

# Rock pools (gnammas) in the Gibson Desert of Western Australia: unique formation and reasons for their limited biological diversity

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## Abstract

Rock pools (gnammas) have a random distribution on rock pavements over much of Australia. In the climatically benign south, they are common and have a diverse fauna, but those in deserts are rarer, structurally different and scarcely surveyed. A widely spaced set of gnammas in the Gibson Desert of Western Australia were sampled in mid-2017 and again in mid-2018 using a pond net and a plankton net. The gnammas are in lateritic rock, and have a distinctive pipe-like form and mode of origin. The latter involves vertical solution of weathered rock, aided by kangaroos excavating for water as the pools dry. This is different from the granite pans and pits in southern Australia. Mean alpha diversity of macroinvertebrate communities in these mid-Western Australian gnammas is 5.9 species, drawn from a metacommunity of eight crustacean species, with perhaps a few insect individuals from an array of 21 species (gamma diversity). Invertebrate dispersal is extremely limited with crustaceans surviving dry periods as passively distributed eggs and insects recolonising actively from the wetter west during each filling event. Poor dispersal, plus the small size and homogeneity of habitat within the pipe gnammas, limits biotic diversity.

**KEYWORDS:** Geomorphology, diversity, dispersal, branchiopod crustaceans, aquatic insects.

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## INTRODUCTION

Australia has a remarkable variety and number of inland rock pools formed largely by chemical corrosion. Usually they are known generically as ‘gnammas’, originally coined by the Noongar people of southwest Australia for pits in granite. These retain rainwater and once were an essential source of drinking water for human survival (Bayly 2011). Geologists and biologists in Australia have adopted the term for any rock pool, shallow or deep, formed by chemical corrosion in any rock type (including sandstone, limestone, quartzite, basalt, etc.) across Australia, each with characteristic geomorphology and processes of formation.

Although such landscape features have been variously recognised worldwide for centuries (e.g. Borlase 1769), the first substantive Australian work on their geomorphology dealt with granite outcrops on the northwestern Eyre Peninsula in South Australia (Twidale & Corbin 1963) and recognised pan gnammas, (shallow with flat floors) pit gnammas (deep, largely hemispherical bowls) and armchair gnammas (bevelled hollows in slopes). Recently Twidale & Bourne (2018) revised interpretation of processes in gnammas but omitted details of pit gnammas and did not refer to pipe gnammas in laterite in deserts (Bayly *et al.* 2011), which at the time were an inadequately described type of gnamma of the remote inland.

Detailed biological work on the pan gnammas of southwestern Australia (Bayly 1982, 1997; Pinder *et al.* 2000; Jocqué *et al.* 2007; Timms 2012a, b; Brendonck *et al.* 2015) recognised a distinctive fauna that Brendonck *et al.* (2016) considered the richest in the world for rock pools. Many faunal elements have special adaptations for living in shallow, crystal-clear waters with short seasonal hydroperiods (Brendonck *et al.* 2016). The deeper pit gnammas with longer hydroperiods and murkier waters support a largely different, far less diverse fauna with few special adaptations that is essentially a eurytopic fauna similar to that of any nearby freshwater pool (Timms 2014a). By contrast, the desert-pipe gnammas of Bayly *et al.* (2011) in the Victoria Desert of southeastern Western Australia apparently have a restricted eurytopic and depauperate fauna, which they explained by their extreme isolation and hence strong dispersal restrictions as well as the small size of the pools.

This paper aims to explore the geomorphology of pipe gnammas in the Gibson Desert of central inland Western Australia and provide an explanation for their formation. The second, more important, aim is to expand the biological database for inland pipe gnammas of Western Australian deserts to help explain their limited biological diversity. Biological collections were made from the Gibson Desert pipe gnammas during two periods with different rainfall conditions and from twice as many gnammas (or three times in a comparison of just pipe gnammas) as visited by Bayly *et al.* (2011).

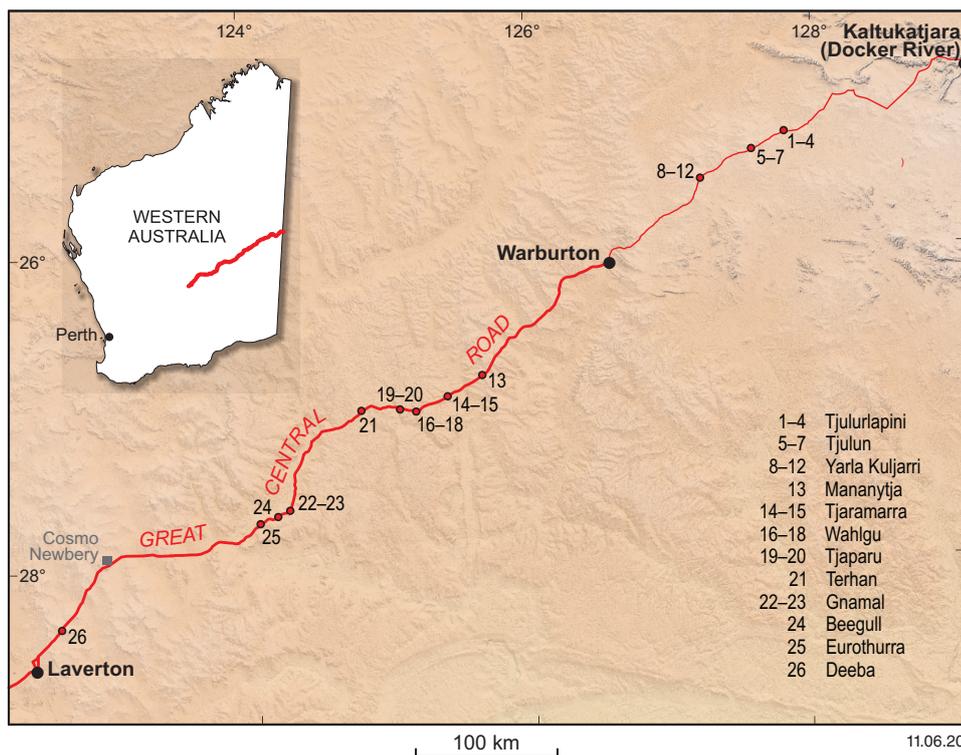
## STUDY AREA AND METHODS

Twenty-six rock holes adjacent to the Great Central Road between Laverton in Western Australia and the Northern Territory border to the east were visited twice in 2017–18 (Figs 1, 2; Appendix 1). The countryside is largely sandy with areas/ridges of lateritic rock and some exposed granite at Cosmo Newby. The area lies in the Canning and Officer basins, the Musgrove Province and on the edge of the Yilgarn Craton (Beard 2002; Appendix 1). The trip of July 1–4, 2017 followed 310.6 mm of rain during the previous six months (measured at Warburton, about midway along the transect; Fig. 1; Bureau of Meteorology 2018), so that all rock holes held water, and most were full (the wet trip). By contrast, during May 18–21, 2018 most of the pools were dry following low rainfall (33.8 mm) over the previous six months (the dry trip).

On the first visit to each pool, rock hollow depth was measured with a flexible steel tape and its average diameter determined by two measurements at right angles. Volumes were calculated using  $V = \pi r^2 z$  where  $V$  = volume,  $r$  = average radius and  $z$  = depth. On the second trip it was noted that many of the holes were not quite vertical having been excavated by kangaroos searching for water. Whereas the depths of some holes changed by up to 5% due to these excavations, these changes were not added to the database. Conductivity was determined with an ADWA332 meter and turbidity was measured in a Secchi disc tube calibrated in Nephelometric Turbidity Units (NTU). This tube does not measure turbidity lower than 5 NTU so very clear waters were not accurately differentiated. If a pool was dry on the second trip a c. 500 g sample of bottom soil was taken from the upper 5 cm for later incubation to check on crustaceans likely to grow on wetting.

Where possible, zooplankton was collected with a small plankton net (opening 10 × 8 cm and 50 cm long, net mesh 159  $\mu$ m) for one minute by swishing it around at various levels in the pools. Microfauna smaller than 160  $\mu$ m, including rotifers, were not studied. Macroinvertebrates were caught with a 1 mm mesh pond net, 25 cm wide and 20 cm high with a 25 mm opening on a D frame. This net was swept through the pool three to four times for a total of no more than two minutes. Macroinvertebrates were sorted in a white tray, and representatives of all species caught were preserved in ethanol for later identification, with the remainder returned alive to the pools together with all tadpoles caught. All zooplankton collected was preserved in ethanol for later study. Though the study was not quantitative, relative abundances in the collections were estimated on a log scale (<10 = 0.1 to 0.9 depending on exact number; 10–99 = 1; 100–999 = 2; 1000–9999 = 3; >10000 = 4).

We used the correlation coefficient to test a possible relationship between gnamma size and alpha diversity, and a student's t-test to look for significant differences between two groups of gnammas (an east grouping of #1–10 and a west grouping of #14–23). The groups represent two distinct and geographically separate clusters of the randomly spaced gnammas along the transect (Fig. 1). Ten gnammas from each group were analysed to match the number in groups of other gnamma types in previous investigations (Timms 2012a, b; 2014a) and to eliminate differences due to unequal numbers involved. A Mantel test was used to test for autocorrelation between sites and their distance apart. To test questions of faunal relationships between these groups of gnammas, we used multivariate analyses with PRIMER (v5) (Clarke & Gorley 2001). We used



**Figure 1.** Location of the Great Central Road through the Gibson Desert showing the positions of studied gnammas.



**Figure 2.** Examples of pit gnammas: (a) Site 11, Karla Kuljarra, protected against camels by a Patjarr Spider; and (b) Site 15, Tjaramarra.

average abundance values collected over many visits to the Wheatbelt localities, whereas abundances for all the Gibson sites are from the 2017 field trip. Otherwise, the collecting and analyses protocols for all the data are similar. Field and laboratory counts were log-transformed ( $\log_{10}(x+1)$ ) and a similarity matrix was constructed using the Bray-Curtis similarity coefficient. Non-metric multidimensional scaling (nMDS) ordination was then performed to visualise patterns in assemblage composition among the data sets. One-way analysis of similarities (ANOSIM) was then used to test significance of the differences. In these ANOSIMs, the magnitude of the associated  $R$  statistic value was used as an absolute measure of difference between paired groups. In general, if  $R > 0.75$ , groups are clearly distinguishable, if  $R > 0.5$ , groups overlap but are clearly different, and if  $R < 0.25$ , groups are typically indistinguishable (Clarke & Gorley 2001). Finally, similarity percentage analysis was performed to determine the species characteristic of each for four major groups identified in the nMDS (the Gibson pipes, the Wheatbelt pits and two groups of the Wheatbelt pans) and those that distinguish between these major groups (Clarke 1993).

## RESULTS

Of the 26 gnammas studied in the Gibson Desert, the mean depth was 116.8 cm, mean diameter 130.4 cm and mean volume when full was 2.09 m<sup>3</sup> (Table 1). These figures hide considerable variation, so that extreme depths combined with extreme volumes cause the volumes to be the most variable parameter (Table 1). Whereas the typical shape is a wide vertical pipe, many gnammas have outward sloping walls at least on one side, where kangaroos actively dig as the pool approaches dryness. Unfortunately, pools closest to the road often contained bottles, tin cans, car parts and ad hoc depth sticks. Some had cobbles, the most notable being Beegull, which is not a pipe gnamma as are all the others but a plunge pool along a waterway. The Cosmo Newbury area was also different by having granite outcrops, but there were no pit gnammas (sensu Timms 2013a) presently deep enough for study, all being almost, if not entirely, full of sediment.

Water was always fresh and pools were either almost clear or somewhat turbid, i.e. values had a bimodal distribution, explained in many cases by catchments of either bare rock or exposed soil. Electrical conductivity and turbidity values were higher in the dry trip, though data were scant on the second trip (Table 1). These values are indicative only, as they undoubtedly vary with stage of filling and seasonal productivity/turbid inflows (Timms 2017).

Alpha diversity (i.e. momentary species richness) of macroinvertebrates in the pools averaged 5.9 with 3.3 crustacean species and 2.6 insects per pool, with the later more variable than the former (Tables 1, 2). Alpha diversity was unrelated to pool depth, pool volume or pool clumping, except for insect diversity, which is related to pool volume ( $r = 0.502$ ,  $P < 0.01$ ). Crustacean individuals were always more numerous than insect individuals (crustaceans 10 to >10000 per collection, usually >1000, while insects were generally < 100 for dipterans and <10 for others, often just 1–2). Overall, eight species of crustaceans and 21 insect species were encountered—the additional insect species found in the dry year of 2018 are accounted for in Table 2. The most common crustaceans were the ostracods *Sarscypridopsis* nr *aculeata* and *Heterocypris* n.sp. BOS1137, and the laevicaudatan *Lynceus baylyi*, whereas the dominant insects were *Chironomus* spp. and the beetles *Sternopriscus multumaculatus* and *Eretes australis* (Table 2). Rehydration of muds collected on the 2018 trip did not add to crustacean diversity (Table 2), but largely confirmed existing distributions, with the exception of *Mesocyclops brooksi*, which was not observed in any culture.

Distribution of species is patchy. Among the crustaceans, *Lynceus baylyi* is absent from the Tjulun group, *Daphnia carinata* is absent from gnammas east of Wahlgu and *Moina australiensis* so far has not been found west of the Yarla Kuljara group (Table 2). Insect distribution is even more random, though the more common species appear somewhat regularly throughout the study area (Table 2). We found no evidence of spatial autocorrelation from a Mantel test ( $p=0.976$ , 9999 permutations). However, by a t-test, which assumes independence among samples, insects were significantly different ( $t = 0.0362$ ,  $P < 0.05$ ) between the east pools (#1–10,  $n=1.5$  species per pool) and the west

pools (#14–23,  $n=3.0$  species per pool) where mean pool volumes were similar ( $t = 0.4744$ ,  $P > 0.05$ ).

## DISCUSSION

The pipe gnammas of the western deserts have a distinctive geomorphology, with a wide near vertical pipe averaging 110 cm deep and 130 cm diameter (Bayly *et al.* 2011; Table 1, Appendix 1). These gnammas have formed in laterite, seemingly by long-term dissolution of the cementing chemicals binding the rock. Once a surface depression forms, a pipe can develop as solution is largely vertical from the overlying pooled water. The side walls are rough with harder remnants of the lateritic conglomerate rock protruding. At many sites, deepening is promoted by excavation by kangaroos. In the past, Aboriginal people may have removed sediment to create larger water storages to aid survival.

Similar gnammas, called native wells, are known in lateritic rocks in central western Queensland (e.g. near Jundah, Windorah; BV Timms, unpublished data). All these pipe gnammas are distinctive and different from the pit gnammas on granite, which generally are pudding-basin shaped or canoe-shaped (Timms 2014a, b; Twidale & Corbin 1963; Twidale & Bourne 2018). The most similar pit gnammas are some vertical cylinders, partly cut by surface water descending to a void below (Twidale & Bourne 2018)—their walls are smooth and with no animal activity involved in their formation.

Water in the desert pipe gnammas is always fresh, though with a minor increase in salts due to evaporation. It is rare for gnamma waters across Australia to be hyposaline, the exception being a few western Nullarbor granitic pools (Timms 2012b). Water clarity is generally in the same range as for pit gnammas (Timms 2014a, b) and for most not quite as crystal clear as in pan gnammas. Clarity decreases as the pools dry, but algae blooms colouring them green were not observed in the desert as in some pit gnammas in agricultural areas to the southwest (Timms 2014a).

For crustaceans, there is strong concordance between the results obtained by Bayly *et al.* (2011) for eight pipe gnammas in the Great Victoria Desert and the present results for the Gibson Desert; for both studies

*Lynceus baylyi* (*Lynceus* sp. nov. in Bayly *et al.* 2011), *Moina australiensis*, *Sarscypridopsis* and *Heterocypris* were important taxa. *Daphnia* was not recorded in the former study and neither were Hemiptera or Coleoptera. These differences could be sampling anomalies due to fewer sites sampled in the Victoria Desert, or lower diversity due to lower mean annual rainfall (Gentilli 1986) imposing shorted hydroperiods (Brendonck *et al.* 2015) or poorer dispersal due to greater spatial distribution of gnammas there (Vanschoenwinkel *et al.* 2008a).

At an alpha diversity of 5.9 in the Gibson pipe gnammas (Table 1) and 4.6 in those in the Victoria Desert (Bayly *et al.* 2011), the faunas of these desert pipe gnammas are depauperate compared to almost all groups of gnammas so far studied in Australia. Pit gnammas on Yilgarn granite to their southeast averaged 8.2 and those on Eyre Peninsula, South Australia, averaged 9.1 species (Timms 2014b). Pan gnamma faunas are usually much more diverse, with an alpha diversity of about 30 species per pan in the Western Australian Wheatbelt (Timms 2012a), and lower (8.1 - 9.7) in eastern Australia (Timms 2012a, 2014a, 2017). The exception is Stanthorpe, Queensland, at 5.6 species in its much shallower pan gnammas (Timms *et al.* 2019). These pan gnamma species are part of a metacommunity, with figures per rock outcrop and district much higher than for individual pans—the latter reaching at least 220 in southwest Australia (Pinder *et al.* 2000). These figures do not include microfauna, which generally are a minor component—rotifers averaging just four species per pool in nine groups of rock pools in Western Australia (Pinder *et al.* 2000).

Comparative figures for the metacommunities of the deeper gnammas are even more instructive. Gibson Desert pipes appear to support a more diverse community than the Victoria Desert pipes (29 vs 14 species; Bayly *et al.* 2011), although three times as many pipes were examined in the Gibson Desert and insects were identified to genus or species level rather than to family level as in the Victoria Desert study. The limited fauna of desert pipes in both areas is obvious in comparison with the pits of the wetter Yilgarn region of Western Australia, where the metacommunity totals 82 taxa (Timms 2014) compared to about 35 overall in the desert pipes (this study, plus Bayly *et al.* 2011).

**Table 1.** Various parameters of the gnammas with year assessed.

Parameter	n	Mean ± SD	Range
Geomorphology (2017)	26	Depth 116.8 ± 31.1 cm Diameter 130.4 ± 63.8 cm Volume 2.09 ± 2.42 m <sup>3</sup>	37–170 cm 70–275 cm 0.06 – 8.12 m <sup>3</sup>
Physicochemical features (2017)	26	Conductivity 117 ± 199 µS/cm Turbidity 18.8 ± 17.8 NTU	97–463 µS/cm 5–32 NTU
Physiochemical features (2018)	4	Conductivity 448 ± 410 µS/cm Turbidity 60.0 ± 68.5 NTU	221–1282 uS/cm 5–150 NTU
Species richness (2017)	26	Crustaceans 3.27 ± 1.31 Insects 2.58 ± 2.35	0–5 2–11
Species richness (2018)	4	Crustaceans 0.25 Insects 2.25	0–1 1–6

**Table 2.** Species list for the Gibson gnammas

Crustacea	Records	2017*	2018* <sup>^</sup>
<i>Lynceus baylyi</i>	15	1, 3, 10–12, 14–17, 19–21, 24–26	1, 2, 9–11, 14, 17, 19–21, 24
<i>Daphnia carinata</i> s.l.	8	2–5, 8, 10, 11, 14, 15	2–6, 8–11, 14
<i>Moina australiensis</i>	6	14–18, 25	14–15
<i>Heterocypris</i> n. sp. BOS1136	1	24	
<i>Heterocypris</i> n. sp. BOS1137	18	1–3, 8, 10–24	1–4, 8–10, 14–15, 18–22, 24
<i>Ilyodromus</i> ? <i>viridulus</i>	1	24	
<i>Sarscypridopsis</i> nr <i>aculeata</i>	23	1–4, 6–9, 11–26	1–3, 6–12, 18–20, 24–25
<i>Mesocyclops brooksi</i>	7	1, 2, 8, 9, 12, 21, 26	
<b>Insecta</b>			
<i>Hemicordulia tau</i>	1	26	
<i>Micronecta</i> sp.	1		26
<i>Anisops gratis</i>	1	1	
<i>Anisops hyperion</i>	6	1, 7, 15, 20, 21, 24	
<i>Anisops stali</i>	9	6, 7, 15, 19–21, 23, 24	26
<i>Anisops thienemanni</i>	3	15, 24, 26	
<i>Agraptocricia hirsuta</i>	2	1, 15,	
<i>Agraptocoruxa parvipunctata</i>	4	21, 24, 26	26
<i>Antiporus gilberti</i>	1		26
<i>Enochrus</i> sp.	1	24	
<i>Eretes australis</i>	7	1, 6, 7, 13, 21, 23, 24	16–17, 23
<i>Hyphydrus elegans</i>	1	26	
<i>Necterosoma</i> sp.	1	26	
<i>Sternopriscus multimaculatus</i>	13	2, 4, 7, 11, 12, 14, 16, 18–21, 24	26
unidentified tanypodine	1	26	
<i>Chironomus alternans</i>	10	8–12, 14–15, 19, 21, 24	26
<i>Chironomus australis</i>	3	15, 16, 18	
<i>Chironomus tepperi</i>	4	15, 19, 21, 24	
<i>Dasyhelea</i> sp.	1	17	
<i>Cryptochironomus</i> sp.	4	20–22, 24	
<i>Culex australicus</i>	4	9, 13, 14, 23	
<b>Arachnida</b>			
Mite	2	10, 24	

\* individual gnammas referred to by their numbers given in Figure 1

<sup>^</sup> cultured crustaceans in italics; extant insects collected in 2018.

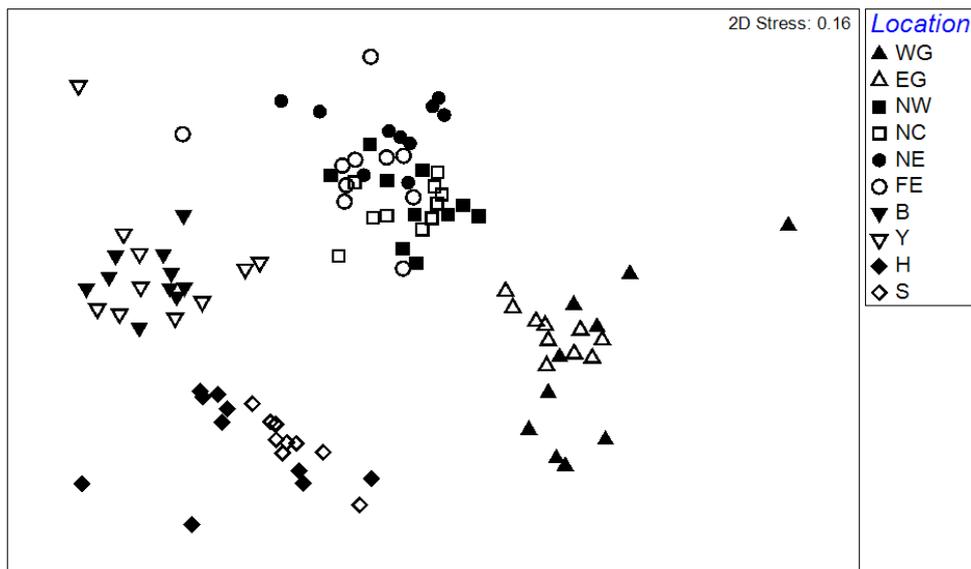
Much of the invertebrate fauna of the desert pipe gnammas is a limited subset of that in Yilgarn pit gnammas, although the only laevicaudatan present in the desert pipes is distinctive; *Lynceus baylyi* is almost entirely restricted to desert gnammas compared to the common *Lynceus magdaleanae* of the Yilgarn pits (Timms 2013b). Cladocerans are the same at the alpha species level (*Daphnia carinata* sensu lato and *Moina australiensis*) whereas among the ostracods there is uncertainty due to taxonomic limitations—genera are shared but there may be differences among the species present. As for the pits, there is a vast difference in community composition between the desert pipes and Yilgarn/Pilbara pan gnammas. The pans have a variety of branchiopods, cladocerans, ostracods, copepods, and a wider range of insects (Bayly 1982, 1997; Pinder *et al.* 2000; Jocque *et al.* 2007; Timms 2012a, b).

Ordination of the pipe gnammas with pit and pan gnammas in southern Western Australia reveals the pipes have a community structure separate from that of both pit gnammas and pan gnammas in other parts of the state (Fig. 3). Both Gibson groups cluster near the lower right-hand corner, the four groups of pit gnammas are also to the right, whereas the pans form a cluster, in two groups,

to the left. Three of the four major groups are significantly different from one other (i.e.  $R > 0.75$ ) and even the southeastern pans are largely different ( $R$  between 0.5 and 0.75) from the northern pans (Table 3). The species most typical of the four groups are (a) *Sarscypridopsis* nr *aculeata*, *Lynceus baylyi*, and *Heterocypris* sp. for the Gibson pipes; (b) *Chironomus tepperi*, *Cypridopsis* sp., and *Sternopriscus multimaculatus* for the Wheatbelt pits; (c) *Boeckella longirostris*, *Amphibolis* sp., and *Paralimnadia badia* from the northwest pans; and (d) *Boeckella opaqua*, *Pleurispina* sp., and *Ceriodaphnia* sp. in the southeast pans.

As Bayly *et al.* (2011) noted, the fauna in these desert pools is severely restricted by ineffective dispersal, particularly as it is hindered by the small surface area of water available to receive dispersants among vast areas of sand and rock—this is especially so for insects which must colonise each filling. In addition, the habitat is relatively homogeneous within the pipes and macroscopic plants are almost entirely absent. The one Victoria Desert pool with macrophytes had an extra three cladocerans and an ostracod (Bayly *et al.* 2011).

It is likely that limitations on dispersal ability are responsible for the patchy distribution of many species in the Gibson Desert (Table 2). Branchiopod



**Figure 3.** Ordination diagram of two groups of 10 each of Gibson pipe gnammas (EG = #1–10; WG = #13–22) with 4 groups of 10 each of pit gnammas in the northern and eastern Wheatbelt on Yilgarn granite of Western Australia and 4 groups of similarly located pan gnammas. Data for gnammas other than the pipes from Timms (2012a, b, 2014a). Pit gnammas: NW = near Beacon, NC = near Trayning; NE near Yanneymooning; FE = near Hyden. Pan gnammas: B = near Paynes Find; Y = near Yanneymooning; H = near Hyden; S = near Norseman.

**Table 3.** ANOSIM statistic R for pairwise tests between G = Pipe gnamma sites in Gibson desert, W = pit gnamma sites in Wheatbelt, N = pan gnamma sites in northern Wheatbelt and S = southeastern sites in Wheatbelt.

Pairwise tests	R statistic
G, W	0.845
G, N	0.950
G, S	0.905
W, N	0.914
W, S	0.947
N, S	0.619

crustaceans are often dispersed by waterbirds and/or wind (Vanschoenwinkel *et al.* 2008a; Rogers 2014), but with no water birds observed during field trips and with the orifice of the pipes being extremely small, and so catching little dust, dispersal opportunities for crustaceans are particularly poor in the Gibson Desert. Mammals are also known to disperse eggs on occasions (Vanschoenwinkel *et al.* 2008b, 2011) and it is possible kangaroos may infrequently disperse small eggs via their fur. Insect distribution is particularly patchy (Table 2) because new colonization is needed after each refill, and few hemipteran and coleopteran individuals are successful in finding pipes, making the process even more disordered. The greater abundance of insects in western pools suggest colonization is from the west under the influence of the dominant westerly winds and the more numerous wetlands to the west, e.g. Laverton wetlands. For dipterans, adults apparently persist around only a few pools when they dry and nearly all recolonization is restricted to these pools. For example, mosquitoes rarely, if ever, are found at pools hundreds of kilometres from source wetlands (Service 1997). This inefficient dispersal is reflected in the limited correlation between pool size and diversity, a feature of the pit gnammas of the Yilgarn granites (Timms 2014a).

Davis *et al.* (2018) show that latitude is a driver in diversity in various habitats across the arid biome, including rock pools. However, they fail to note the

fundamental difference between shallow pan and deeper pit/pipe-gnamma communities (see above). It is thus invalid to compare Pilbara pans with Victoria Desert pipe gnammas as only similar geomorphic units should be compared. When this is done there is still a decrease of diversity with some increase in latitude if, for instance, the Pilbara pan at 20° 44'S (with an alpha diversity of 18.5; Pinder *et al.* 2010) is compared with structurally similar Walga Rock pans at 27° 24'S (alpha diversity 10.6; Timms 2012a). However, even this difference is misleading as the reduction in alpha diversity is due principally to different hydrologies (Brendonck *et al.* 2011) and not, in the first instance, to latitude.

## CONCLUSIONS

The wide pipe-like morphology of pipe gnammas, with kangaroos contributing to their enlargement, makes them unique. By comparison with other gnammas, invertebrate diversity is particularly low with mean species richness of only 5.9 per pool. The laevicaudatan *Lynceus baylyi* and undescribed species of *Heterocypris* and *Sarscypridopsis nr aculeata* ostracods dominate among the crustaceans, but among insects there is an array of hemipterans, coleopterans and dipterans with *Sternopriscus multumaculatus* and *Chironomus* spp. the most widespread. There are severe limitations on dispersal of all species.

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## APPENDIX

**Table 1.** Location and physical characteristics of the gnammas along the Great Central Road.

number	Name	Coordinates	total depth (cm)	diameter (cm)	volume (m <sup>3</sup> )	Species Richness		
						Crustaceans	Insects	Total
1	Tjulurlapini 1 (N)	25°18'00.54"S, 127°49'02.16"E	100	110	0.95	4	3	7
2	Tjulurlapini 2 (middle)	25°18'00.54"S, 127°49'02.28"E	105	113	1.05	4	1	5
3	Tjulurlapini 3 (middle)	25°18'00.84"S, 127°49'02.28"E	72	85	0.41	5	0	5
4	Tjulurlapini 4 (SW)	25°18'00.66"S, 127°49'01.92"E	142	255	7.25	3	1	4
5	Tjulun 1 (N)	25°24'42.78"S, 127°35'11.46"E	37	118	0.40	1	0	1
6	Tjulun 2 (middle)	25°24'43.08"S, 127°35'11.04"E	144	268	8.12	1	2	3
7	Tjulun 3 (S)	25°24'43.14"S, 127°35'10.86"E	93	103	0.77	0	2	2
8	Yarla Kuljarri 1 (N)	25°35'50.82"S, 127°13'31.56"E	150	90	0.95	5	2	7
9	Yarla Kuljarri 2 (middle)	25°35'51.36"E, 127°13'31.14"E	112	70	0.43	3	2	5
10	Yarla Kuljarri 4 (middle)	25°35'51.42"S, 127°13'31.20"E	118	73	0.49	4	2	6
11	Yarla Kuljarri 6 (S)	25°35'51.42"S, 127°13'31.26"E	40	78	0.06	4	2	6
12	Yarla Kuljarri 9 (SW)	25°35'51.96"S, 127°13'31.50"E	132	128	1.70	4	2	6
13	Mananytja	26°50'12.66"S, 125°39'37.02"E	130	73	0.54	2	1	3
14	Tjaramarra N	26°50'02.94"S, 125°24'44.28"E	105	185	2.82	3	2	5
15	Tjaramarra S	26°50'08.46"S, 125°24'39.24"E	128	173	3.01	5	6	11
16	Wahlgü N	27°03'37.56"S, 125°11'07.56"E	170	98	1.28	4	1	5
17	Wahlgü W	27°03'38.16"S, 125°11'05.82"E	110	108	1.01	4	1	5
18	Wahlgü SE	27°03'38.34"S, 125°11'06.90"E	120	130	1.59	3	3	6
19	Tjaparu N	27°02'35.52"S, 125°04'12.36"E	148	102	1.21	3	5	8
20	Tjaparu S	27°02'35.58"S, 125°04'12.42"E	105	90	0.67	4	2	6
21	Terhan	27°02'39.18"S, 124°47'47.28"E	125	275	7.42	4	7	11
22	Gnamal NE	27°40'06.30"S, 124°15'47.34"E	115	62	0.35	4	1	5
23	Gnamal SW	27°40'06.84"S, 124°15'48.00"E	125	85	0.71	1	2	3
24	Beegull	27°42'19.56"S, 124°10'34.20"E	125	242	6.74	4	10	14
25	Eurothurra	27°44'45.78"S, 124°02'57.18"E	152	132	2.08	3	1	4
26	Deeba	28°22'06.66"S, 122°35'43.38"E	135	145	2.23	3	6	9
<b>means</b>			116.8	130.4	2.09	3.27	2.58	5.85