An outback oasis: the ecological importance of bilby burrows

S. J. Dawson[1] , L. Broussard[2], P. J. Adams[1,3], K. E. Moseby[4], K. I. Waddington[5], H. T. Kobryn[1], P. W. Bateman[6] & P. A. Fleming[1]

1 Environmental and Conservation Sciences, School of Veterinary and Life Sciences, Murdoch University, Murdoch, WA, Australia
2 Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA
3 Invasive Species, Department of Primary Industries and Regional Development, South Perth, WA, Australia
4 School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia
5 Buru Energy, Perth, WA, Australia
6 School of Molecular and Life Sciences, Curtin University, Perth, WA, Australia

Abstract

Ecosystem engineers are species that have a role in creating and maintaining certain habitat traits that are important for other species. Burrowing species do this by creating subterranean refugia from predation and thermal extremes, but also providing foraging opportunities through soil movement and by increasing local landscape heterogeneity. In this study, we used camera traps to monitor the burrows of greater bilbies (*Macrotis lagotis*), a vulnerable Australian marsupial, in an area subject to frequent disturbance by fire. We tested the hypothesis that bilby burrows provide refuge for other species and therefore their presence increases biodiversity. In total, 45 taxa – 22 bird, 16 reptile and 7 mammal taxa – were recorded interacting with 127 burrows across 7 sites. Species richness was greater at burrows compared with vegetation away from burrows, while abundance was no different. There was no difference in species assemblage for bilby burrows that were actively maintained by bilbies compared with abandoned burrows, although there was more activity at bilby maintained burrows. A wildfire allowed us to test the ad hoc hypothesis that the use of bilby burrows was greater when vegetation cover was removed by fire. We recorded significant differences in species assemblage interacting with burrows after fire, although overall species richness and abundance did not change. The response of individual species was variable; for example, burrows provide a refuge for smaller species (such as mice and small reptiles), and may therefore protect them from the effects of fire. Where they persist, bilbies provide an important ecosystem engineering service, as their burrows support a broad range of species. Further reduction in the distribution of the bilby is therefore likely to have a flow-on effect on biodiversity, impacting species that use their burrows for refuge.

Introduction

Ecosystem engineers are animals that, through multiple processes, modify the physical environment and in doing so create and maintain habitat that benefits other species (Jones *et al.* 1994; Jones, Lawton & Shachak, 1997; Jones *et al.* 2010). Ecosystem engineers can create and maintain habitat by changing water flows (Wright, Jones & Flecker, 2002), creating microhabitats (Campos-Arceiz, 2009), modifying vegetation structure (Valeix *et al.*, 2011) or changing nutrient cycling (James, Eldridge & Hill, 2009; Platt *et al.*, 2016). Examples of this diverse group include beavers (*Castor canadensis*) building dams (Wright *et al.*, 2002; Bartel, Haddad & Wright, 2010), termites (Isoptera) creating refugia in colony mounds (Dangerfield, McCarthy & Ellery, 1998; Fleming & Loveridge, 2003; Jouquet *et al.*, 2011), the shells of marine molluscs (Mollusca) providing habitat heterogeneity in benthic environments (Gutierrez *et al.*, 2003), and proboscideans changing the structural complexity of vegetation by damaging trees and creating large and permanent game trails (Pringle, 2008; Haynes, 2012). All these taxa have marked effects on the surrounding community (Jones *et al.*, 1997; Wright & Jones, 2004).

In Australia, one of primary processes driven by ecosystem engineers is the bioturbation of soil by digging mammals, many of which have suffered significant population and range declines (James & Eldridge, 2007; Fleming *et al.*, 2014).

Bioturbation by digging mammals can increase water infiltration, capture organic matter, increase nutrient cycling, and increase plant germination and growth (see Fleming *et al.*, 2014 for review). Burrowing species (as a subset of digging species), in particular, are among the most important ecosystem engineers, as their construction of burrows increases habitat heterogeneity (Ceballos, Pacheco & List, 1999; Davidson, Detling & Brown, 2012), modifies nutrient cycling (Wesche, Nadrowski & Retzer, 2007; Chapman, 2013; Gharajehdaghipour *et al.*, 2016), provides foraging opportunities (Read *et al.*, 2008; Desbiez & Kluyber, 2013), and provides shelter for burrow commensals (Jackson & Milstrey, 1989; Kinlaw, 1999; Kinlaw & Grasmueck, 2012; Hofstede & Dziminski, 2017).

Other taxa may interact with burrows for a variety of reasons. Burrow commensals may use the burrows of other species for shelter from predators (Layne & Jackson, 1994; Waterman & Roth, 2007), shelter from fire (Friend, 1993), foraging for food (Desbiez & Kluyber, 2013) or for thermal refuge (Walde *et al.*, 2009; Pike & Mitchell, 2013). The loss of burrowing ecosystem engineers can, therefore, have negative effects on ecosystem health and related biodiversity (Crain & Bertness, 2006; Fleming *et al.*, 2014). Given that the persistence of some taxa depends on the presence of burrows excavated by another species (Vaughan, 1961; Milne, Bull & Hutchinson, 2003), reductions in population size or range of burrowing species may cause cascading declines in those species reliant on burrows (Desmond, Savidge & Eskridge, 2000; Davidson *et al.*, 2012; Dziadzio & Smith, 2016).

The greater bilby (*Macrotis lagotis*) is a fossorial species of bandicoot (Thylacomyidae) once widespread across much of Australia but now largely restricted to arid parts of the mainland. Nationally, bilby populations are thought to be declining (Woinarski, Burbidge & Harrison, 2014). Bilbies are industrious excavators, capable of digging multiple large burrows (up to 2 m deep) within hours (Smyth & Philpott, 1968; Johnson, 1989). They live in scattered populations of 2–3 individuals (Johnson, 1989), and use up to 18 burrows at a time (Moseby & O'Donnell, 2003). Bilbies regularly dig new burrows and abandon old ones (Moseby & O'Donnell, 2003), resulting in burrow densities (including abandoned burrows) of up to 47 burrows km^{-2} (this study). Given their abundance when present, it is therefore unsurprising that a range of species have been recorded using bilby burrows, including echidnas (*Tachyglossus aculeatus*), brush-tailed mulgara (*Dasycercus blythi*), spinifex hopping mice (*Notomys alexis*) and sand goannas (*Varanus gouldii*), as well as a range of invertebrates, including hemipterans and coleopterans (Read *et al.*, 2008; Hofstede & Dziminski, 2017). Under the right conditions, burrows of some species can last for over 30 years (Witz, Wilson & Palmer, 1991; Burbidge, Short & Fuller, 2007; Hofstede & Dziminski, 2017), and even abandoned burrows are still used by a range of species (Witz *et al.*, 1991; Hofstede & Dziminski, 2017). Burrowing animals can therefore create long-lasting habitat and refuge legacy.

While many studies have previously identified burrow commensals by physically deconstructing the burrow and trapping each individual specimen (e.g. Witz *et al.*, 1991) or using

pitfall traps with drift fences (e.g. Read *et al.*, 2008), these methods may not capture the full range of interactions with burrows (e.g. birds that forage at the mouth of the burrow rather than use the burrow itself). Motion-triggered camera traps provide a method of remotely monitoring the use of burrows and the associated sand apron by other taxa (literature reviewed in Table 1).

We used camera traps to identify vertebrate species using burrows, testing the hypothesis that there was greater biodiversity associated with the burrows compared with adjacent undisturbed locations, and that maintained burrows would show greater use than abandoned burrows. A wildfire also allowed the opportunity to test the ad hoc hypothesis that removal of vegetation by fire makes bilby burrows more important as refuge. Such information will help to predict the impacts of further declines, and inform management strategies.

We addressed three predictions in these data:

1 compared with surrounding vegetation, bilby burrows are associated with greater species richness and abundance and support a different community composition;
2 removal of adjacent vegetation by fire increases use of bilby burrows; and
3 burrows actively maintained by bilbies would be used more than burrows that have been abandoned by bilbies.

Materials and methods

The study was conducted at seven sites in the West Kimberley region, in north Western Australia (18°00′S, 123°00′E), the distance between a site and its nearest neighbour ranged from 2.6 to 19.5 km. The region is part of the Dampierland Bioregion (Thackway & Cresswell, 1995) with a tropical, monsoonal climate and an average of 600 mm of rainfall a year predominantly during summer (November to April). There were two broad vegetation types across the study: Pindan vegetation (five sites; Table 2), and Fitzroy Plains (two sites; Table 2) (Beard, 1990). Pindan sites were on gently undulating sandplain with red earthy soils, with vegetation consisting of a sparse eucalypt-dominated woodland over a thick *Acacia* spp. dominated midstory, with a grassy understory of *Chrysopogon* spp., *Sorghum* spp. and *Triodia* spp. (Kenneally, Edinger & Willing, 1996). The Fitzroy Plains were characterized by red sandplains with dunes, with scattered *Eucalyptus* spp., *Acacia* spp. and *Grevillea* spp. woodland over a low open *Senna notabilis* shrubland, with open grassland of *Triodia* spp. and *Sorghum* spp. Generally speaking, while key structuring plant species are similar between both sites, the understorey is more open in the Fitzroy plains, and contains predominantly hummock grasses, rather than the tussock grasses of the Pindan sites.

Once located, each of seven sites (bilby 'populations') were searched by two people, on multiple parallel transects (separated by 20 m) to locate bilby burrows, after which cameras were deployed on as many burrows as possible. Each transect was walked until no sign had been recorded for ~300 m, ensuring the full extent of the population had been sampled. Burrows generally consisted of a single excavated hole with a

Table 1 Studies that have recorded burrow commensals and taxa interacting with burrows using camera traps, and additional important studies conducted using other methods. Species richness in each taxon is not reported in all listed studies.

Reference	Country	Climate	Burrower	No. of species			
				Mammals	Reptiles & amphibians	Birds	Total
Studies using camera traps							
Current study	Australia	Tropical	Bilby (Macrotis lagotis)	7	16	22	46
Hofstede & Dziminski (2017)	Australia	Arid	Bilby (M. lagotis)	6	7	4	20
Thornett et al. (2017)	Australia	Semi-arid	Southern hairy-nosed wombat (Lasiorhinus latifrons)	4	5	15	24
Mori, Menchetti & Balestrieri (2015)	Italy	Mesic	European badger (Meles meles)	8	—[a]	—[a]	8
Desbiez & Kluyber (2013)	Brazil	Tropical	Giant armadillo (Priodontes maximus)	18	3	3	24
Agha et al. (2017)	United States	Arid	Desert tortoise (Gopherus agassizii)	10	7	14	33
Dziadzio & Smith (2016)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)	11	8	18	37
Alexy et al. (2003)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)	4	8	0	12
Lee et al. (2010)	United States	Arid	Pygmy rabbit (Brachylagus idahoensis)	22	3	18	43
Additional key studies (not using camera traps)							
Jackson & Milstrey (1989)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)				60
Jones & Franz (1990)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)				
Kinlaw & Grasmueck (2012)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)				
Layne & Jackson (1994)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)				
Witz et al. (1991)	United States	Tropical	Gopher tortoise (Gopherus polyphemus)				19
Ceballos et al. (1999)	Mexico	Arid	Prairie dogs (Cynomys spp.)				
Desmond et al. (2000)	United States	Semi-arid	Prairie dogs (Cynomys spp.)				
Hawkins & Nicoletto (1992)	United States	Semi-arid	Kangaroo rat (Dipodomys spp.)				
Kinlaw (1999)	United States	Arid	Multiple species				

[a]Mori et al. (2015) only recorded the mammal assemblage.

Table 2 Location and information appropriate to each study population used in the study

Site	Bilby activity	Vegetation	Dates of survey	No. camera trap sites (trap nights) Burrows	No. camera trap sites (trap nights) Control	Temperature during study (mean ± 1SD °C)[c]	Type of cameras used
Grass-seed	Yes	Pindan	Jun-Nov 2015	32 (2346)	19 (2031)	31.1 ± 11.7	HC500, HC600, PC900
		Pre-fire	Jun-Sept 2015	23[a] (1524)	19 (1356)	30.6 ± 11.9	HC500, HC600, PC900
		Post-fire	Sept-Nov 2015	20[a] (822)	19 (675)	32.5 ± 11.3	HC500, HC600, PC900
Peter	Yes	Fitzroy Plain	Jul-Nov 2015	37 (1797)	0	30.6 ± 12.9	HC500, UXR6
Bore	Yes	Pindan	Jul 2014, May–Sept 2016	32 (1034)	0	28.0 ± 11.1	HC500 HC600
Kurrajong	Yes	Pindan	Dec 2015 – Jun 2016	15 (122)	0	31.2 ± 10.8	HC500, HC600, PC900
Josh	No[b]	Fitzroy Plain	Jun–Jul 2015	5 (70)	0	23.1 ± 9.9	HC500, UXR6
Yakka-munga	Yes	Pindan	Oct-Nov 2015	3 (30)	0	35.2 ± 9.6	HC500, UXR6
Judi	Yes	Pindan	Dec 2015	3 (12)	0	35.2 ± 10.3	HC600

[a]Eleven burrows monitored in both periods.

[b]Recent sign at the site suggests bilby had only recently vacated the site.

[c]Temperature data taken from camera trap images. All images, including by-catch, was used to calculate this mean, to avoid bias towards peak activity times.

domed profile (approximately 120 × 150 mm), together with the excavated soil pile, which is flattened to make an 'apron' in front of it, and has also had been pushed back by the bilby such that a shallow depression ~50 mm deep tended to form directly in front of the burrow entrance. Burrows were often, but not consistently, dug at fallen tree limbs, or below grassy tussocks. Bilby burrows were distinguished from those of other burrowing species following Moseby, Nano & Southgate (2012). Only *Varanus panoptes* excavate similar-sized burrows at these study sites, although their burrows are easily distinguished due to their lateral elongation and relatively small sand apron.

The seven sites were monitored between 3 and 196 consecutive days, between June 2014 and September 2016 (Table 2). The duration of camera deployment was determined by the availability of cameras, seasonal access to the sites, battery life and memory card capacity of cameras, and the need to survey multiple sites for replication. We have dealt with the differences in effort between surveys through rarefaction methods.

Camera trapping

'Burrow' camera traps were set 1.5–2 m from the opening of the burrow, positioned to view both the mouth of the burrow (to capture individuals entering or exiting burrows) and surrounds (a 1 m radius around the mouth of the burrow), to capture animals not directly entering the burrow. At our longest-term monitored site, for comparison (acting as controls), we used cameras deployed evenly throughout the population, set in an identical manner ('Grass-seed' population only; Table 2, Fig. 1). The location of these cameras was determined by their use in a concurrent study, however there was no consistent difference in vegetation between control cameras and burrow cameras.

All cameras were attached to a metal stake at 400 mm height. Where possible, cameras were orientated in a southerly direction to avoid glare from the sun triggering the camera (Meek, Ballard & Fleming, 2012). Any grass that was likely to trigger the camera was removed, while being careful not to unnecessarily expose the burrow to predators. Four models of Reconyx (Reconyx Inc., Holmen, WI, USA) camera were used: three 'still' cameras (HC500, HC600 and PC900), and one 'still/video' camera (UXR6) (Table 2). Still cameras were set to PIR trigger, five rapid-fire images, no quiet period, high sensitivity and with no white flash. Still/video cameras were set to PIR trigger, normal sensitivity, three photo burst and videos were excluded from analysis. Data from cameras that were disturbed (pushed off target) were discarded.

Image analysis

All vertebrates recorded in images were identified to species or genus level (for animals such as rodents; Table 3) and tagged in the metadata using EXIFPRO (Kowalski & Kowalski, 2012). All unidentified species and invertebrates were excluded from analysis. Images were also categorized based on the action of the animal, with images classified as follows:
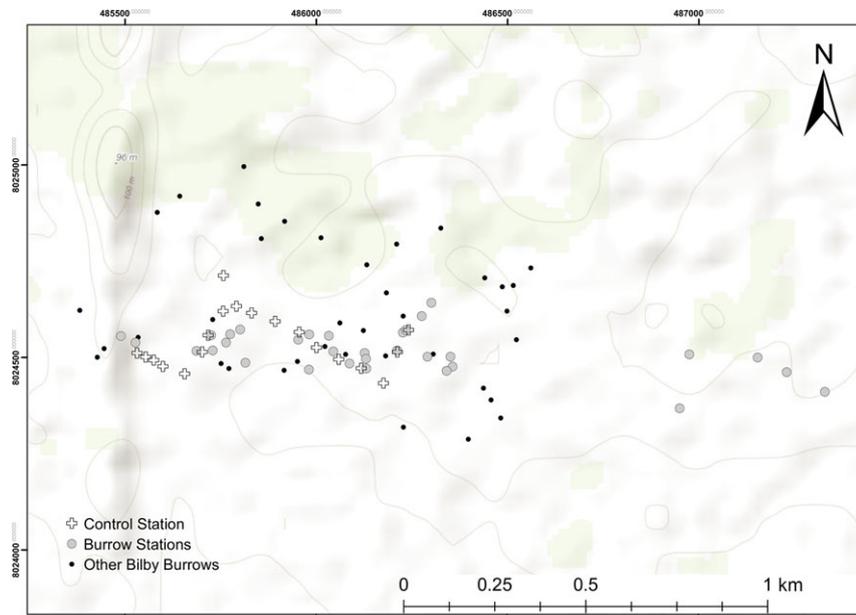
Figure 1 'Grass-seed' population, showing all burrows located during monitoring, as well as those that were monitored by camera, and the location of control cameras.

1 'Interacting' (i.e. a potential 'burrow-commensal' species): a spatial threshold for categorizing behavior was used because interpretation of behavior (such as foraging or sheltering) from still photographs is subjective. An individual was therefore scored as 'interacting' with the burrow if they were within the target area (including the burrow itself, the depression at the front of the burrow and the apron). We did not attempt to classify animals as entering or exiting, as camera traps often missed such events, especially for fast-moving species.

2 'Passing': any individual caught on camera but not within the target area was classified as 'passing'.

Image metadata was extracted using package 'CAMTRAPR' (ver 0.99.8) (Niedballa, Courtiol & Sollmann, 2017). The threshold of independence was set to 10 min, so that consecutive detections of the same species at the same site were considered the same individual. Cattle were excluded from analysis.

Comparisons

We addressed three experimental questions.

Burrows vs. control cameras

We compared between burrows and control stations for the 'Grass-seed' site only (data prior to the site being burnt). Community composition was compared between 19 control stations and 21 burrow stations. No comparison was made between control stations (at 'Grass-seed') and burrow stations at other sites. Given control stations only had 'passing' captures, both 'passing' and 'interacting' captures were used from burrow stations.

Effect of fire on burrow use

At the 'Grass-seed' site, burrows and control cameras were monitored before and after fire. Community composition was compared between 21 burrows before and 19 burrows after, and 18 control sites before and 18 control sites after. Only 'interacting' captures were used for this analysis.

Maintained vs. abandoned burrows

Burrows were classified as 'maintained' if bilbies were observed maintaining burrows within the time of monitoring (removing dirt from the mouth of the burrow); otherwise the burrow was considered to have been abandoned. Community composition was compared for 87 burrows (59 maintained, 28 abandoned) with 45 species. Burrows that had only one species interact with it were treated as outliers and excluded community analysis, but were included in the tests of trap rate. Given control stations only had 'passing' captures, both 'passing' and 'interacting' captures were used from burrow stations.

Statistical analysis

Three measures of vertebrate community were calculated to address each research question:

1 *Species richness*. To account for significant differences in survey effort, an individual-based rarefaction curve was created in ESTIMATES v9.1.0 (Colwell, 2013). Rarefaction resamples from a reference sample (the survey data), and produces an estimate of the expected number of species and its unconditional standard deviation (Colwell, 2013). The

Table 3 A list of the taxa identified interacting with bilby burrows, as well as the taxa identified at control sites. The third column indicates if species were significantly more likely to be recorded interacting (+) or passing (−), or equal (=). Only taxa with >10 total captures were tested. Taxa that were classified as burrow-commensals are in bold

	Species	Common name	Passing	Interacting		Control
Mammal	*Macrotis lagotis*	Greater bilby	48	943	+ ***	83
	***Pseudomys* spp.**[a]	Mouse	693	472	− ***	13
	Lagorchestes conspicillatus	Spectacled hare-wallaby	48	50	=	125
	Notamacropus agilis	Agile wallaby	91		− ***	323
	Felis catus	Feral cat	14	45	+ ***	56
	Canis familiaris[b]	Dingo	5	12	=	15
	Notomys alexis	Spinifex hopping mouse	9	2		
	Vulpes vulpes	Red Fox		2		
	Tachyglossus aculeatus	Short beaked echidna	1			
	Trichosurus vulpecula	Brush tailed possum		1		2
	Osphranter rufus	Red Kangaroo				1
Bird	***Pardalotus rubricatus***	Red-browed pardalote	4	330	+ ***	
	Rhipidura leucophrys	Willie wagtail	116	95	=	
	Pomatostomus temporalis	Grey-crowned babbler	21	63	+ ***	
	Pardalotus striatus	Striated pardalote		70	+ ***	
	Geopelia cuneata	Diamond dove	56	1	− ***	
	Lichenostomus virescens	Singing honeyeater	27	20	=	
	Grallina cyanoleuca	Magpie lark	33	1	− ***	
	Corvus spp.[c]	Torresian crow/Little crow	25	1	− ***	
	Colluricincla harmonica	Grey shrike-thrush	8	13	=	
	Artamus cinereus	Black-faced woodswallow	16	2	− **	1
	Malurus melanocephalus	Red-backed fairywren	1	16	+ ***	
	Cracticus nigrogularis	Pied butcherbird	3	13	+ *	
	Geopelia striata	Peaceful dove	5			
	Poephila acuticauda	Long-tailed finch	3	2		
	Anthus novaeseelandiae	Australasian Pipit	1	3		
	Falco berigora	Brown falcon		4		
	Malurus lamberti	Variegated fairywren		4		
	Acanthiza apicalis	Inland thornbill	3			
	Coracina novaehollandiae	Black-faced cuckoo-shrike	2	1		
	Lichenostomus keartlandi	Grey-headed honeyeater	3			
	Microeca fascinans	Jacky winter	2	1		
	Cincloramphus mathewsi	Rufous songlark	2			
	Coturnix ypsilophora	Brown quail	2			
	Falco cenchroides	Nankeen kestrel	2			
	Gerygone fusca	Western gerygone		2		
	Mirafra javanica	Horsfield's bushlark	2			
	Ocyphaps lophotes	Crested pigeon	2			
	Ardeotis australis	Australian bustard	1			5
	Artamus personatus	Masked woodswallow	1			
	Burhinus grallarius	Bush stone-curlew				1
	Centropus phasianinus	Pheasant coucal				1
	Chrysococcyx basalis	Horsfield's bronze-cuckoo		1		
	Dacelo leachii	Blue-winged kookaburra	1			
	Hamirostra melanosternon	Black-breasted buzzard				1
	Lalage suerii	White-shouldered triller	1			
	Lichmera indistincta	Brown honeyeater		1		
	Podargus strigoides	Tawny frogmouth	1			
	Turnix pyrrhothorax	Red-chested buttonquail		1		
Reptile	***Varanus panoptes***	Yellow-spotted monitor	13	202	+ ***	4
	Pogona minor	Dwarf beared dragon	13	111	+ ***	
	Ctenophorus spp.[d]	Dragon	17	30	=	
	Varanus acanthurus	Spiny-tailed monitor	2	26	+ ***	
	Varanus tristis	Black-tailed monitor	5	23	+ ***	
	Diporiphora sp.		22	4	− ***	

Table 3 Continued.

	Species	Common name	Passing	Interacting	Control
	Scincidae sp.		5	13	+ *
	Lophognathus gilberti	Gilbert's dragon	3	6	
	Strophurus ciliaris	Northern spiny-tailed gecko	3	6	
	Agamid sp.		4	4	
	Tiliqua multifasciata	Centralian blue-tongued skink		5	
	Varanus brevicauda	Short-tailed pygmy monitor	1	4	
	Varanus eremius	Pygmy desert monitor	1	3	
	Ctenotus sp.		2	1	
	Pseudechis australis	Mulga snake		2	
	Anilios sp.			1	
	Chlamydosaurus kingii	Frilled-necked lizard	1		
Unknown	Unknown		18		
	Unknown Bird		12	1	− **
	Unknown *Cracticus* sp.		7	5	=
	Unknown *Malurus* sp.		5	1	
	Unknown lizard		2	3	
	Unknown varanid			1	
	Total species (excluding unknowns and bilbies)		**49**	**45**	

[a]Likely *Pseudomys delicatulu*s (Delicate mouse), *P. nanus* (Western Chestnut Mouse), and *Leggadina lakedownensis* (Lakeland Downs Short-tailed Mouse).
[b]Jackson *et al.* (2017).
[c]Likely *Corvus orru* and *C. bennetti*.
[d]Likely *Ctenophorus isolepsis* and *C. caudicintus*.
* indicates $P<0.05$, ** indicates $P<0.01$, and *** indicates $P<0.001$.

Chao1 estimator was used for all asymptotic estimates of species richness (Chao, 1984). In addition, species richness estimates were extrapolated to three times the sample size (number of individual captures) (Colwell *et al.*, 2012). We used 95% confidence intervals of each curve (extrapolation), and species richness estimate (rarefaction) to test for differences in species richness (Gotelli & Colwell, 2001; Colwell, Mao & Chang, 2004).

2 *Activity*. The trap rate of all species interacting with burrows was calculated as the number of individual trap events per trap day (to account for differences in trap effort between sites). Trap rate was compared by fitting a generalized linear model with a negative binomial distribution to the number of captures, with the treatment included as a categorical predictor variable, and the trap effort as an offset term, in the package MASS (Ver. 7.3-49) (Venebles & Ripley, 2002). The significance of the predictor variable was then tested by performing an ANOVA test on the fitted model. Modeling was conducted in R (R Core Team, 2018).

3 *Community composition*. For each site or treatment, a data matrix was produced with one row for each camera station and a column with capture rate for each species; camera stations that only captured one species were excluded from analysis. Species assemblage comparisons between sites or treatments were performed using a one-way Analysis of Similarity (ANOSIM) to test for significant differences, followed by a Similarity Percentage (SIMPER) to explore which species accounted for differences in assemblage (program PAST; Hammer, Harper & Ryan, 2001). The data were plotted using non-metric Multi-Dimensional Scaling (MDS) using a Bray-Curtis similarity matrix. All captures (interacting and passing) were used to address questions 1 and 2, while only the captures of animals interacting with burrows were included to address question 3. The proportion of captures that were passing and interacting were compared to using a binomial test, which compares observed frequencies against an expected 50:50 distribution. Species that were significantly more likely to interact with burrows than pass them were classed as burrow-commensals (Table 3).

Results

Data were gathered from 5414 trap days at 127 burrows. Other than bilbies, 45 animal taxa interacted with (maintained and abandoned) bilby burrows; 37 were identified to species, while eight were identified to genus (e.g. *Pseudomys, Corvus, Ctenophorus*) (Table 3). Of the species interacting with burrows, 16% were mammal, 36% reptile/amphibian and 49% were bird species. The greatest raw species richness was 13 species recorded at a single burrow in the 'Grass-seed' site.

In total, 4013 independent captures of animals were recorded: 1389 records (34.6%) were animals interacting with the burrow and 2624 records (65.4%) were animals passing the burrow. This meant that 11 species (excluding bilbies) were significantly more likely to interact with a burrow than pass it (Table 3), and were therefore considered burrow-commensals.

At least seven mammal species (not including bilbies) were recorded interacting with burrows. Only one mouse, *Notomys alexis*, could be identified to species, while *Pseudomys* spp. could not be distinguished. *Pseudomys* spp. accounted for the most raw captures of interactions with burrows, and were often

seen entering burrows; however, they were more often recorded passing burrows. While *Pseudomys* spp. were more likely to pass a burrow (n = 693 records) than interact with it (n = 472 records), they were frequently recorded entering and exiting burrows on camera, and were therefore considered burrow-commensals.

Spectacled hare wallabies (*Lagorchestes conspicillatus*), dingoes (*Canis familiaris*) and cats (*Felis catus*) often investigated the mouth of burrows, but were never recorded entering them (Fig. 2). Agile wallabies (*Notamacropus agilis*), and short-beaked echidna (*Tachyglossus aculeatus*) were recorded passing, but did not interact with burrows (Table 3).

Twenty-two bird taxa interacted with maintained and abandoned burrows, and only one could not be identified to species (*Corvus* sp., n = 1 records). Pardalotes (*Pardalotus rubricatus* and *P. striatus*) were the most frequently recorded bird species interacting with burrows (n = 330 and 70 records), often digging their own burrows into the side walls of bilby burrow entrances (Fig. 2).

Sixteen reptile species were recorded interacting with burrows, (Table 3); 10 of these were identified to species, the remaining six taxa could not be reliably identified (*Ctenophorus* sp., *Diporiphora* sp., *Ctenotus* sp., *Anilios* sp., Scincidae spp. and Agamidae spp.). Five varanid species were recorded; *Varanus panoptes* was the most frequently recorded reptile species interacting with burrows (n = 202 records) (Fig. 2).

Burrows vs. control cameras

While there was no difference in the asymptotic estimate of species richness between burrow and control cameras, this is likely to be due to the variation in species richness between control cameras (Fig. 3). Conversely, the extrapolation curves suggest a greater species richness at burrows. There was no difference in trap rate (χ^2 = 0.795, d.f. = 1, P = 0.372). There was a significantly different community composition for bilby burrows compared with control sites (Fig. 4a; ANOSIM, R = 0.69, P < 0.001). Differences in community composition were due to more frequent captures of *Pseudomys* spp. and *Rhipidura leucophrys* (SIMPER: 32.09%, 9.92%) at burrows, and more captures of *N. agilis* and *L. conspicillatus* (SIMPER: 16.66%, 11.73) at control stations (Fig. 5).

Effect of fire on burrow use

Fire did not cause a significant change in species richness (Fig. 3) nor was there a difference in trap rate at bilby burrows before and after fire (χ^2 = 0.201, d.f. = 1, P = 0.654). At control sites, fire had no effect on the species richness, although there was a significant decrease in trap rate after fire (χ^2 = 55.038, d.f. = 1, P < 0.001). *Pogona minor* and *Pseudomys* spp. capture rates at burrows increased after fire (Fig. 5), while the three most common bird species (*R. leucophrys*, *Pardalotus rubricatus* and *Burhinus grallarius*) were less often recorded interacting with burrows after fire. The difference in community composition of taxa at burrows before and after fire did not reach statistical significance (ANOSIM,

R = 0.05, P = 0.048). There were, however, significant differences in the assemblage at control stations before and after fire (ANOSIM, R = 0.27, P < 0.001). Differences in community composition at control sites was due to a decline of trap rate for *N. agilis* (SIMPER: 50.5%), *L. conspicillatus* (SIMPER: 31.0%) and *F. catus* (SIMPER: 9.8%) after fire (Fig. 5).

Maintained vs. abandoned burrows

Species richness (Fig. 3) and activity (χ^2 = 1.031, d.f. = 1, P = 0.310) were greater at maintained burrows than abandoned ones. Despite these overall differences, there was no significant difference in the community composition of taxa interacting with burrows between maintained and abandoned burrows (Fig. 4b; ANOSIM, R = −0.019, P = 0.804). There was a greater range in community composition at maintained burrows than at abandoned burrows, that is, the community composition at maintained burrows is more varied than at abandoned burrows (Fig. 4b).

Discussion

Whether they are actively maintained or abandoned, bilby burrows support a distinct faunal community. Bilby burrows are likely to provide thermal buffering and humidity refuge for small species, shelter from predators, access to dug soil and access to a vertical soil bank (for other burrowing species), as well as access to food resources (e.g. leaf litter invertebrates, seeds, small vertebrate prey) that may be less accessible on undug soil surfaces. These factors make bilby burrows important resources across a hot and sparsely vegetated landscape which can be challenging, particularly for small vertebrates.

Forty-five taxa of mammal (excluding bilbies), bird and reptiles were recorded interacting with bilby burrows; 11 of these taxa were classified as burrow commensals as they were either significantly more likely to interact with a burrow than pass it (e.g. *V. panoptes*), or were recorded entering and exiting burrows multiple times (e.g. *Pseudomys* spp.). Burrow commensal species included small mice, a range of small birds, and various medium-sized reptiles. *Pardalotus* spp. birds regularly made their own burrows in the vertical walls of bilby burrows, while bilby burrows became more important refuges for some species (e.g. *P. minor*) after fire removed vegetation cover from one site.

This study represents the largest camera trap catalogue of taxa interacting with bilby burrows to date. Overall species richness was greater at burrows than in the adjacent vegetation, and the assemblage was significantly different. In general, large herbivores were seen more at control sites, while small and medium-sized mammals were more associated with burrows. This probably reflects the different shelter requirements of animals of different body sizes, as small species may be more susceptible to both predation and thermal stress, and may therefore be more likely to require physical shelter than larger species. This supports the assertion that taxa interacting with burrows are a distinct community. Areas where burrowing species are present demonstrate an increase in abundance of
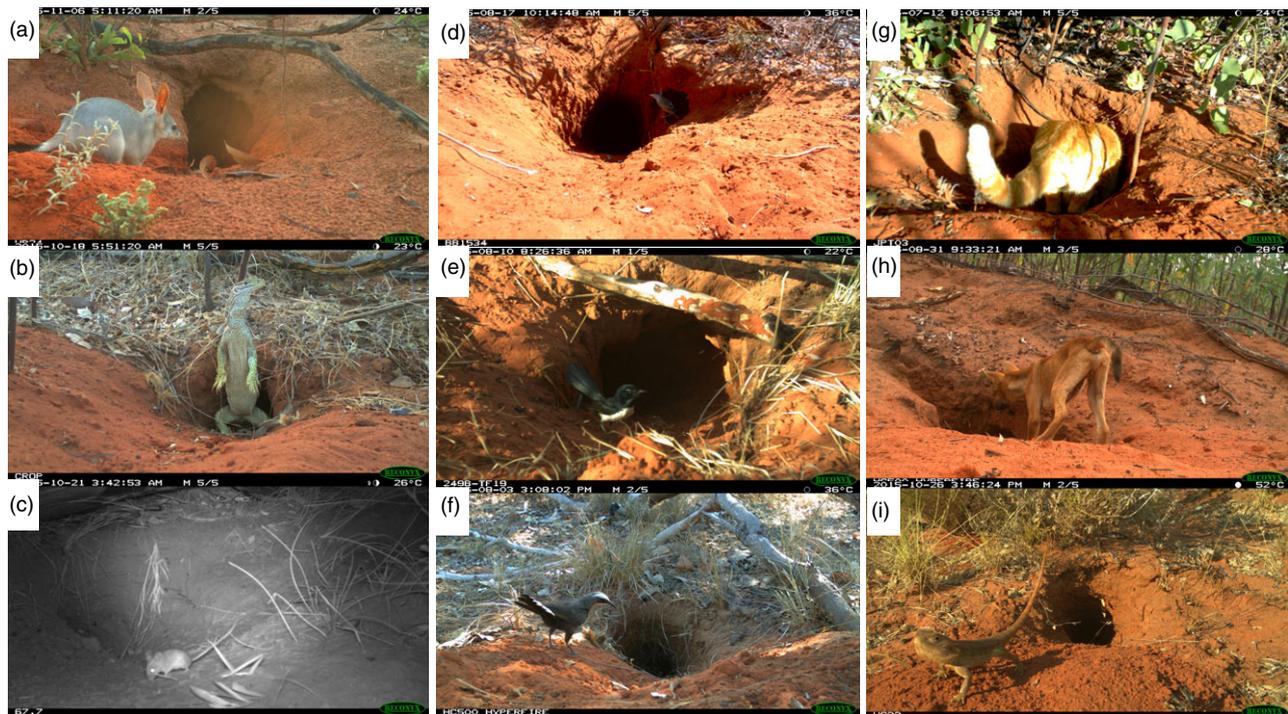
Figure 2 Example photos of a selection of the taxa recorded interacting with burrows. (a) *Macrotis lagotis*, (b) *Varanus panoptes*, (c) *Pseudomys* spp., (d) *Pardalotus rubricatus*, (e) *Rhipidura leucophrys*, (f) *Pomatostomus temporalis*, (g) *Felis catus*, (h) *Canis familiaris*, (i) *Pogona minor*.

arthropods (Davidson & Lightfoot, 2007; Read *et al.*, 2008), and lizards (Davidson, Lightfoot & McIntyre, 2008), and support more diverse communities of small mammals (Ceballos *et al.*, 1999).

The use of burrows by some species increases after fire, when alternative cover is removed. The change in community composition at control sites after fire was far greater than the change at burrow sites. The change in community composition at control sites was driven by terrestrial herbivores (*Notamacropus agilis*, *Lagorchestes conspicillatus*) vacating the area after fire, and there was also a reduction in the use of burrows by the four most common bird species suggesting that they similarly vacate an area after fire. By contrast, some species using bilby burrows were more likely to be recorded after fire. For example, the increase in records of *P. minor* may indicate an increased reliance on burrows after the shelter afforded by undergrowth is removed, which is supported by this species' selection for cover in vegetation or leaf litter (Craig *et al.*, 2007). *Pseudomys* spp. had similar trap rates at burrows pre- and post-fire, suggesting that removal of vegetation has little short-term effect on the use of burrows. In respect to gopher tortoise (*Gopherus polyphemus*) burrows, cotton mice (*Peromyscus gossypinus*) similarly show no change in refuge selection after fire removes the vegetation (Derrick, Conner & Castleberry, 2010).

Although there was greater species richness at maintained bilby burrows, there was no significant difference in community composition between maintained and abandoned burrows. This finding supports those of previous studies of bilbies (Hofstede & Dziminski, 2017), and gopher tortoises (Witz *et al.*, 1991), indicating that even un-maintained burrows are important resources for other species. A burrow, even abandoned, evidently provides resources for other species. In the West Kimberley, old bilby burrows may remain open without maintenance by a bilby for at least 1 year, depending on substrate and cattle trampling (Dawson, unpub. data). Similarly, boodies (*Bettongia lesueur*), a burrowing marsupial of a similar size to bilbies, dig extensive warrens, and if dug into calcrete substrate, may remain in the landscape for over 30 years (Burbidge *et al.*, 2007). Given bilbies show little site fidelity (Johnson, 1989), the ecological 'footprint' of an individual is likely much larger than its home range, as it includes the burrows it has previously excavated. Bilbies may therefore provide legacy shelter and heterogeneity.

We propose three broad categories of burrow commensal relationships observed in this study.

Firstly, some species semi-permanently reside in the same burrow (e.g. *Pseudomys* spp. and *Varanus panoptes*). Some of these species can excavate their own burrows, but appear to capitalise on the provision of a bilby burrow. A similar community of species (i.e. *V. gouldii*, *T. aculeatus*, *N. alexis*, *Dasycercus blythi*) permanently inhabit bilby burrows in other regions of Australia (Hofstede & Dziminski, 2017). Similarly, permanent habitation of burrows has been recorded for a range
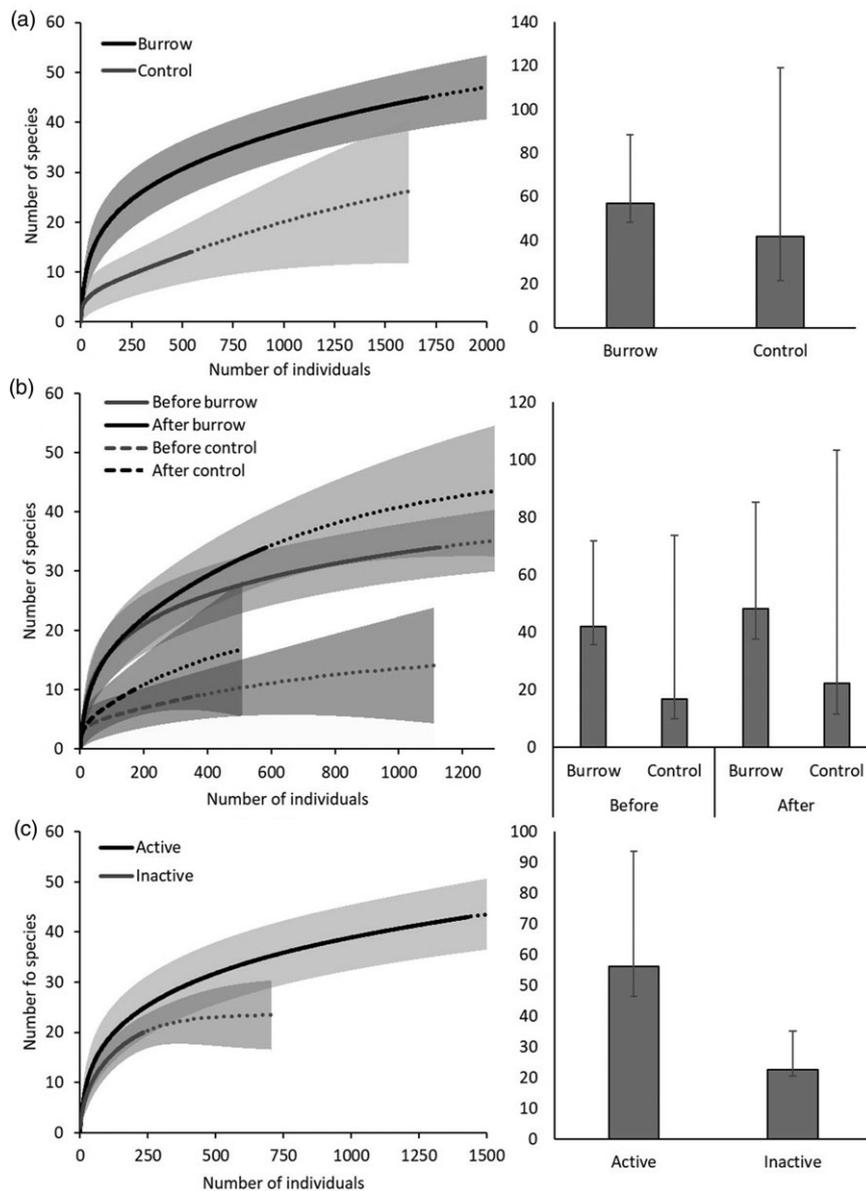
Figure 3 Species richness estimates calculated using individual-based extrapolation (left column), and individual based rarefaction, giving an asymptotic species richness estimate (right column). 95% confidence intervals are used throughout, and data is extrapolated to three times the original sample size. (a) The species richness is likely to be greater at burrow sites, however the 95% confidence intervals overlap due to high variation at control cameras. (b) The species richness does not change after fire. (c) The species richness is greater at maintained burrows than abandoned burrows

of species throughout the world (Ceballos *et al.*, 1999; Waterman & Roth, 2007; Kinlaw & Grasmueck, 2012).

The second category of relationship is that of species that re-engineer bilby burrows, capitalizing on opportunities afforded by the burrow; for example, using the vertical walls of the entrance to create their own burrows (e.g. pardalotes) or digging into the soft soil of the spoil heap. The structural irregularity of the burrows appears to make a preferred nesting site and presumably provides and thermal and anti-predator

benefit as well. Similarly, Florida Mouse (*Podomys floridanus*) often re-engineer burrows of gopher tortoises, creating complex series of subterranean tunnels (Jones & Franz, 1990; Kinlaw & Grasmueck, 2012).

The last category is that of species that use the mouth of the burrow and apron (while not necessarily or very infrequently, entering the burrow itself). This category included birds and lizards that rest in the shade and lizards that bask on the open apron, and also forage in the shallow depression in
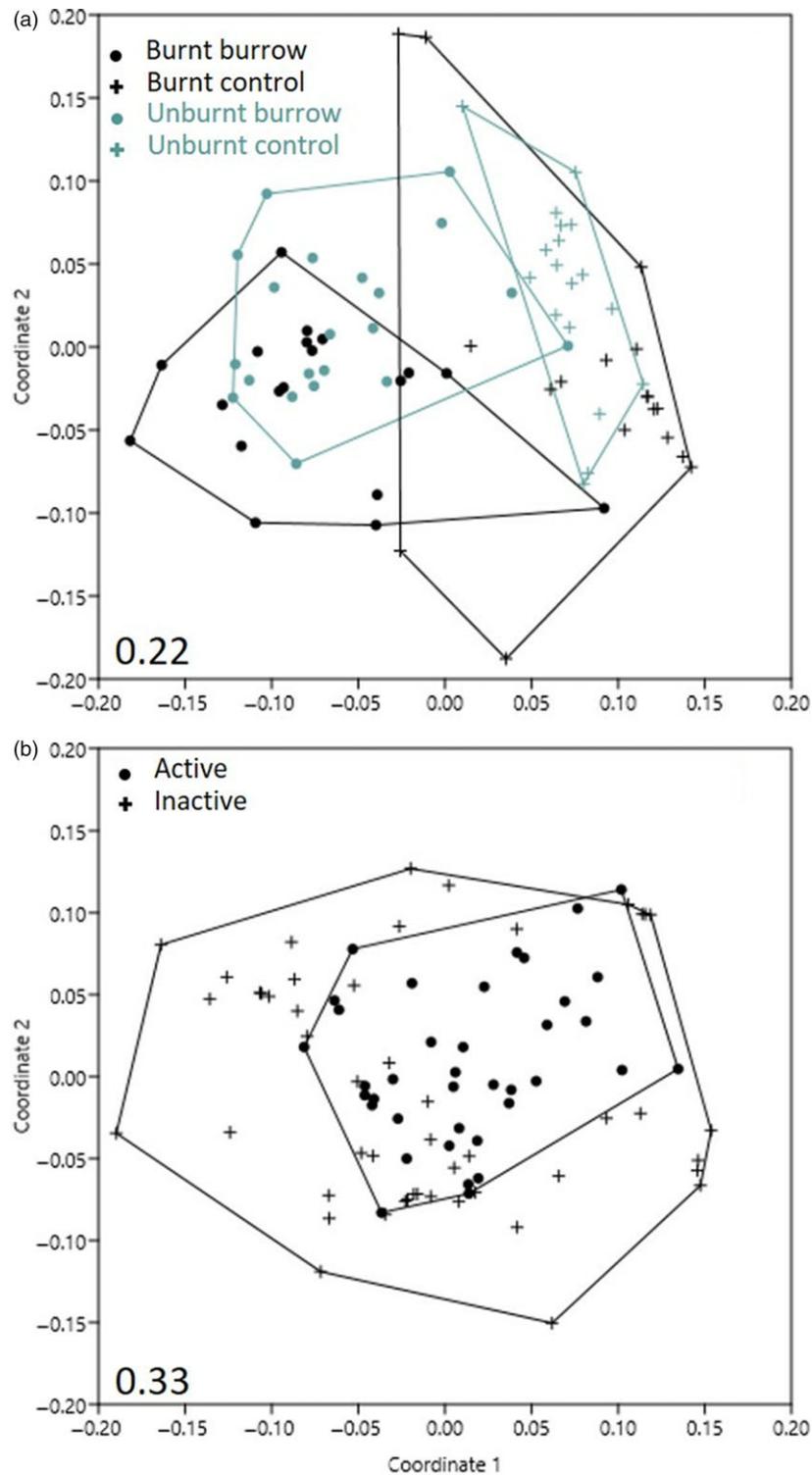
Figure 4 Community composition for taxa interacting with bilby burrows, each datum point represents a single burrow or control site monitored by camera trap. Datum points close to each other have similar communities, and the level of overlap between groups shows the level of similarity between treatments/populations, the significance of which is tested using an ANOSIM. Stress values are shown in the bottom left corner. (a) The species assemblage at unburnt burrows and unburnt control camera stations at the Grass-seed population were significantly different. Similarly, unburnt burrows and burnt burrows had the same assemblage, while the assemblage at control sites changed significantly after fire. (b) The community assemblage at maintained burrows was not different from abandoned burrows.
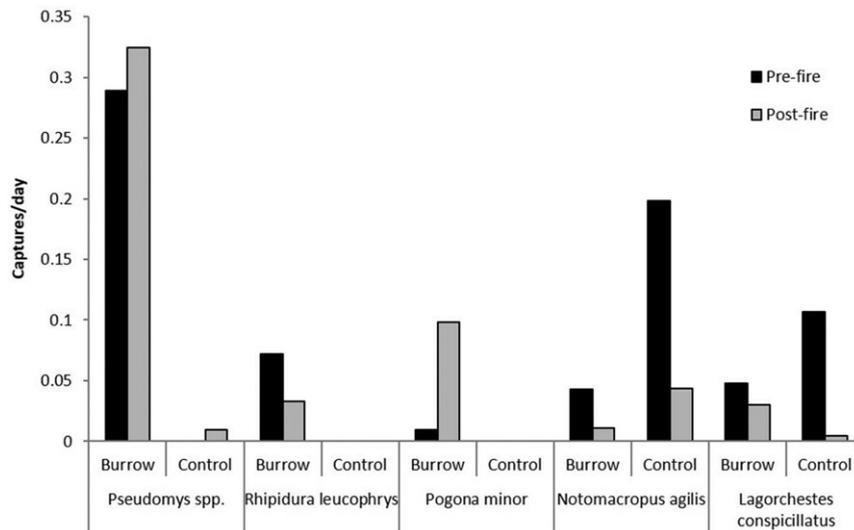
Figure 5 Trap rate (capture per day) of the 6 most common taxa at the 'Grass-seed' site, across all burrows, before and after fire. Difference in species trap rate between burrows and control stations is compared using only the black bars.

front of the burrow, which often acts as a trap for leaf litter (Newell, 2008; James, Eldridge & Moseby, 2010; Chapman, 2013) and in turn supports invertebrates that are often associated with the burrow or the apron (Read *et al.*, 2008). This category was the best represented in the current study, which was likely to reflect our use of camera traps, as opposed to excavating burrows. A range of mammals (Desbiez & Kluyber, 2013) and birds (Dziadzio & Smith, 2016) have similarly been recorded using the apron of burrows while not entering the entrance of the burrow. We conclude that the resources provided by the burrow apron, such as litter and invertebrates for foraging (Read *et al.*, 2008; Desbiez & Kluyber, 2013), shade (Dziadzio & Smith, 2016), or increased soil moisture (Chapman, 2013) benefit a range of species that, until the use of camera traps for monitoring, were largely excluded from analysis of burrow commensals. Furthermore, in this last category we include predators such as feral cats, foxes and dingoes, as they were commonly observed investigating the mouth of burrows. Predators are often observed investigating the burrow of potential prey species (Sillero-Zubiri & Gottelli, 1995; Agha *et al.*, 2017; Hofstede & Dziminski, 2017) presumably to concentrate search effort on areas of higher activity.

Future research investigating the reasons species have for interacting with burrows may benefit from using fencing or netting burrows, to separate species that inhabit the burrows, from those that interact while passing (e.g. Read *et al.*, 2008).

Limitations

In the current study, we were conservative in our classification of animal behavior by not classifying captures as entering or exiting a burrow unless absolutely sure, unlike other previous studies (e.g. Hofstede & Dziminski, 2017; Thornett, Ostendorf & Taggart, 2017). While camera trapping can under-represent reptiles and invertebrates (Meek *et al.*, 2012), we also found

that cameras frequently did not detect even relatively large species, such as bilbies, entering burrows that they were shown later to have been occupying, indicating that movement in or out of the burrow often did not trigger the cameras. However, this conservative approach may have caused misleading results for some species. For example, *Pseudomys* spp. were recorded passing burrows more than interacting with them, even though there were records of this taxa entering and exiting burrows. We believe *Pseudomys* spp. exited and entered burrows at high speed, which in addition to their small body size, caused cameras to fail to trigger in most instances. Future studies that do not rely solely on the use of cameras could reveal more about the behavior of such animals.

It is possible that some of the difference observed between control and burrows cameras was due to burrows sometimes being located at surface irregularities (the base of trees, shrubs, or mounds of dirt), that may dissuade larger species from walking over the burrow. However, there was no consistent difference in vegetation density between control and burrow cameras, we therefore consider it unlikely that this introduces any significant bias.

Conclusion

Our results show that a diverse range of taxa interact with bilby burrows, indicating that camera trapping is a valuable method for identifying species that interact with burrows, supporting the findings of previous studies (Table 1). Bilby burrows are important features in the landscape, and may provide an important shelter resource for many species, especially after fire. We echo the calls of Hofstede & Dziminski (2017) that bilby burrows should be considered alongside the traditional text book examples of burrowing ecosystem engineers: gopher tortoises, prairie dogs (*Cynomys* spp.) and the kangaroo rat (*Dipodomys* spp.) (Table 1 and references therein). Future

studies of the importance of bilby burrows should investigate differences in biodiversity between sites with burrows and those without, as has been conducted in the United States and Mexico (Ceballos *et al.*, 1999; Desmond *et al.*, 2000).

Acknowledgements

Authors' contributions

PB, PF originally formulated the idea. SD and PF developed methodology and performed statistical analyses. SD, PA, PB and PF conducted fieldwork. SD and LB conducted imaging analysis. SD, KM, PW and PF wrote the manuscript. PA, KW and HK provided helpful comments on drafts.

References

Agha, M., Smith, A.L., Lovich, J.E., Delaney, D., Ennen, J.R., Briggs, J., Fleckenstein, L.J., Tennant, L.A., Puffer, S.R., Walde, A., Arundel, T.R., Price, S.J. & Todd, B.D. (2017). Mammalian mesocarnivore visitation at tortoise burrows in a wind farm. *J. Wildl. Manag.* **81**, 1117–1124.

Alexy, K.J., Brunjes, K.J., Gassett, J.W. & Miller, K.V. (2003). Continuous remote monitoring of gopher tortoise burrow use. *Wildl. Soc. Bull.* **1973–2006**(31), 1240–1243.

Bartel, R.A., Haddad, N.M. & Wright, J.P. (2010). Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. *Oikos* **119**, 883–890.

Beard, J.S. (1990). *Plant life of western Australia*. Kenthurst: Kangaroo Press, 319 p.-illus., col. illus., maps. ISBN 864172796

Burbidge, A., Short, J. & Fuller, P. (2007). Relict *Bettongia lesueur* warrens in Western Australian deserts. *Aust. Zool.* **34**, 97–103.

Campos-Arceiz, A. (2009). Shit happens (to be useful)! Use of elephant dung as habitat by amphibians. *Biotropica* **41**, 406–407.

Ceballos, G., Pacheco, J. & List, R. (1999). Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *J. Arid Environ.* **41**, 161–172.

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scand. J. Stat.* **11**, 265–270.

Chapman, T.F. (2013). Relic bilby (*Macrotis lagotis*) refuge burrows: assessment of potential contribution to a rangeland restoration program. *Rangel. J.* **35**, 167–180.

Colwell, R.K. (2013). EstimateS: statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R.K., Mao, C.X. & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**, 2717–2727.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L. & Longino, J.T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J. Plant Ecol.* **5**, 3–21.

R Core Team (2018). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Craig, M.D., Garkaklis, M.J., St. J Hardy, G.E., Grigg, A.H., Grant, C.D., Fleming, P.A. & Hobbs, R.J. (2007). Ecology of the western bearded dragon (*Pogona minor*) in unmined forest and forest restored after bauxite mining in south-west Western Australia. *Australian Journal of Zoology* **55**, 107–116.

Crain, C.M. & Bertness, M.D. (2006). Ecosystem engineering across environmental gradients: implications for conservation and management. *AIBS Bull.* **56**, 211–218.

Dangerfield, J., McCarthy, T. & Ellery, W. (1998). The mound-building termite Macrotermes michaelseni as an ecosystem engineer. *J. Trop. Ecol.* **14**, 507–520.

Davidson, A.D. & Lightfoot, D.C. (2007). Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* **30**, 515–525.

Davidson, A., Lightfoot, D. & McIntyre, J. (2008). Engineering rodents create key habitat for lizards. *J. Arid Environ.* **72**, 2142–2149.

Davidson, A.D., Detling, J.K. & Brown, J.H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* **10**, 477–486.

Derrick, A.M., Conner, L.M. & Castleberry, S.B. (2010). Effects of prescribed fire and predator exclusion on refuge selection by Peromyscus gossypinus Le Conte (cotton mouse). *Southeast. Nat.* **9**, 773–780.

Desbiez, A.L.J. & Kluyber, D. (2013). The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. *Biotropica* **45**, 537–540.

Desmond, M.J., Savidge, J.A. and Eskridge, K.M. (2000). Correlations between burrowing owl and black-tailed prairie dog declines: a 7-year analysis. Papers in Natural Resources: 162.

Dziadzio, M.C. & Smith, L.L. (2016). Vertebrate use of gopher tortoise burrows and aprons. *Southeast. Nat.* **15**, 586–594.

Fleming, P.A. & Loveridge, J.P. (2003). Miombo woodland termite mounds: resource islands for small vertebrates? *J. Zool.* **259**, 1–8.

Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E. & Hardy, G.E.S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mamm. Rev.* **44**, 94–108.

Friend, G.R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biol. Cons.* **65**, 99–114.

Gharajehdaghipour, T., Roth, J.D., Fafard, P.M. & Markham, J.H. (2016). Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. *Sci. Rep.* **6**, 1–7. srep24020

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391.

Gutierrez, J.L., Jones, C.G., Strayer, D.L. & Iribarne, O.O. (2003). Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* **101**, 79–90.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001). PAST: paleotological Statistics software package for education and data analysis. *Palaeotol. Elctr.* **4**, 9.

Hawkins, L. & Nicoletto, P. (1992). Kangaroo rat burrows structure the spatial organization of ground-dwelling animals in a semiarid grassland. *J. Arid Environ.* **23**, 199–208.

Haynes, G. (2012). Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology* **157**, 99–107.

Hofstede, L. & Dziminski, M.A. (2017). Greater bilby burrows: important structures for a range of species in an arid environment. *Aust. Mammal.* **39**, 227–237.

Jackson, D. & Milstrey, E. (1989). The fauna of gopher tortoise burrows Gopher tortoise relocation symposium proceedings. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Technical Report. 5: pp. 86–98.

Jackson, S.M., Groves, C.P., Fleming, P.J.S., Aplin, K.P., Eldridge, M.D.B., Gonzalez, A. & Helgen, K.M. (2017). The Wayward Dog: is the Australian native dog or Dingo a distinct species? *Zootaxa* **4317**, 201–224.

James, A.I. & Eldridge, D.J. (2007). Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biol. Cons.* **138**, 351–359.

James, A.I., Eldridge, D.J. & Hill, B.M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecography* **32**, 723–732.

James, A.I., Eldridge, D.J. & Moseby, K.E. (2010). Foraging pits, litter and plant germination in an arid shrubland. *J. Arid Environ.* **74**, 516–520.

Johnson, K.A. (1989). Thylacomidae. In *Fauna of Australia: Mammalia*, vol 1B: 625–635. Walton, D.W. & Richardson, B.J. (Eds). Canberra: Australian Government Publishing Service.

Jones, C.A. & Franz, R. (1990). Use of gopher tortoise burrows by Florida mice (*Podomys floridanus*) in Putnam County, Florida. *Fla. Field Nat.* **18**, 45–51.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). *Organisms as Ecosystem Engineers*: 130–147. Springer New York: Ecosystem Management. New York.

Jones, C.G., Gutiérrez, J.L., Byers, J.E., Crooks, J.A., Lambrinos, J.G. & Talley, T.S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos* **119**, 1862–1869.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–1957.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C. & Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *Eur. J. Soil Biol.* **47**, 215–222.

Kenneally, K.F., Edinger, D.C. & Willing, T. (1996). *Broome and beyond: plants and people of the Dampier Peninsula, Kimberley, Western Australia*. Perth: Department of Conservation and Land Management, Como, Western Australia.

Kinlaw, A. (1999). A review of burrowing by semi-fossorial vertebrates in arid environments. *J. Arid Environ.* **41**, 127–145.

Kinlaw, A. & Grasmueck, M. (2012). Evidence for and geomorphologic consequences of a reptilian ecosystem engineer: the burrowing cascade initiated by the gopher tortoise. *Geomorphology* **157**, 108–121.

Kowalski, M. and Kowalski, M. (2012). EXIFPro 2.0. California.

Layne, J.N. & Jackson, R.J. (1994). Burrow use by the Florida mouse (*Podomys floridanus*) in south-central Florida. *Am. Midl. Nat.* **131**, 17–23.

Lee, J.E., Larsen, R.T., Flinders, J.T. & Eggett, D.L. (2010). Daily and seasonal patterns of activity at pygmy rabbit burrows in Utah. *West. N. Am. Nat.* **70**, 189–197.

Meek, P.D., Ballard, G. & Fleming, P. (2012). *An introduction to camera trapping for wildlife in Australia*. Canberra: Invasive Animals Cooperative Research Centre.

Milne, T., Bull, C.M. & Hutchinson, M.N. (2003). Use of burrows by the endangered pygmy blue-tongue lizard, *Tiliqua adelaidensis* (Scincidae). *Wildl. Res.* **30**, 523–528.

Mori, E., Menchetti, M. & Balestrieri, A. (2015). Interspecific den sharing: a study on European badger setts using camera traps. *Acta Ethologica* **18**, 121–126.

Moseby, K.E. & O'Donnell, E. (2003). Reintroduction of the greater bilby, *Macrotis lagotis* (Reid) (Marsupialia: Thylacomyidae), to northern South Australia: survival, ecology, and notes on reintroduction protocols. *Wildl. Res.* **30**, 15–27.

Moseby, K., Nano, T. & Southgate, R.I. (2012). *Tales in the sand: a guide to identifying Australia arid zone fauna using spoor and other signs*. Ecological Horizons.

Newell, J. (2008). *The role of the reintroduction of Greater Bilbies (Macrotis lagotis) and Burrowing Bettings (Betongia lesueur) in the ecological restoration of an arid ecosystem: foragin diggings, diet, and soil seed banks*. Adelaide: University of Adelaide.

Niedballa, J., Courtiol, A. and Sollmann, R. (2017). camtrapR: camera trap data management and preparation of occupancy and spatial capture-recapture analyses. R package version 0.99.8.

Pike, D. & Mitchell, J. (2013). Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Anim. Conserv.* **16**, 694–703.

Platt, B.F., Kolb, D.J., Kunhardt, C.G., Milo, S.P. & New, L.G. (2016). Burrowing through the literature: the impact of soil-disturbing vertebrates on physical and chemical properties of soil. *Soil Sci.* **181**, 175–191.

Pringle, R.M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* **89**, 26–33.

Read, J.L., Carter, J., Moseby, K.M. & Greenville, A. (2008). Ecological roles of rabbit, bettong and bilby warrens in arid Australia. *J. Arid Environ.* **72**, 2124–2130.

Sillero-Zubiri, C. & Gottelli, D. (1995). Diet and feeding behavior of Ethiopian wolves (*Canis simensis*). *J. Mammal.* **76**, 531–541.

Smyth, D.R. & Philpott, C.M. (1968). Field notes on rabbit bandicoots, *Macrotis lagotis* Reid (Marsupialia), from central Western Australia. *Trans. R. Soc. S. Aust.* **92**, 3–17.

Thackway, R. and Cresswell, I. (1995). *An interim biogeographic regionalisation for Australia: a framework for establishing the national system of reserves, Version 4.0.* Canberra: Australian Nature Conservation Agency: 88.

Thornett, E., Ostendorf, B. & Taggart, D.A. (2017). Interspecies co-use of southern hairy-nosed wombat (*Lasiorhinus latifrons*) burrows. *Aust. Mammal.* **39**, 205–212.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biol. Cons.* **144**, 902–912.

Vaughan, T.A. (1961). Vertebrates inhabiting pocket gopher burrows in Colorado. *J. Mammal.* **42**, 171–174.

Venebles, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*. New York: Springer.

Walde, A.D., Walde, A.M., Delaney, D.K. & Pater, L.L. (2009). Burrows of desert tortoises (*Gopherus agassizii*) as thermal refugia for horned larks (*Eremophila alpestris*) in the Mojave Desert. *Southwest. Nat.* **54**, 375–381.

Waterman, J.M. & Roth, J.D. (2007). Interspecific associations of Cape ground squirrels with two mongoose species: benefit or cost? *Behav. Ecol. Sociobiol.* **61**, 1675–1683.

Wesche, K., Nadrowski, K. & Retzer, V. (2007). Habitat engineering under dry conditions: the impact of pikas (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. *J. Veg. Sci.* **18**, 665–674.

Witz, B.W., Wilson, D.S. & Palmer, M.D. (1991). Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. *Am. Midl. Nat.* **126**, 152–158.

Woinarski, J., Burbidge, A. & Harrison, P. (2014). *Action plan for Australian mammals 2012*. Collingwood: CSIRO Publishing.

Wright, J.P. & Jones, C.G. (2004). Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* **85**, 2071–2081.

Wright, J.P., Jones, C.G. & Flecker, A.S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**, 96–101.