fire (Hoffman & Brown 1984), and *P. fimbria* occurred in recently burnt vegetation in large numbers.

In all cases hand pollination increased fruit set compared with open pollinated flowers (Fig 1). Five species had between 80 to 100 % fruit set. Only *Pterostylis recurva* showed little difference between the hand pollination treatment and open pollination. The species that provided a food reward had a higher fruit set from open pollination than the other species, but *Pterostylis recurva*, which offers no nectar had almost equivalent results to those that do.

Discussion

A number of studies has compared Western Australian and southern South African systems and concluded that they have general similarities but

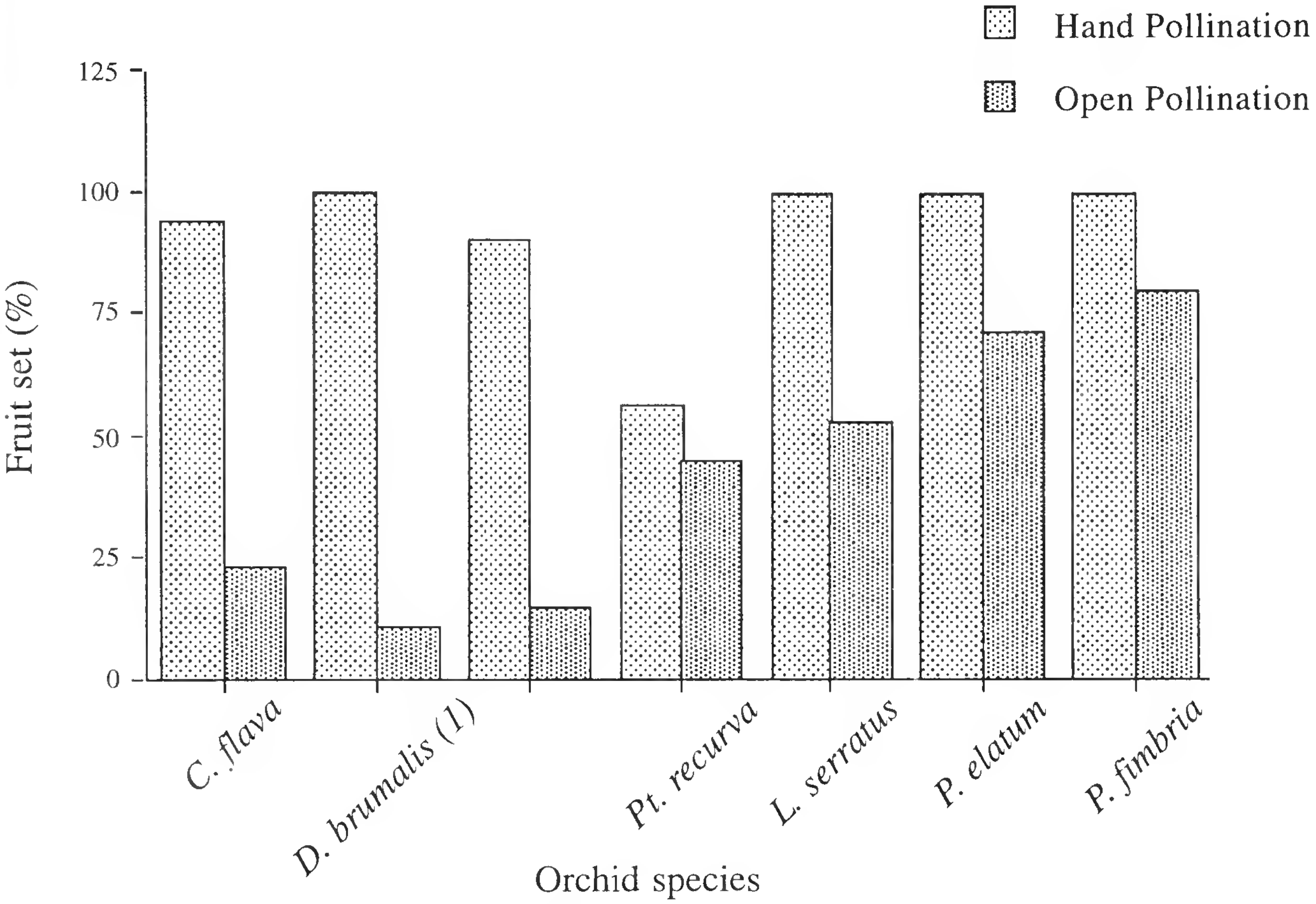

Figure 1. Fruit set of hand and open pollinated orchid species.

differences in some specific areas (Cowling *et al.* 1994). A South African study of the pollen limitation of Cape wildflowers by Johnson & Bond (1997) found that fruit set was frequently limited by pollen availability. The pollen limitation of fruit set in five of the six terrestrial orchids examined here agrees with Johnson & Bond's (1997) model. Therefore the Western Australian system appears to operate similarly to the South African system, at least in relation to orchids.

Our study also confirmed the generalisation from other orchid studies that species with pollinator rewards show higher fruit set than deceptive or mimic species (Johnson & Bond 1997; Neiland & Wilcocks 1998). However one species *P. recurva* which grew in a very shaded site showed little increase in fruit set with supplemental pollen. This may indicate resource limitation in the low light environment. Most *Pterostylis* species tend to grow in shaded sites (Ladd, personal observations) and may also show similar resource limitation of fruit set.

Caladenia flava is a general food mimic orchid that attracts foragers with dummy structures devoid of either nectar or pollen. The *C. flava* plants were in the same general area as *P. fimbria*, and the contrast between the reasonable natural capsule set of the nectar producer and the absence in the general mimic is striking (Fig 1). There were few yellow flowered species in the area at the time the orchids were flowering which could have acted as models for *C. flava*.

The genus *Diuris* shows elements of Batesian mimicry, as its species mimic papilionoid legumes such as *Daviesia* and *Oxylobium*, and the orchids are pollinated by bees that utilise pollen and nectar offered by these legumes (Adams & Lawson 1993; Dafni & Bernhardt 1988; Nilsson 1992). Pollination effectiveness should be greatest when a low density, non-rewarding species mimics the flowers of a model species offering copious rewards at a much higher density (Dafni 1984; Weins 1978). This was found in *Thelymitra antennifera* (Dafni & Calder 1987) and in *Orchis* (Dafni & Ivri 1981). The very low natural capsule development in the *Diuris* correlated with a complete lack of nearby flowering legume shrubs at the study sites in 1999. The low fruit production found in this investigation was similar to the very low pollinia deposition by relevant insects for *Diuris maculata*, another Western Australian species (Beardsell *et al.* 1986).

Many Australian terrestrial genera, such as *Prasophyllum*, are stimulated to flower in increased numbers after fire. However, Adams & Lawson (1993) could find no reports on the effects of fire on pollinator activity or pollination rates. In this study *Prasophyllum fimbria* was in an area that had been burnt in the previous summer, and was flowering abundantly, compared to the other species. The observation that large numbers of fruit were produced by the species after fire indicates that the nectar reward was a strong lure for insects to repopulate the area. However *Lyperanthus* does not require fire to induce flowering (Hoffman & Brown 1998), indicating that nectariferous species may also be successful in undisturbed vegetation.

Populations of plants are increasingly subjected to size reduction and fragmentation through human action. Some studies show plants in smaller populations generally receive fewer visits from pollinators and the availability of pollen may become limiting for fruit set (Briggs & Leigh 1996; Lamont *et al.* 1993). While there are examples where species populations are buffered against pollinator loss (Bond 1994), this may only be short term. Cunningham (2000) investigated the fruit set efficiency of *Acacia brachybotrya* and *Eremophila glabra* in linear strips of vegetation and those in bigger fragments. It was found that a depressed pollination in the linear strips of vegetation occurred, causing lower fruit set than for the same species in the larger reserves. Similarly in a study of an orchid (*Pterygodium catholicum*) the plants in a small remnant native vegetation patch showed no seed set while populations in a larger remnant did set low numbers of fruit (Donaldson *et al.* 2002). If the situation of depressed pollination occurs widely in orchids, particularly non-nectariferous species which are extremely pollen limited under natural conditions, the system will be heavily impacted and conservation biology of such species will need to consider how to improve pollination effectiveness.

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Comparison of the vegetation of the islands in Shoalwater Bay (Rockingham, Western Australia) with that of the coastal bushland

E Rippey[1,2], J J Rippey[2], B Green[2] & J N Dunlop[2]

[1]Department of Geography, University of Western Australia. Crawley WA 6009
[2]Friends of the Shoalwater Islands Marine Park, % Rockingham Environmental Centre,
Safety Bay Road, Rockingham WA 6168
email: jjrippey@cyllene.uwa.edu.au

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Abstract

Surveys were conducted of the vegetation of three areas in and around Shoalwater Bay: a strip of foreshore (Mersey Point), a headland (Point Peron), and a string of islands. Each survey area measured about 15 ha. The differences between the two mainland reserves and the islands are of particular interest. Only 23% of the plant species recorded occurred in all three reserves. It appears that human activities have been directly responsible for many of the changes in the flora of the mainland reserves, while seabirds influence the plant cover of the islands. At Mersey Point, a large proportion of species appear to have been introduced by the dumping of garden rubbish. At Point Peron, the vegetation has been affected by frequent fires, so that fire-resistant species are favoured. On the islands, seabirds play a major role in determining the nature of the vegetation by virtue of their trampling and the guano that they deposit. The findings of this investigation provide a baseline for further monitoring and for evaluation of future management measures.

Keywords: Shoalwater Bay, coastal vegetation, island vegetation, Western Australia

Introduction

Shoalwater Bay lies off the west coast at Rockingham, 50 km south of Perth. It is enclosed to the east by the mainland beach, to the west by a string of small islands, and to the north by the Point Peron Peninsula (Fig 1). Mersey Point Reserve, a narrow foredune strip occupying the southern end of the mainland beach, Point Peron the rocky headland at the tip of the Cape Peron Peninsula, and the vegetated islands (Penguin, 12.5 ha; Seal, 1.2 ha; Bird, 0.9 ha; Middle Shag, 0.4 ha) make up the three reserves under consideration. Each covers about 15 hectares. All three areas have been registered as regionally significant under the state Bush Forever programme (Anon 2000).

The aim of this study was to survey the flora of the three reserves, to investigate the reasons for differences between them, and to look at the management implications. Bushland remnants are considered valuable for two main reasons (Briggs 1984). The great majority of the Perth metropolitan area has been cleared, and these remnants provide the best indication available of the composition of the pre-existing vegetation at any particular site. The reserves also provide habitat for native fauna, that is of particular value if there are links by corridors to other bushland remnants. Such links effectively enlarge the area of bushland, providing a larger genetic pool for uncommon species with the corridors allowing free movement of birds, pollinators, seed distributors *etc*. Point Peron and Mersey Point Reserves both have links with other bushland, as they form the extremities of a 200 ha reserve, albeit with narrow corridors.

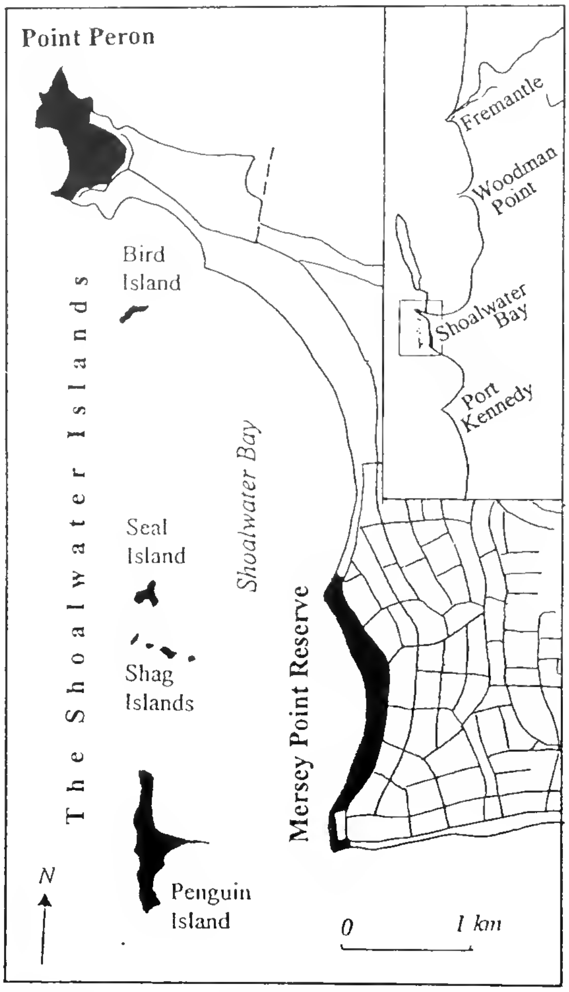

Figure 1. Locality map showing Shoalwater Bay surrounded by Mersey Point Reserve, Point Peron and the Shoalwater Islands.

Work on urban bushland shows that bush remnants suffer constant disturbance, mainly associated with human activities such as increasing fragmentation by paths and clearings, enrichment of the naturally low nutrient soils, frequent fires and the introduction of exotic species, both plant and animal (Piggott & Loneragan 1995). Some disturbance appears to be necessary to maintain species diversity, but frequent or intense disturbance decreases diversity (Hobbs & Huenneke 1992).

The Shoalwater Bay Reserves have all been subject to a century of severe disturbance. Holiday makers have used the area extensively and their activities were largely unrestricted until the late 1980s. Much of the surface of all three areas has been denuded at various times. The central eastern part of Mersey Point Reserve, which originally consisted of high dunes, was bulldozed level in the 1960s to allow ocean views and easy access to the sea for the developing suburbs of Rockingham. Point Peron was the site of an artillery battery during World War II. On Penguin Island the north and south plateaux were scraped clear by guano collectors early in the twentieth century (Chape 1984) leaving large areas still denuded in the 1950s. Human impacts are less dramatic at present, particularly on the islands, where the only access permitted is to parts of Penguin Island. Despite this protection, however, the islands are especially vulnerable to disturbance, as they form what is effectively a fragmented reserve with a very high edge to area ratio. Mersey Point also has a high edge to area ratio owing to its elongated shape.

For the three Shoalwater Bay Reserves, disturbance falls into three main categories, fire, nutrient enrichment and weed invasion.

Fire

The frequency of fire in bushland areas in Perth can be correlated with proximity to urban development and the level of human activity (Piggott & Loneragan 1995). Kings Park experienced 10 fires *pa* between 1944 and 1994 (Dixon *et al.* 1995), Star Swamp Bushland Reserve about one *pa* between 1948 and 1987, and still fewer occurred at the outlying Woodman Point and Yule Brook Reserves (Piggott & Loneragan 1995). About 50% of fires in Kings Park are the result of arson (Dixon *et al.* 1995), and for the Perth region as a whole 30% of fires are arson-related with another 30% having escaped from control burning or burning of rubbish (Robley 1983). The responses of different native species to fire differ (Wycherley 1984), and frequent burning can change the composition of the flora. Species that can respond rapidly are advantaged, particularly native species capable of resprouting such as *Acacia rostellifera*, and exotic species of both annuals and resprouting perennials. The most vulnerable species are obligate reseeders that are killed by fire, such as *Templetonia retusa*. These take several years to replenish the seedbank and progressive loss of species can result from repeated burning (Ford 1985). Fire is not common on the offshore islands, and there is no record of wildfire on the Shoalwater Islands.

Soil enrichment

Here again the processes on the islands are very different from those in the mainland reserves. On the mainland the native plants are suited to soils that are naturally low in nutrients, and enrichment occurs as a result of human action, for example, through fertiliser run-off from adjacent grassed areas or from dumping of garden rubbish (Hobbs 1995a). Mersey Point is at risk as it encompasses several pockets of lawn and the reserve lies opposite a row of suburban gardens.

On the islands the situation is different. Some of the problems of lawned areas adjacent to bushland probably exist around the lawn on Penguin Island, but there is enormous enrichment of much of the soil from the guano of thousands of seabirds, which use the islands for nesting and roosting. The number of pairs of pied cormorants (*Phalacrorax varius)* nesting on the islands has increased from a total of about 150, nesting on one island or another in the 1940s, to about 1000 distributed between all islands each year (Rippey *et al.* 2002a). Pelicans (*Pelecanus conspicillatus*), the other major guano producers of the region, have nested here since 1999 and silver gulls (*Larus novaehollandiae*), none of which nested on Penguin Island in the 1940s (Serventy & White 1943) now number thousands of pairs (Dunlop *et al.* 1988).

Little has been written on the ecology of Perth's seabird islands compared with that of urban bushland areas, but an ecological cycle was described by Gillham (1961). She suggested that the climax community of native shrubs, including *Nitraria billardierei*, was damaged or killed by trampling and droppings during a nesting episode, and was replaced by coprophilic native species, especially *Malva australiana*, until recovery of the climax community occurred. Further nesting sometimes left nothing but annual weeds or even bare ground, at which stage the area became unsuitable for nesting, and recovery commenced.

Weed invasion

Over 1000 introduced plant species have become naturalised in Western Australia, more than half of which are present in bushland (Keighery 1994) or natural ecosystems and are termed environmental weeds (Humphries *et al.* 1991). Key stages in the establishment of weeds have been identified (Anon 1999) whereby species are introduced, become established, produce a large number of propagules, and after what may be a considerable time lag, disperse, sometimes through 'nascent foci' of outlying populations (Hobbs & Saunders 1995).

The ability of exotic species to invade is a function of the characteristics of both the species and the site invaded (Hobbs & Huenneke 1992). Davis *et al.* (2000) suggest that a surplus of available nutrients in an area underlies invasion, and Hobbs (2000) refines this by suggesting that disturbance which increases the supply of a limiting resource favours invasion. While disturbance can take many forms (for example fire, grazing, soil disturbance, nutrient inputs, trampling, fragmentation), weed invasion is particularly enhanced by a combination of soil distubance and increased nutrients (Hobbs & Huenneke 1992).

Plant invasion can affect the environment at three levels. At the genetic level the number of individuals of native species can be reduced below the minimum necessary for persistence, at the species diversity level the number of species present and their distribution can be reduced, and at the ecosystem level the functioning of the ecosystem can be changed. Thus the ability of native species to survive, and their abundance, can be reduced, fire regimes can be altered, and even nutrient cycling, hydrology and energy budgets can change (Mack *et al.* 2000). Geomorphological processes can also be altered, and the problems of plant invasion and the difficulty of repair are greatest where ecosystem function is damaged (Anon 1999).

Locality and Methods

During 1997-1999, the Friends of the Shoalwater Islands Marine Park conducted botanical surveys of the Mersey Point reserve, Point Peron and the Shoalwater islands. The names of non-native species are preceded by an asterisk (*).

Locality

The reserve at Mersey Point consists of a narrow foreshore 1.6 km long between the beach and the sea-front houses of Rockingham. Point Peron has a coastline of rugged cliffs with a beach to the south-west, and undulating dunes to the east. The islands consist mainly of sandy plateaux surrounded by cliffs up to 5 m high undercut by the sea, and talus slopes where caves have collapsed. There is a west-facing beach on Penguin Island and eastern beaches on Penguin and Seal Islands.

The geology of the area consists of aeolianite limestone overlain by calcareous sand dunes. The islands and Point Peron are remnants of a limestone ridge, parallel to the mainland, partially inundated at the start of the Holocene. The ridge eroded and the sand was deposited on the mainland shore ten kilometres to the east. The mainland coast has prograded during the Holocene to within a kilometre of the string of islands, which are now linked by sandbars, and in the case of Point Peron by a peninsula, to the mainland. The sandbar to Penguin Island from Mersey Point can be crossed on foot at low water.

Climate

The climate is Mediterranean with over 800 mm rain *pa*, falling mainly in the cool winter months, while summer months are dry, windy and hot with daily maximum temperatures averaging 30 °C in January and February. Salt is blown in from the sea and some 200 kg is deposited on every hectare annually (Hingston & Gailitis 1976). All three areas are subject to the influence of waves and the prevailing south westerly winds.

Tenure

Mersey Point is a C Class reserve vested in the Shire of Rockingham for the purpose of recreation. The reserve encompasses three car parks, one with a tea-room and landscaped garden, one with an informal boat ramp, and the third with a lawned picnic area. There are several walkways to the beach.

Point Peron is a C Class reserve vested in the Ministry for Sport and Recreation for the purpose of recreation. It is managed by the Department of Conservation and Land Management under a Cabinet Agreement pending completion of a management plan. Rehabilitation work has been carried out recently, with revegetation and installation of paths and fences.

Penguin Island is an A Class reserve managed by the Department of Conservation and Land Management for the purpose of recreation. The smaller islands are A Class nature reserves for the conservation of flora and fauna. Public access is only permitted to Penguin Island, where visitors are restricted to the beaches, a lawned recreation area on the eastern tombolo, and two boardwalks between the eastern and the western beaches.

In October/November 1997 volunteers carried out a botanical survey of the islands in Shoalwater Bay. On Penguin Island, nine east-west transects consisting of a chain of plots 2 m wide by 5 m in length were used to record plant species and approximate percentage cover. Plants were collected and identified on the smaller islands with transects being carried out later by the authors on the longest axis on Middle Shag, Seal and Bird Islands. A herbarium of pressed plants was prepared and identification of the majority of species checked by the Western Australian Herbarium. Results (Rippey *et al.* 1998) are repeated here, with the addition of eight relics of earlier non-native plantings; **Araucaria heterophylla*, **Agonis flexuosa*, **Eucalyptus gomphocephala*, **E. utilis*, **Melaleuca lanceolata*, **M. nesophila*, **Tamarix* sp and **Ficus* sp.

A similar survey was conducted for the reserve at Mersey Point the following spring in October 1998 with four east-west transects. Follow-up collections were made later that month and in the following month with two traverses along the north-south axis. Species growing in watered, lawned areas were excluded.

One of the authors (BG) provided the initial plant list for Point Peron. She had organised the recent rehabilitation of the Point Peron reserve which involved research into the flora and collection of seed and cuttings for cultivation for later replanting. One east-west transect was carried out in October 1999. Numerous other visits were made to all three reserves during 2000 and 2001.

Plant nomenclature is taken from Paczkowska & Chapman (2000) and Bodkin (1993) in the case of **Agave attenuata* and **Sansevieria trifasciata*. Species lists were compared with lists of native species recorded from cuspate forelands situated to the north and south of the study area, Woodman Point (Powell & Emberson 1981) and Port Kennedy (Trudgen 1988) (see Fig 1).

In October 2001, soil samples were taken from Mersey Point, Point Peron, Middle Shag Island, the east and west parts of Bird Island and from the southern promontory and the eastern tombolo of Penguin Island. Samples could not be collected from Seal Island nor the northern promontory of Penguin Island as seabirds were nesting there throughout the spring. The sample from each area consisted of three cores of surface soil mixed together, each core measuring 5 cm in diameter and 10 cm in depth. Analysis was done by CSPB Futurefarm.

Results

Altogether 146 species were identified from the three sites, 76 species at the Mersey Point reserve, 86 species at

Table 1

Total number of native and alien species in each of the survey areas.

Location	Native	Alien	all spp
The islands	42	46	88
Mersey Point	28	48	76
Point Peron	40	46	86

Point Peron and 88 species on the Shoalwater islands (see Appendix). A total of 55 species (38%) were native and 91 (62%) were introduced. Mersey Point reserve has a higher proportion of introduced species than the other two areas (Table 1). About 23% of species collected are common to all three locations. This core group of 33 species consists of 18 native species (*Carpobrotus virescens, Alyxia buxifolia, Olearis axillaris, Senecio lautus, Rhagodia baccata, Threlkeldia diffusa, Lepidosperma gladiatum, Acanthocarpus preissii, Scaevola crassifolia, Conostylis candicans, Acacia cyclops, Acacia rostellifera, Myoporum insulare, Hardenbergia comptoniana, Spinifex hirsutus, Spinifex longifolius, Clematis linearifolia* and *Spyridium globulosum*) and 15 introduced species (**Tetragonia decumbens, *Trachyandra divaricata, *Arctotheca calendula, *Sonchus oleraceus, *Cakile maritima, *Euphorbia peplus, *Euphorbia terracina, *Fumaria capreolata, *Lagurus ovatus, *Pelargonium capitatum, *Romulea rosea, *Eucalyptus gomphocephala* (native to the Western Australian coast but planted in the areas surveyed), **E. utilis, *Stenotaphrum secundatum* and **Anagallis arvensis*).

These common species occur widely along the coast and the native species, in particular, account for the majority of the plant cover at the three Shoalwater reserves, and indeed for the coastal dunes of the Perth region. The natives are perennials and consist of 12 shrubs varying from prostrate to 5 metres tall, two climbers, one herb, two large grasses and a sedge. The aliens are mainly small annuals, with the addition of two low spreading perennials, two cormous species, a perennial grass and two trees.

Over 50% of the species recorded (77 of 146) only occurred in one of the three areas (Table 2). The differences between the numbers of native and alien plant species found at each location, and the numbers of each which are unique to that location, are not statistically significant using the χ^2 test (P>0.05).

Table 2

The number of species that only occur in one of the three survey areas.

Location	Unique Native	Unique Alien	Unique Total	Unique species as % of total species in that area
The islands	9	18	27	30%
Mersey Point	4	23	27	36%
Point Peron	7	16	23	27%
TOTAL	20	57	77	52%

Some species, such as **Araucaria heterophylla* (Norfolk Island Pine) and **Eucalyptus utilis* (Coastal Moort), are introduced species planted intentionally, while others such as **Eucalyptus gomphocephala* (Tuart) are native to the district but unlikely to be found naturally in this habitat. Bushland/urban interface areas such as these are often 'improved' and 'rehabilitated' over the years, thus it is not always easy to determine whether a species was brought in intentionally or arrived by chance.

Mersey Point

Of 76 species found at Mersey Point, 33 are the core species found in all 3 areas, and a further 35 are aliens, most which are common garden plants. Introductions include **Tropaeolum majus* (Nasturtium), **Agapanthus praecox* (Agapanthus), **Opuntia stricta* (Prickly Pear), **Lantana camara, *Senecio tamoides* (Canary Creeper), **Cynodon dactylon* (Couch Grass), as well as a reed and several fleshy rockery plants. One of these succulent plants **Cotyledon orbiculata* had not been recorded as a weed in the Perth area previously but is a noted weed of offshore islands near Albany. All these weed species are well established and many are spreading. **Opuntia stricta* is forming a small grove of about 25 plants. **Schinus terebinthifolia* (Japanese Pepper), **Leptospermum laevigatum* (Victorian tea tree) and **Rhamnus alaternus* (Buckthorn) are large shrubs or trees that appear to be spreading and are considered a threat elsewhere (Hussey *et al.* 1997).

Point Peron

Acacia rostellifera thickets cover most of the Point, particularly to the east, and introduced annuals, particularly **Euphorbia terracina* and grasses, form much of the understory. Native shrubs on the higher dunes include *Acacia cochlearis, Melaleuca huegelii, Templetonia retusa, Spyridium globulosum, Olearia axillaris, Solanum symonii* and *Anthocercis ilicifolia*. A weed unique to this area is **Echium plantagineum* (Paterson's curse).

The islands

Eighty eight species were recorded for the islands, 85 of which are found on Penguin Island (including 8 planted species). A total of 24 species occur on the smaller islands, including *Malva australiana, *Chenopodium album* and **C. murale* that were not recorded on Penguin Island.

Nitraria billardierei and *Rhagodia baccata* are natives that do particularly well on islands, but are less common (although widespread) along the mainland coast. *Nitraria* grows on the limestone talus slopes of all the Shoalwater islands. *Rhagodia* is a spreading shrub that covers a greater proportion of Penguin Island than any other species, although it is rare on the smaller islands.

Four Malvaceae are found on the islands. **Malva dendromorpha* is the dominant species on the small islands forming dense thickets 2 m high. **M. parviflora* forms restricted meadows on Penguin, Seal and east Bird Island. A few **M. linnaei* were located on Penguin Island. The native *M. australiana* was recorded in comparatively

Table 3

Soil composition in the three reserves; available nitrogen (nitrate N plus ammonium N), available phosphorus, and available potassium (mg kg^{-1}) and pH.

	N	P	K	pH
Mainland: Mersey Point	27	68	21	7.9
Point Peron	3	17	15	8.4
Penguin Is: southern promontory	19	314	34	7.7
eastern promontory	33	68	30	7.8
Bird Island west	288	771	259	7.1
east	477	767	1378	8.2
Middle Shag Island	499	850	737	6.7

small numbers on Middle Shag Island, and one plant was found on each of Seal and Bird Islands.

Most aliens on the islands are annuals, such as **Melilotus indica* and grasses **Lolium rigidum*, **Hordeum leporinum* and **Bromus diandrus* which can form lush meadows in the wet season. **Lycium ferocissimum* found on Penguin Island, is a dense thorny shrub which has survived attempts at eradication over three years.

Soils

Analyses of the soils taken from Mersey Point, Point Peron and the islands showed that available nitrogen, phosphorus and potassium levels tended to be very high on the small islands (Table 3).

Discussion

Inter-reserve comparisons can be helpful in assessing the completeness of the flora in particular sites if the reserves are similar in size, location, *etc* and if recording methods are similar. Two floral surveys have been done each at Woodman Point (80 ha) and Port Kennedy (1000 ha), which are cuspate forelands lying 18 km north and 9 km south of Shoalwater Bay respectively. Sixty-six native species were listed for Woodman Point by Powell & Emberson (1981) and a total of 161 species, of which 94 were native, by Keighery (2001). Fifty-five species, of which 46 were native, were recorded for Port Kennedy, excluding those listed as wetland species (Trudgen 1988). A single list of 240 species, of which 172 were native, for the wider Port Kennedy area (Keighery & Keighery 1993) was not useful for comparison.

The 18 core species found in all three Shoalwater Bay areas also occurred at Woodman Point and Port Kennedy, apart from *Alyxia buxifolia* at Woodman Point and *Clematis linearifolia* at Port Kennedy. However 12 native species were recorded at both Woodman Point and Port Kennedy that were not found at Shoalwater Bay: *Acacia lasiocarpa*, *Callitris preissii*, *Dianella revoluta*, *Diplolaena dampieri*, *Gompholobium tomentosum*, *Hemiandra pungens*, *Kennedia prostrata*, *Leucopogon parviflorus*, *Desmocladus flexuosus*, *Melaleuca systena*, *Phyllanthus calycinus* and *Schoenus grandiflorus*. Certainly some of these species could have occurred at one or other of the mainland Shoalwater Bay sites. The disparity between the three Shoalwater sites and the difference in size between them and the much more extensive Woodman Point and Port Kennedy areas makes further comparison unhelpful.

The three Shoalwater reserves surveyed are in close proximity to one another and their geology is similar, but the mainland reserves differ from the islands in that the ecosystems have different dynamics and are subject to different disturbance processes. Fire has only been a problem at Point Peron. Nutrient enrichment of the soil dominates the ecology of seabird islands, where there is a massive nutrient subsidy from the ocean via seabirds that feed at sea and deposit guano on the islands (Anderson & Polis 1999; Mizutani & Wada 1988). On the mainland, urban bushland remnants generally derive any additional nutrients from neighbouring parks and gardens. Weed invasion is of major importance in all three reserves. A very high proportion of the species recorded are aliens, 63% 53% and 52% for Mersey Point, Point Peron and the islands respectively. This compares with only 26% for the Perth region (Marchant *et al.* 1987) and 12% for Western Australia as a whole (Paczkowska & Chapman 2000). Many of these introduced species are widespread annual herbs and grasses such as **Lagurus ovatus*, **Euphorbia terracina*, **E. peplus* and **Sonchus oleraceus* that invade following disturbance.

Mersey Point

There is a swale beside the road down the eastern side of Mersey Point Reserve which is used for dumping garden rubbish. Heaps of lawn cuttings and garden clippings of various ages can be found here, with the garden plants and introduced succulents listed for Mersey Point, opposite the gardens from which they originated. Some species such as **Nerium oleander* could have been planted originally in landscaping works. The lawned areas (watered, fertilised and mown) are at risk of infiltrating adjacent bushland, and like the composting rubbish are capable of changing the nutrient balance of the bushland.

The disturbance of the broad strip of foreshore sands beside the beach comes mainly from the wind and sea. This area is thinly covered by four perennial species, two native spinifex grasses of foredunes and **Pelargonium capitatum* and **Trachyandra divaricata* which are coastal species that colonise denuded areas.

Point Peron

Frequent fires have occurred in recent years at Point Peron (11 during the summer of 1999-2000; B Green, unpublished observations). These appear to be the result of arson, and there was associated vehicle activity and destruction of fences. Point Peron is less overlooked by the suburbs of Rockingham than the other two reserves and this isolation may make it more vulnerable to vandalism.

Comparison of our results with a previous vegetation survey (Keating & Trudgen 1986) makes it possible to gauge the effects of fires. Unfortunately few introduced species were included in the 1986 species lists, but vegetation communities were mapped. In 1986 the most widespread vegetation community at Point Peron was *Acacia rostellifera-Alyxia buxifolia* heath, covering about 40% of the area. This was a very mixed community with a further 16 native shrubs, herbs and creepers listed in addition to the two dominant species. Today little of this mixed native heath survives. Under a regime of frequent burning, annuals and species that can survive fire can be advantaged. *Acacia rostellifera* which can be rejuvenated by fire, as it resprouts from damaged trunks and from underground parts, becomes senescent and starts to die out after about 20 years (McArthur 1996). At Point Peron, *Acacia rostellifera* now covers most of the eastern dunes area, with introduced alien annuals, particularly **Euphorbia terracina* and grasses forming much of the understorey. Most of the *Acacia* is young regrowth vegetation, and it is very dense in some sheltered areas.

It cannot be stated that any native species have disappeared or appeared as a result of fire, particularly as some species may always be overlooked by researchers, but three shrubs, *Leucopogon parviflorus*, *Acacia lasiocarpa* and *Diplolaena dampiera* were listed by Keating & Trudgen (1986) and not found in our survey, and *Dodonaea aptera* was unlisted by these authors but was found in our survey. The high number of introduced annual grasses and herbs recorded in our survey could well be associated with the recent fires. These species now dominate the vegetation in some areas and dominate the understorey in others. Such weeds not only invade burned areas but also die back in summer forming tinder that makes the area still more fire-prone. At least one species, **Echium plantagineum*, was probably brought in by earthmoving machinery during rehabilitation efforts.

The islands

Comparison with earlier vegetation surveys showed that on Penguin Island 12% of native species had been lost over the past 40 years but on the small islands the loss had been much more dramatic, 67% on Seal Island, 82% on Bird Island and 43% on Middle Shag Island (Rippey *et al.* 1998). The trend, which is continuing, is not the direct result of human action, but is primarily due to changes in soil nutrient levels and trampling during nesting by increasing numbers of cormorants, and since 1999 a group of pelicans. The vegetation cycle described by Gillham (1961) is still identifiable on the southern and eastern parts of Penguin Island, where these species do not nest. Here the vegetation is damaged and enriched in patches where smaller seabirds such as silver gulls, and little penguins (*Eudyptula minor*) nest, giving annual weeds an opportunity to grow until the dominant perennials such as *Rhagodia baccata* reestablish. However areas used for nesting by the major guano producing bird species of the region, pelicans and cormorants, have undergone a radical vegetation change. On the north of Penguin Island and on the small islands, the native vegetation has virtually disappeared with the exception of *Nitraria billardierei* on the talus slopes. **Malva dendromorpha* often dominates as 2 m high thickets. On the islands of Brittany (France), this species is regarded as being more tolerant of high guano levels than any other (Gehu & Gehu-Franck 1961). Annual weeds such as **Lolium rigidum*, **Bromus diandrus*, **Urtica urens*, **Chenopodium album* and **C. murale* are also common. The Gillham cycle has been replaced by a situation where **M. dendromorpha* and annual alien species dominate and persist. Unfortunately this makes the islands vulnerable to erosion as the annuals disappear completely during the hot, dry and windy summer months, and **M. dendromorpha* dies back to a clump of leaves on the top of a bare stem, with little or no understorey.

Change in vegetation as a result of nesting by seabirds is well recognised. For example on the north-east coast of Scotland in sites used by herring gulls *Larus argentatus* (Sobey & Kenworthy 1979), and on the Riou archipelago off Marseilles (France) where there has been a population explosion of yellow legged gulls *Larus cachinnans* (Vidal *et al.* 1998), trampling, manuring, digging, and collection of nest material has resulted in loss of species diversity and dominance by annual and ruderal species. In Scotland it was noted that no annuals were present in non-affected sites; in the French study the disappearance of indigenous species was emphasised.

The native *Malva australiana* is being supplanted by **M. dendromorpha*, and by 2002 Middle Shag Island was the only Shoalwater Bay island on which it persisted. This *M. australiana* of the island variety (formerly *Lavatera plebeia* var *tomentosa*) is one of only 18 'obligate/semi-obligate ornithocoprophilic' vascular plant species in the world (Yugovic 1998). **Lycium ferocissimum* (African boxthorn) is a dangerous introduction capable of changing the character of the island vegetation entirely.

Management implications

Invasion by weeds is the most obvious problem of the Shoalwater reserves. Current thinking suggests that if causes of invasion are understood and addressed then the chances of success are greater than if weeds are removed (Adair & Groves 1998). Identification of the factors that make a site vulnerable to invasion, the degree of disturbance, and its management may lead to more effective control programmes (Hobbs & Humphries 1995). Early control of weeds is seldom possible because of the difficulty of predicting which plants will become pests (Csurhes & Edwards, 1998). Panetta (1993) suggests that the best indicator is their weediness elsewhere. *Malva dendromorpha*, however, is not considered troublesome outside Australia, although it has caused concern on Mud Islands in Victoria and on West and Wright Islands in South Australia (Rippey *et al.* 2002b). In the two mainland reserves at Shoalwater Bay much of the disturbance and weed introduction is of human origin, and in such situations an accepted approach is to strive for community awareness and involvement. Practical measures that can be of help include the delineation of lawned areas with paths or fences to maintain discrete recreation areas. Fences can prevent dumping if all else fails. Species planted in landscaping enterprises should be selected with care as many of those that establish easily can readily naturalise.

The pre-European fire regime is not known. Very frequent fires are not desirable, but occasional fires benefit many native species, and in addition, controlled fires are useful for reducing fuel loads to prevent major fires. Fire management can thus be a compromise between the needs of native flora and safety concerns (Hobbs 1995b). Well known management techniques for sites such as Point Peron where arson is the cause of fires, are education and community watch, together with weed control, the use of buffer zones or firebreaks, and control of wildfires that do occur.

On the islands, where increased numbers of large seabirds nest regularly or continuously, there is no point in attempting to restore the pre-existing native vegetation. Revegetation efforts would best be approached using only those native species which are tolerant of very high guano levels such as *Malva australiana, Carpobrotus virescens* in rocky areas and *Nitraria billardierei*. Removal of **Malva dendromorpha*, the seeds of which have a prolonged dormancy, requires a long-term commitment and would have to be carried out on all islands and the wider mainland coastline to prevent reintroduction.

M. australiana of the island variety is an attractive native species with limited geographical distribution, capable of existing in enriched soils, and it would be regrettable to lose it.

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Appendix.

Species list for the Shoalwater Islands, Mersey Point Reserve and Point Peron (list for islands from Rippey *et al.* 1998). * denotes introduced species. p denotes species present.

Plant families	Plant Names	Mersey Pt	Pt Peron	Islands
Agavaceae	**Agave americana*	p	p	
	**Agave attenuata*	p		
	**Sansevieria trifasciata*	p		
Aizoaceae	**Carpobrotus edulis*		p	
	Carpobrotus virescens	p	p	p
	**Galenia pubescens*		p	p
	**Tetragonia decumbens*	p	p	p
	Tetragonia implexicoma		p	p
Amaryllidaceae	**Agapanthus praecox*	p		
Anacardiaceae	**Schinus terebinthifolia*	p		
Apiaceae	*Apium prostratum*			p
Apocynaceae	*Alyxia buxifolia*	p	p	p
	**Nerium oleander*	p		
Araucariaceae	**Araucaria heterophylla*	p		p
Asphodelaceae	**Trachyandra divaricata*	p	p	p
	**Asphodelus fistulosus*		p	
Asteraceae	**Arctotheca calendula*	p	p	p
	**Arctotheca populifolia*		p	
	**Arctotis stoechadifolia*		p	
	**Conyza* sp	p	p	
	**Hypochaeris* sp		p	
	Leucophyta brownii			p
	Olearia axillaris	p	p	p
	**Osteospermum ecklonis*	p		
	Ozothamnus cordatus		p	p
	Senecio lautus	p	p	p
	**Senecio tamoides*	p		p
	**Sonchus oleraceus*	p	p	p
Boraginaceae	**Echium plantagineum*		p	
Brassicaceae	**Brassica rapa*			p
	**Brassica tournefortii*	p		
	**Cakile maritima*	p	p	p
	Lepidium foliosum			p
	**Raphanus raphanistrum*		p	p
	**Sisymbrium orientale*	p		p
Cactaceae	**Opuntia stricta*	p		
Caryophyllaceae	**Polycarpon tetraphyllum*			p
	**Sagina maritima*			p
Chenopodiaceae	**Atriplex prostrata*			p
	**Chenopodium album*			p
	**Chenopodium ambrosioides*			p
	**Chenopodium murale*			p
	Enchylaena tomentosa		p	p
	Rhagodia baccata	p	p	p
	Salsola tragus	p	p	
	Sarcocornia quinqueflora			p
	Sarcocornia sp		p	
	Threlkeldia diffusa	p	p	p
Convolvulaceae	**Cuscuta epithymum*	p		
	Wilsonia backhousei		p	p
Crassulaceae	**Aeonium arboreum*	p		
	**Cotyledon orbiculata*	p		
	**Crassula glomerata*	p	p	
	Crassula closiana			p
Cyperaceae	*Isolepis nodosa*	p	p	
	Lepidosperma gladiatum	p	p	p
Dasypogonaceae	*Acanthocarpus preissii*	p	p	p
	Lomandra maritima		p	
Dilleniaceae	*Hibbertia cuneiformis*	p		
Dipsacaceae	**Scabiosa atropurpurea*		p	
Euphorbiaceae	**Euphorbia paralias*		p	
	**Euphorbia peplus*	p	p	p
	**Euphorbia terracina*	p	p	p
	**Euphorbia* sp	p		
Frankeniaceae	*Frankenia pauciflora*		p	p

Plant families	Plant Names	Mersey Pt	Pt Peron	Islands
Fumariaceae	**Fumaria capreolata*	p	p	p
	**Fumaria muralis*		p	
Geraniaceae	**Erodium moschatum*			p
	**Pelargonium capitatum*	p	p	p
Goodeniaceae	*Scaevola crassifolia*	p	p	p
Haemodoraceae	*Conostylis candicans*	p	p	p
Iridaceae	**Romulea rosea*	p	p	p
Lamiaceae	**Lavandula* sp	p		
Lauraceae	*Cassytha racemosa*		p	p
Malvaceae	**Malva dendromorpha*		p	p
	**Malva linnaei*		p	p
	Malva australiana			p
	**Malva parviflora*			p
Mimosaceae	*Acacia cochlearis*	p	p	
	Acacia cyclops	p	p	p
	Acacia rostellifera	p	p	p
	Acacia saligna	p		
Moraceae	**Ficus* sp		p	p
Myoporaceae	*Eremophila glabra*		p	p
	Myoporum insulare	p	p	p
Myrtaceae	*Agonis flexuosa*	p		p
	**Eucalyptus erythrocorys*	p		
	**Eucalyptus gomphocephala*	p	p	p
	**Eucalyptus utilis*	p	p	p
	**Leptospermum laevigatum*	p	p	
	Melaleuca huegelii		p	
	Melaleuca lanceolata		p	p
	**Melaleuca nesophila*	p		p
Oleaceae	**Olea europea*	p		
Onagraceae	**Oenothera drummondii*	p	p	
Oxalidaceae	**Oxalis pes-caprae*	p		p
Papilionaceae	*Hardenbergia comptoneana*	p	p	p
	Jacksonia furcellata	p		
	**Lupinus consentinii*		p	
	**Lupinus* sp	p		
	**Medicago polymorpha*	p	p	
	**Melilotus indicus*			p
	Templetonia retusa		p	
Pittosporaceae	*Pittosporum ligustrifolium*		p	p
Poaceae	**Ammophila arenaria*		p	
	**Arundo donax*	p		
	Austrostipa elegantissima		p	p
	Austrostipa flavescens			p
	**Avena barbata*	p	p	
	**Avena fatua*		p	p
	**Brachypodium distachyon*		p	
	**Bromus diandrus*			p
	**Bromus* sp		p	
	**Cynodon dactylon*	p		
	**Ehrharta longiflora*			p
	**Ehrharta* sp		p	
	**Hordeum leporinum*		p	p
	**Lagurus ovatus*	p	p	p
	**Lolium perenne*			p
	**Lolium rigidum*		p	p
	**Parapholis incurva*		p	p
	**Poa annua*			p
	Poa poiformis		p	
	Spinifex hirsutus	p	p	p
	Spinifex longifolius	p	p	p
	Sporobolus virginicus			p
	**Stenotaphrum secundatum*	p	p	p
Polygonaceae	*Muehlenbeckia adpressa*		p	p
Primulaceae	**Anagallis arvensis*	p	p	p
Ranunculaceae	*Clematis linearifolia*	p	p	p
Rhamnaceae	**Rhamnus alaternus*	p		
	Spyridium globulosum	p	p	p
Santalaceae	*Exocarpus sparteus*			p
	**Leptomeria preissiana*	p		

Plant families	Plant Names	Mersey Pt	Pt Peron	Islands
Sapindaceae	*Dodonaea aptera*		p	
Solanaceae	*Anthocercis ilicifolia*		p	
	**Lycium ferocissimum*			p
	**Solanum linneanum*	p		
	**Solanum nigrum*			p
	Solanum symonii		p	
Tamaricaceae	**Tamarix* sp			p
Tropaeolaceae	**Tropaeolum majus*	p		
Urticaceae	*Parietaria* sp		p	p
	**Urtica urens*			p
Verbenaceae	**Lantana camara*	p		
Zygophyllaceae	*Nitraria billardierei*	p		p
Total	**91 146**	**76**	**86**	**88**

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Notes on ....

Podocyte complexity and terrestriality in frogs

H Y Chan, J E O'Shea, P C Withers & T Stewart

Zoology, School of Animal Biology M092, University of Western Australia, Crawley WA 6009

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Abstract. We extend Richter & Splechtna's (1996) study of the morphology of amphibian podocytes with respect to habitat aridity and water regulation, and describe the method for calculating complexity index of podocyte pedicels. Our results show that *Notaden nichollsi*, the most terrestrial species examined so far, has the highest podocyte complexity. The relationship between podocyte complexity and habitat suggests that glomerular filtration rate is an important parameter related to habitat aridity and water regulation in frogs.

Introduction

Amphibians are found in habitats ranging from fully aquatic to fully terrestrial and sometimes extremely arid. The permeable skin of most amphibians allows substantial trans-cutaneous water and solute flux, and frogs have an effective water regulation system comprising a very distinct lymphatic system, kidneys and bladder (Steen 1929; Ewer 1952; Bentley *et al.* 1958; Middler *et al.* 1968; Bentley 1969; Shoemaker & Nagy 1977; Shoemaker *et al.* 1992).

Water regulation by frogs is determined in part by glomerular filtration rate (GFR), the rate of water entry into the lumen of the renal tubules (Heller 1950). GFR is determined morphologically by the microstructure of podocyte cells that cover glomerular capillaries, as well as physiological factors such as plasma hydrostatic and colloid osmotic pressure. The pedicels (foot-like projections) of podocytes form filtration slits, the number and size of which influences GFR.

Richter & Splechtna (1996) used scanning electron microscopy to examine the complexity of podocytes for a variety of frogs differing in terrestriality. They distinguished five types of podocyte process systems, and suggested that podocyte pedicel microstructure was correlated with habitat *i.e.* podocyte complexity increases with terrestriality. Aquatic frogs have fewer high-branching levels than terrestrial species. We examine podocyte complexity for the Australian frog *Notaden nichollsi*, and *Xenopus laevis* and *Bufo marinus*, using a similar protocol to Richter & Splechtna (1996).

Materials and Methods

A desert spadefoot toad (*Notaden nichollsi*) and a cane toad (*Bufo marinus*) were killed by double pithing, and a perfused and fixed South African clawed toad (*Xenopus laevis*) was obtained from other experiments. Frog kidneys were perfusion-fixed with 4% paraformaldehyde in cacodylate buffer and post-fixed with osmium-thiocarbohydrazide (Richter & Splechtna 1996). They were then mounted on SEM stubs and critical point dried. A Philips 505 scanning electron microscope was used to locate glomeruli on the kidney surface, then a Field Emission Scanning Electron Microscope JSM 6300F was used for higher resolution imaging.

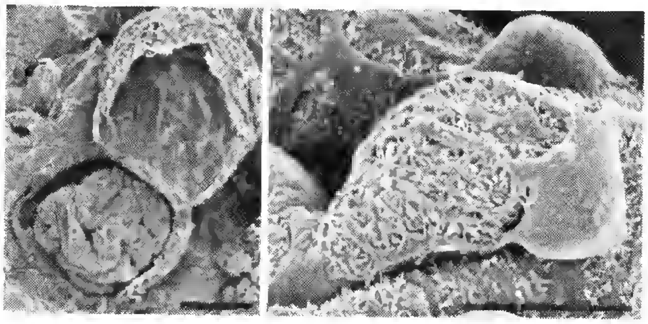

Figure 1. High resolution photomicrographs of *Bufo marinus* podocytes showing glomerulus within a Bowman's capsule (left; scale bar 50 µm) and podocytes on the glomerular capillaries (right; scale bar 10 µm).

Podocytes on the surface of glomeruli in the kidney of frogs were difficult to locate, and it was also difficult to obtain photographs of the podocytes with sufficient resolution for clear definition of the branching patterns. Nevertheless, we obtained photomicrographs (*e.g.* Fig 1) for the calculation of podocyte complexity for three species, the aquatic *Xenopus laevis* (n =1 individual, 3 glomeruli, 5 podocytes), the mesic terrestrial *Bufo marinus* (n = 1; 1 glomerulus, 3 podocytes) and the arid terrestrial *Notaden nichollsi* (n = 1; 1 glomerulus, 2 podocytes).

Podocyte complexity index

Richter & Splechtna (1996) did not provide any detail of the methodology for calculating the index for podocyte complexity, but merely cited Laskowski & Pohlit (1974), a biophysical book published only in German. So, we describe here our interpretation of the methodology required to replicate Richter & Splechtna's (1996) calculations.

Firstly, the number of branches in each branching level (from 1 to 4) of a podocyte cell body is determined. Primary level podocyte processes branch out to secondary level processes, and then to tertiary and quaternary levels. In determining branch levels in each podocyte group, the main branch always retains the status of the previous branch level. The main branch is defined as the initial branch extending from the cell body, and with the continuation that provides the maximum branching complexity.

After the branching levels are determined, the total number of branch endings is counted, and the fraction (P_i) of branch endings belonging to each branch level is calculated. For each group, P_i is multiplied by the branch level (Z_i), and the complexity index (bit value) for each podocyte cell body is calculated by summing the P_iZ_i values. The complexity index is defined such that the higher the bit value, the more complex the structure is. An example of how to determine the branching levels of

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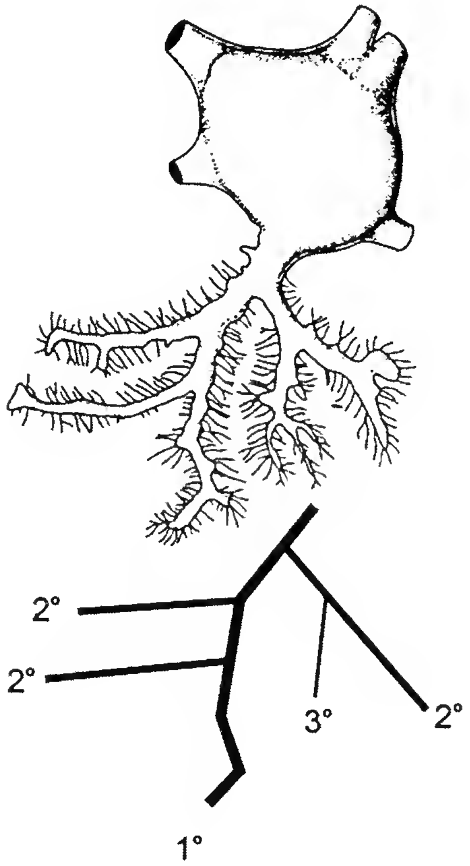

Total number of branch endings = 5

	P_i	Z_i	P_iZ_i
1°	1/5	1	1/5
2°	3/5	2	6/5
3°	1/5	3	3/5
			10/5 = 2.0 bit

Figure 2. Example of calculation of podocyte complexity index for branching level for podocyte pedicels (type III, from Richter & Splechtna 1996) using schematic of primary pedicel branch (1°), secondary branches (2°) and tertiary branch (3°).

the processes of podocytes is shown in Fig 2. The podocyte complexity index for an individual podocyte is determined by taking the average SP_iZ_i value for several randomly selected podocyte cell bodies.

Results and Discussion

The average complexity index obtained for pedicels of podocytes from *X. laevis* was low, at 1.27 bits; it was 2.32 bits for *B. marinus*; and was highest (2.46 bits) for *N. nichollsi*. The bit value obtained for *X. laevis* was very close to that of Richter & Splechtna (1996). Direct comparison between the complexity indices obtained in this study with those of Richter & Splechtna (1996) shows a strong relationship between podocyte pedicel complexity and terrestriality (Fig 3), presumably mediated by variation in glomerular filtration rate.

The podocyte pedicel index for *N. nichollsi*, the most arid terrestrial amphibian examined so far, is also the highest value measured, conforming well with the pattern established by Richter & Splechtna (1996). Further studies of additional species will clearly be productive in more fully documenting the relationship between podocyte microstructure, kidney function and water balance for the many and diverse species of anuran amphibians.

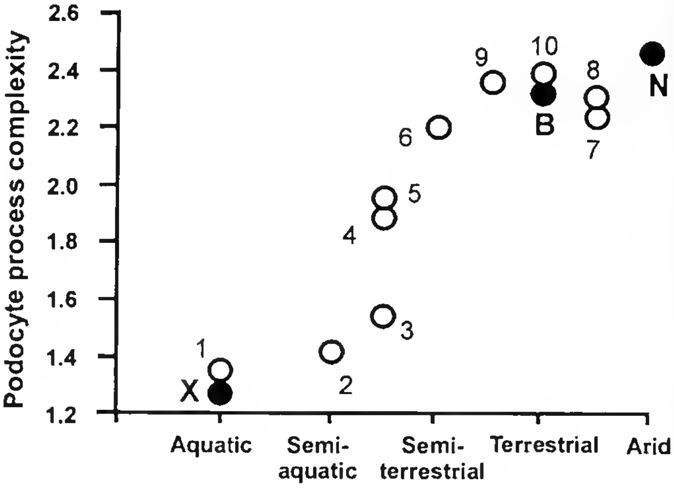

Figure 3. Relationship between habitat and podocyte complexity (adapted from Richter & Splechtna 1996). Values from the present study are *Xenopus laevis* (X; 1.27 bits), *Bufo marinus* (B; 2.32 bits) and *Notaden nichollsi* (N; 2.46 bits). Species from Richter & Splechtna (1996) are; 1, *Xenopus laevis*; 2, *Rana ridibunda*; 3, *Rana esculenta*; 4, *Bombina variegata scabra*; 5, *Discoglossus pictus*; 6, *Rana lessonae*; 7, *Alytes cysternasii*; 8, *Bufo regularis*; 9, *Rana temporaria*; 10, *Rana dalmatia*.

Acknowledgements: Collection of frogs was under permit from the Department of Conservation and Land Management, and experimentation was under approval from the Animal Ethics Committee of the University of Western Australia. We thank the Neurobiology Research Group of the Department of Zoology (UWA) for perfused and fixed *Xenopus laevis* specimens.

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Obituary: R Dennis King

May 1942 – January 2002

Dennis King was a generous man. Generous with his time, knowledge and expertise. Dennis was always willing to share his knowledge and enthusiasm, particularly for goannas, with fellow scientists and others interested in nature.

Born in Calgary (Canada) in 1942, Dennis moved to Vancouver at a young age, went to Magee High School, and then to the University of British Colombia to undertake Bachelors' and Masters' degrees in zoology, which he completed in 1968. He subsequently accepted an Australian Wool Board scholarship to undertake a PhD at the University of Adelaide. Initially intending to study birds, however, he saw the light early and changed to goannas. His PhD topic 'Temperature regulation in the Sand goanna *Varanus gouldii* (Gray)' was completed in 1977, and was awarded in 1978.

After completing his formal qualifications, Dennis worked with the Western Australian Agricultural Protection Board. Much of his work focussed on the biology and control of rabbits and other feral exotic species such as goats. He was a major player in the research into sodium monofluoroacetate (1080), a naturally occurring substance in some Australian plants of the genus *Gastrolobium*, and the resulting tolerance of some native species to the toxin. Because of this tolerance, 1080 has been used for many years to control introduced vertebrate pests without posing a risk to native animals. The use of 1080 to control foxes, in particular, has led to the increase in numbers of endemic species of small animals in some areas, and the removal of some of these from the list of endangered species. Dennis considered his work on fluoroacetate-tolerance in native species as his most important work outside his love of reptiles.

His 130 plus publications reflected his two areas of scientific interest; the management and control of vertebrate pests, and research into goannas. With Brian Green he published a book: 'Goannas: The Biology of Varanid Lizards', which is in its second edition. More recently he wrote, in association with Eric Pianka from the University of Texas, a section for a book on Komodo Dragons, a publication of the Smithsonian Institution. At the time of his death he was writing/editing a book with Eric Pianka, 'Varanoids of the World', which will address what is known about this fascinating genus of lizards.

After his retirement in 1996, Dennis developed his long standing links with the Western Australian Museum, becoming an Honorary Associate, and was often seen in the lower basement of the museum peering into bottles of preserved goannas, extracting ticks from their skin or parasites from their intestinal tract, or studying other tissues and organs. Dennis sustained an interest in the biology of goannas over a period of more than 30 years, and would readily share his wealth of knowledge with any one that would ask. His research interests and his approach to life resulted in a wide circle of friends on many continents.

A vocal conservationist, Dennis willingly shared his views on how well we were managing the natural environment with whoever would listen. He enjoyed field trips to the remoter sections of the Australian bush, even when it became physically taxing because of complications resulting from his diabetes.

In his early years, Dennis was a keen sportsman, playing basketball and lacrosse and competing in athletics. In later years he remained a keen observer of a number of sports. He enjoyed good food of any sort, including the Asian varieties, good wine and good conversation.

Our memory of Dennis is commemorated in the specific epithet of *Varanus kingorum* (Storr), named in 1980 for Drs Dennis and Max King for their contributions to study of the Varanidae.

Dr Graham G Thomspon
Edith Cowan University