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The parasites of free-ranging terrestrial wildlife from Australia's south-west

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ABSTRACT

The conservation management of threatened wildlife increasingly relies upon translocations to augment populations. Translocations, however, pose various risks: from the host perspective these include the spread of parasitic disease, whereas from a broader biodiversity perspective translocation may lead to the loss of rare parasites and other dependent fauna. Although Disease Risk Analyses are recommended during translocation planning, knowledge regarding the parasites infecting threatened species or their pathogenicity is often lacking. Between March 2014 and June 2016, woylies (*Bettongia penicillata*) and sympatric marsupials were screened for the presence of endo- and ectoparasites, during two fauna translocations in south-western Australia. Here, we summarise the parasite taxa identified from *B. penicillata*, brush-tailed possums (*Trichosurus vulpecula hypoleucus*) and chuditch (*Dasyurus geoffroii*), including prevalence data for host, parasite taxon and site. Results from the opportunistic sampling of other species (*Isoodon fusciventer*, *Phascogale tapoatafa wambenger*, *Tiliqua rugosa* and *Felis catus*) are also presented. New host–parasite records including *Hepatozoon* spp. from *T. v. hypoleucus*, *Trypanosoma noyesi* from *T. rugosa*, *Ixodes australiensis* and *Ixodes tasmani* from *D. geoffroii*, and *I. australiensis* and *Amblyomma* sp. from a *P. t. wambenger* were identified. This study highlights the importance of monitoring sympatric species, particularly when compiling baseline data of parasite fauna present within translocation sites and enhances our knowledge of parasites infecting terrestrial wildlife within Australia's south-west, a Global Biodiversity Hotspot.

Keywords: *Bettongia penicillata*, *Dasyurus geoffroii*, disease, fauna translocation, *Hepatozoon* spp, host-parasite ecology, *Isoodon fusciventer*, *Phascogale tapoatafa wambenger*, *Tiliqua rugosa*, *Trichosurus vulpecula hypoleucus*, trypanosome, woylie.

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Introduction

Interactions between wildlife, domestic animals and humans are increasing globally, enhancing the likelihood of disease transmission including the spillover of pathogens with zoonotic potential (Leifels *et al.* 2022). As such, wildlife health surveillance for the detection of emerging zoonotic disease continues to receive significant attention. The importance of understanding wildlife pathogen diversity, however, also benefits the conservation management of threatened species and the broader ecosystem (Thompson *et al.* 2010). On the one hand, wildlife disease is poorly understood and although identified as a key threat to some species at risk of extinction (e.g. McCallum 2012), its importance is likely to be globally underestimated. On the other hand, parasites may play key roles in maintaining ecosystem function, through direct and indirect effects on free-living communities (Preston *et al.* 2016; Lymbery and Smit 2023). More research is needed to determine the biological significance of parasites and the effect of altering host–parasite associations on individual hosts (e.g. reproductive fitness, survivorship), host populations (e.g. population health, growth rates) and community interactions (e.g. competition, predation), particularly during conservation management interventions where disease risk may be heightened (e.g. fauna translocations: Ewen *et al.* 2015).

Fauna translocations play a pivotal role in the management of threatened fauna worldwide, with their conservation benefits extending beyond the species being translocated to also re-establish natural ecosystem structures and processes (IUCN/SSC 2013). Within Australia, translocations are increasingly employed to manage threatened fauna, though success rates remain low (Morris *et al.* 2015; Watkins *et al.* 2018). Although introduced predators have been unequivocally identified as a key factor contributing towards the failure of many translocations of medium-sized terrestrial mammals within Australia (Short 2010; Morris *et al.* 2015; Moseby *et al.* 2015), other factors such as disease may also impact translocation outcomes (Thompson *et al.* 2010; Ewen *et al.* 2015; Vaughan-Higgins 2019).

Parasites are often considered a major 'health hazard' during translocations (Ewen *et al.* 2015) and have been associated with translocation failures (e.g. chytridiomycosis: Scheele *et al.* 2021). Parasites also form a vital component of biodiversity (Hudson *et al.* 2006; Dougherty *et al.* 2016) and there is growing evidence to suggest that host immunity and the persistence of host populations may be enhanced if parasites are conserved, rather than eradicated, during translocation (Pizzi 2009; McGill *et al.* 2010; Boyce *et al.* 2011; Rideout *et al.* 2016). Many parasites have coevolved with their host, and do not induce disease under homeostatic conditions (Clark 2011); however, fauna translocations have the potential to disrupt the parasite community within a host (see Northover *et al.* 2018*a*), which may change the host–parasite balance to the detriment of either the host (Telfer *et al.* 2010) or the parasite (Moir *et al.* 2012). Although parasite management during translocations has been reviewed (e.g. Cunningham 1996; Stringer and Linklater 2014; Northover *et al.* 2018*a*) and frameworks to manage disease risk developed (e.g. Ewen *et al.* 2015; Dunlop and Watson 2022), parasites and parasitic disease are still not adequately considered during translocations. To assess both the disease risks associated with translocating wildlife and the extinction risk to parasites and other dependent fauna accompanying translocated wildlife, knowledge regarding the parasite species infecting a host and other sympatric species is required.

The woylie or brush-tailed bettong (*Bettongia penicillata* Gray, 1837) is an Australian macropodoid marsupial (Family Potoroidae), that is currently listed as Critically Endangered (Woinarski and Burbidge 2016). Once abundant across most of southern and central Australia, *B. penicillata* populations suffered catastrophic declines following European settlement (de Tores and Start 2008). By the 1960s populations of *B. penicillata* were confined to three isolated areas: the Upper Warren region [UWR (Kingston and Perup subpopulations)], Tutanning and Dryandra Woodland (henceforth referred to as Dryandra), within south-western Australia (Sampson 1971; Wayne *et al.* 2015). The Tutanning population is now considered functionally extinct (Pacioni *et al.* 2014; A. Wayne pers. comm.).

In response to conservation efforts (namely introduced predator control and translocations) *B. penicillata* numbers recovered, and in 1996 the species conservation status was downgraded (Start *et al.* 1998). Unexpectedly, however, *B. penicillata* populations declined by more than 90% between 1999 and 2006 (Wayne *et al.* 2013). The nature of the declines, with a distinctive spatio-temporal pattern in conjunction with a high prevalence of skin disease, was suggestive of infectious disease (Wayne *et al.* 2015). Health investigations conducted during the decline failed to identify an underlying cause (Wayne *et al.* 2013); however, research has been ongoing, and recovery initiatives have secured the persistence of the species, with the extant UWR and Dryandra populations showing signs of recovery in recent years (National Environmental Science Program Threatened Species Research Hub 2019).

Over the past decade studies have focused on the potential role of trypanosomes (blood-borne parasites) given their pathogenicity and association with *B. penicillata* population declines (Smith *et al.* 2008; Botero *et al.* 2013; Thompson *et al.* 2014*a*; Godfrey *et al.* 2018). The role of viruses has also been explored, though Pacioni *et al.* (2014) found no evidence of exposure to viral pathogens in several *B. penicillata* populations, concluding that viral disease was an unlikely cause of the declines. While Skogvold *et al.* (2017) subsequently detected herpesviruses in *B. penicillata* from Perup Sanctuary, infected hosts ($n = 5$) did not show signs of disease, thus the clinical significance of infection remains uncertain. The role of other parasites (e.g. Rong *et al.* 2012; Northover *et al.* 2018*b*) and stress (e.g. Hing *et al.* 2017) has also been investigated, as has the coextinction risk for the parasite community associated with *B. penicillata* (Thompson *et al.* 2018).

In comparison to *B. penicillata*, knowledge of host–parasite associations in wild populations of sympatric marsupials such as the koomal or brush-tailed possum (*Trichosurus vulpecula hypoleucus*) and chuditch or western quoll (*Dasyurus geoffroii*) is limited, with most records documented from captive animals or those inhabiting urban and periurban environments (e.g. Haigh 1994; Clark 2011; Hillman *et al.* 2018; Loh *et al.* 2018; Egan *et al.* 2021). In wild populations, Thomasz (2014) documented the parasites infecting *D. geoffroii* ($n = 36$) from Julimar Conservation Park and the UWR during a translocation project, and Cooper *et al.* (2018) investigated the *Trypanosoma* spp. infecting *T. vulpecula* ($n = 32$) and *D. geoffroii* ($n = 3$) within the UWR. Molecular surveillance of ticks parasitising marsupials has provided further insight regarding the *Trypanosoma* spp. infecting *T. vulpecula* ($n = 15$) (Krige *et al.* 2021*a*).

Given the poor understanding of the parasite species infecting Western Australia's (WA) native fauna (Wayne *et al.* 2015), the purpose of this study was to screen wild populations of *B. penicillata* and sympatric species (primarily *T. v. hypoleucus* and *D. geoffroii*) within the UWR and Dryandra for the presence of blood-borne, gastrointestinal and ectoparasite taxa to better understand parasite diversity among hosts and between sites. Exposure to *Toxoplasma*

gondii was also examined in a subset of *B. penicillata*. We were particularly interested in documenting the prevalence of host-generalist parasites (i.e. those able, in the same stage of the life cycle, to infect more than one species of host), because they may pose a greater disease risk to declining host populations (De Castro and Bolker 2005) and are more likely to cause emerging infectious disease (Dharmarajan *et al.* 2021). By obtaining a greater understanding of the parasite diversity present within WA's native fauna populations, we hope to improve the management of threatened species and their parasite taxa during future translocations, to better inform Disease Risk Analyses and guide the conservation of parasite species, where these do not pose a disease risk to their hosts.

Methods

Trapping and sample collection

Between March 2014 and June 2016, small mammal trapping was conducted within the UWR and Dryandra in collaboration with the Department of Biodiversity, Conservation and Attractions (DBCA) (under Regulation 4 and 17 Scientific Licences), during two fauna translocations to supplement wild *B. penicillata* populations in south-western WA (see Northover *et al.* (2019*a*) and (2019*b*) for details of trapping regime). Ethics approval was obtained from Murdoch University (permit number RW2659/14). *Bettongia penicillata* were translocated (1) from Perup Sanctuary into two unfenced sites, Walcott and Warrup East, in June 2014; and (2) from six unfenced sites within the UWR (Balban, Boyicup, Corbal, Dudijup, Dwalgan and Winnejup), into an unfenced site within Dryandra in June 2015 (Fig. 1). Animals were monitored for up to 12 months following translocation.

Animals were captured using Sheffield cage traps, which were set at dusk and baited with universal bait (peanut butter, rolled oats and sardines). Trapping equipment and handling bags were cleaned and sterilised prior to each trapping session, but were used for all species, over consecutive days. Bags were shaken out to remove faeces, hair, dirt etc. (or replaced if soiled) after handling each animal to reduce the risk of cross contamination. Fresh newspaper was placed under each trap after each capture, and traps were roughly cleaned (i.e. shaken out or brushed) in the field to remove large bits of faecal material prior to resetting. Except for July 2015 (night trapping), traps were cleared at first light within 3 h of sunrise each day.

Samples were collected from animals at each capture. Individual (target) animals were identified using two uniquely numbered ear-tags. Blood and ectoparasites were obtained using manual restraint in *B. penicillata*, bobtail (shingleback) lizards (*Tiliqua rugosa*), and a brush-tailed phascogale (*Phascogale tapoatafa wambenger*; ectoparasites opportunistically collected by DBCA staff), and under general anaesthesia for all other species. Inhalational anaesthesia

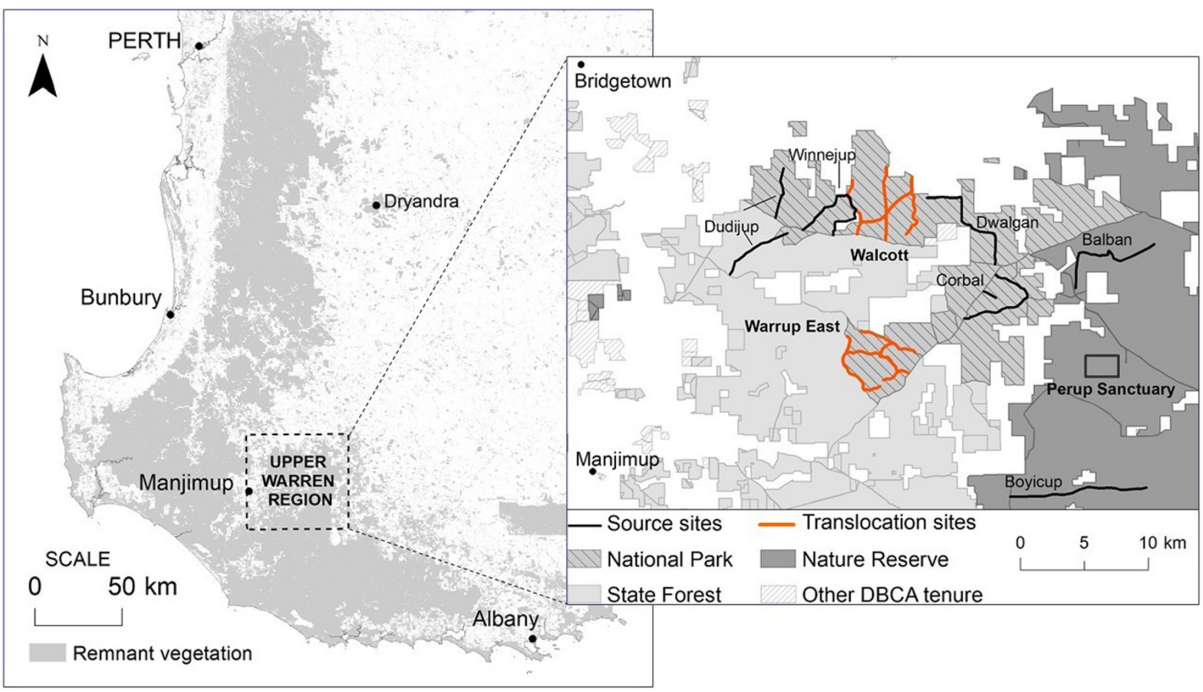

Fig. 1. Map illustrating our study sites within south-western Western Australia. The box (right) shows Walcott and Warrup East (orange) in relation to Perup Sanctuary and the six UWR transects. Dryandra is located roughly 150 km north-east of the Upper Warren region.

using isoflurane in 100% oxygen was delivered via facemask under the supervision of a registered veterinary surgeon in the field.

Parasite analysis

Haemoparasites

Up to 1 mL of blood was collected from the lateral caudal (tail) vein in *B. penicillata*, and either the jugular or tail vein in other marsupials, into EDTA MiniCollect tubes (Greiner Bio-One, Germany), and frozen at −20°C before processing. In *T. rugosa*, up to 0.5 mL of blood was collected from the ventral coccygeal vein. Peripheral blood smears were prepared in the field using the 'wedge' method (see Clark *et al.* 2004) and stained with Diff-Quik prior to mounting with dibutylphthalate polystyrene xylene. Blood smears from a subset of *Trypanosoma*-positive hosts (*B. penicillata* and *T. v. hypoleucus* only) were inspected by light microscopy for the presence of haemoprotozoans. *Trypanosoma* spp. were the main haemoparasites monitored during this study, though the seroprevalence of *T. gondii* was also determined in a subset of *B. penicillata*. Trypanosome detection methods (PCR and Sanger sequencing) have been described by Northover *et al.* (2019*a*). While clade specific primers were used to identify *T. vegrandis*, *T. copemani* and *T. noyesi*, Sanger sequencing was used to identify *T.* sp. ANU2 and *T. gilletti*, as species specific primers for these trypanosomes were not available. Targeted amplicon next generation sequencing of the *Trypanosoma 18S* rDNA loci (see Cooper *et al.* 2018) was performed on samples in which species identification could not be achieved with Sanger sequencing.

Toxoplasma gondii

A commercial modified agglutination test (Toxo-Screen DA, bioMerieux, France) was used as per the manufacturer's instructions to determine the seroprevalence of *T. gondii*. In this test, formalin-treated *T. gondii* antigen was added to the sera and agglutination was expected to occur in the presence of specific IgG antibodies (Couzineau and Baufine-Ducrocq 1970). A denaturing agent (2-mercaptoethanol) was used to avoid agglutination by non-specific IgM antibodies (Couzineau and Baufine-Ducrocq 1970). Each sample used two dilutions (1/40 and 1/4000) and every plate contained a positive, negative, and antigen control. Results were interpreted as per the manufacturer's guidelines, whereby a seropositive result presented as an agglutination mat covering more than half of the well, and a seronegative result presented as a red button. Borderline reactions were retested.

Gastrointestinal parasites

Newspaper was placed under each trap to collect faeces. Faecal samples were preserved in 10% buffered formalin and refrigerated at 4°C until processing. Faeces were examined for the presence of gastrointestinal parasite eggs, oocysts, and larvae, using the modified sodium nitrate ($NaNO_3$) faecal flotation protocol described by Northover *et al.* (2017); see Appendices (Figs 4–7) for criteria used to differentiate gastrointestinal parasite taxa.

Ectoparasites

Each individual was examined in a systematic manner for the presence of ectoparasites (fleas, lice, mites and ticks). A subset of the different ectoparasites observed at the time of sampling were collected from each animal and stored in 70% ethanol. Ectoparasites were morphologically identified by Murdoch University parasitology staff using keys developed by Roberts (1970), von Kéler (1971), Dunnet and Mardon (1974), and Domrow (1987).

Data analysis

For each parasite taxon, prevalence of infection was calculated as the proportion of infected samples using Agresti-Coull 95% confidence intervals for sample sizes >40 and Wilson score 95% confidence intervals (with continuity correction) for sample sizes <40 (Brown *et al.* 2001), assuming a binomial distribution.

Results

Haemoparasites

Bettongia penicillata

The *Trypanosoma* spp. (and piroplasms) infecting *B. penicillata* have previously been documented, based on the analysis of 1211 blood samples from 596 individuals (Northover *et al.* 2019*a*). Here we analysed an additional 194 blood samples from 151 (119 not previously sampled) individuals for the presence of trypanosomes. With both datasets combined (1405 blood samples from 715 individuals) 54.0% of samples were *Trypanosoma*-positive (Table 1); 80 samples could not be identified to species. Prevalence of infection among individuals (i.e. a positive result at any time point during the monitoring period) was 65.3%. Of the remaining 1325 samples, five *Trypanosoma* species (*T. vegrandis*, *T. copemani*, *T. noyesi*, *T. gilletti* and *T.* sp. ANU2) were detected (Table 1). *Trypanosoma vegrandis* was most prevalent, followed by *T. copemani*, *T. noyesi*, *T.* sp. ANU2 and *T. gilletti* (Table 1).

Of the *Trypanosoma*-positive samples that could be identified to species ($n = 679$), the prevalence of *Trypanosoma* spp. coinfection was 23.1% (95% CI: 20.1–26.4%), with up to three *Trypanosoma* species detected in a single host (Appendix Fig. 1). *Trypanosoma* prevalence and diversity varied between sites, with the highest overall prevalence detected within Walcott and the lowest species diversity within Dryandra (Appendix Table 1); *T.* sp. ANU2 and *T. gilletti* were not detected within Dryandra. *Bettongia*

Table 1. Summary of the haemoparasites identified from marsupials during this study [no. infected/no. samples tested (% infected); 95% CI]; N/A means that no samples were examined for this particular host/parasite combination.

Haemoparasite	*B. penicillata*	*T. v. hypoleucus*	*D. geoffroii*
Overall *Trypanosoma* spp. prevalence	759/1405 (54.0%)	262/317 (82.6%)	14/119 (11.8%)
	51.4–56.6%	78.1–86.4%	7.1–19.0%
Trypanosoma vegrandis	402/1325 (30.3%)	77/313 (24.6%)	5/118 (4.2%)
	27.9–32.9%	20.2–29.7%	1.6–9.9%
Trypanosoma copemani	300/1325 (22.6%)	183/313 (58.5%)	8/118 (6.8%)
	20.5–25.0%	52.9–63.8%	3.3–13.1%
Trypanosoma noyesi	100/1325 (7.5%)	65/313 (20.8%)	8/118 (6.8%)
	6.2–9.1%	16.6–25.6%	3.3–13.1%
Trypanosoma sp. ANU2	30/1325 (2.3%)	3/313 (1.0%)	1/118 (0.8%)
	1.6–3.2%	0.2–2.9%	0.0–5.2%
Trypanosoma gilletti	11/1325 (0.8%)	0/313 (0.0%)	0/118 (0.0%)
	0.4–1.5%	0.0–1.5%	0.0–3.9%
Toxoplasma gondii	11/617 (1.8%)	0/4 (0.0%)	N/A
	1.0–3.2%	0.0–60.4%	
Unidentified piroplasms	Present	Present	N/A
Unidentified *Hepatozoon* spp.	Not detected	Present	N/A

penicillata translocated into Dryandra (UWR origin) were also negative for *T. gilletti*. Both trypanosomes and piroplasms (*Theileria* and *Babesia* spp.) were observed in peripheral blood smears from *B. penicillata* (Fig. 2).

A subset of *B. penicillata* blood samples ($n = 617$) collected from 349 individuals was also screened for *T. gondii*, of which 11 samples (1.8%) were positive. Of these, five were from Warrup East (0.8%), four were from Walcott (0.6%; includes two positive results from the same host at different time points) and two were from Dryandra (0.3%).

Trichosurus vulpecula hypoleucus

In total, 317 blood samples collected from 226 individuals were screened for trypanosomes, of which 262 samples (82.6%) were positive (Table 1). Four samples that were positive on general PCR screening, could not be identified to species. Prevalence of infection among individuals was 86.7%. Four *Trypanosoma* species were detected in *T. v. hypoleucus* (*T. copemani*, *T. vegrandis*, *T. noyesi* and *T.* sp. ANU2) (Table 1), including up to three *Trypanosoma* species in a single host (all *T. copemani*, *T. vegrandis*, *T. noyesi* coinfection) (Appendix Fig. 2). Overall, *T. copemani* was most prevalent, followed by *T. vegrandis* and *T. noyesi* (Table 1). *Trypanosoma* sp. ANU2 was detected in only three hosts from Warrup East (Appendix Table 2). Coinfection with two or more trypanosomes was detected in 26.0% (95% CI: 21.0–31.7%) of positive samples. Warrup East had the greatest *Trypanosoma* spp. prevalence (100%) and diversity (Appendix Table 2). An unknown *Hepatozoon* species was identified in three blood smears from *T. v. hypoleucus* (Fig. 3); all three hosts originated from Dryandra and *Trypanosoma* spp. infection (*T. copemani* and *T. vegrandis* coinfection in two cases; *T. copemani* in the other) was also apparent. Trypanosomes and unidentified piroplasms were also detected in blood smears (Fig. 3). Four (UWR) *T. v. hypoleucus* that were screened for *T. gondii* were seronegative.

Dasyurus geoffroii

We screened 119 blood samples from 97 individuals for the presence of trypanosomes. Of these, 14 samples (11.8%) were positive (Table 1); one sample could not be identified to species. Prevalence of infection among individuals was 14.4%. Four *Trypanosoma* species were identified in *D. geoffroii* (Table 1), including up to three *Trypanosoma* species in a single host (Appendix Fig. 3). *Trypanosoma copemani* and *T. noyesi* were equally most prevalent, followed by *T. vegrandis* and *T.* sp. ANU2 (Table 1). Coinfection was detected in 46.2% (95% CI: 20.4–73.9%) of positive samples. Despite the high number of *D. geoffroii* sampled within Dryandra ($n = 54$), only one host was *Trypanosoma*-positive (*T. noyesi*). Except for *T.* sp. ANU2, which was detected in a single host from Warrup East, Walcott had the highest prevalence of *Trypanosoma* spp. infection (Appendix Table 3). *Trypanosoma vegrandis* was not detected in *D. geoffroii* from Warrup East or Dryandra,

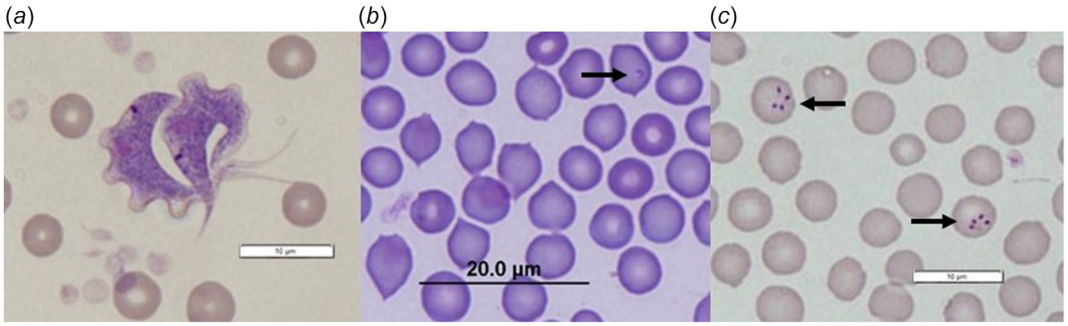

Fig. 2. Haemoparasites identified in peripheral blood smears from woylies (*Bettongia penicillata*): (*a*) *Trypanosoma copemani*; (*b*) *Theileria* sp. (black arrow); (*c*) *Babesia* sp. (black arrows).

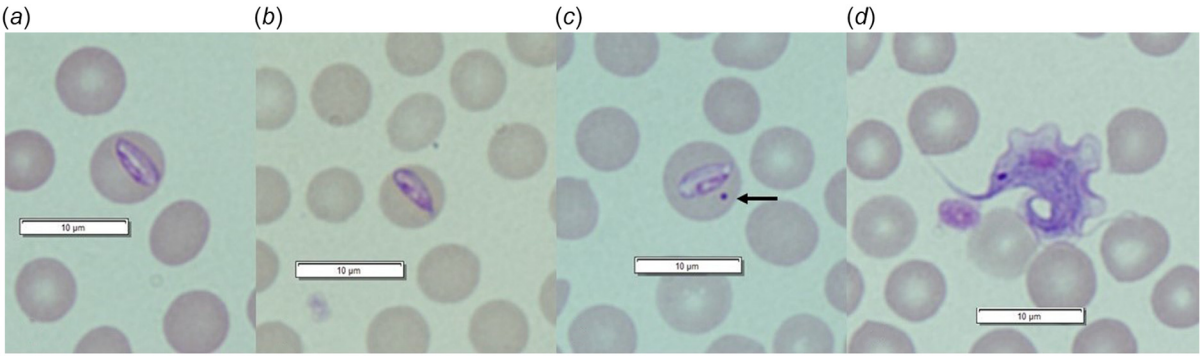

Fig. 3. Unidentified *Hepatozoon* spp. (*a*–*c*), a piroplasm (*c*; black arrow) and a *Trypanosoma* sp. (*d*) identified in blood smears from brush-tailed possums (*Trichosurus vulpecula hypoleucus*).

despite Warrup East (and Walcott) having high *Trypanosoma* spp. diversity.

Other species

Seven *T. rugosa* were screened for the presence of trypanosomes, three of which (42.9%) were positive; *Amblyomma albolimbatum* ticks were parasitising two of the *Trypanosoma*-positive hosts, the third had no visible ectoparasites. *Trypanosoma noyesi* was sequenced from two of the positive samples (Dryandra origin). The third positive sample (UWR origin) could not be interpreted with confidence due to difficulties encountered during the extraction process, thus species-level identification was not pursued. A single feral cat (*Felis catus*) captured during trapping in Warrup East tested negative for *Trypanosoma* spp. on general PCR screening. *Trypanosoma vegrandis* was sequenced in a quenda or south-western brown bandicoot (*Isoodon fusciventer*) from Perup Sanctuary; this was the only *I. fusciventer* screened for trypanosomes.

Gastrointestinal parasites

Bettongia penicillata

We examined 946 faecal samples collected from 377 individuals for the presence of gastrointestinal parasites. Five visually distinctive nematode eggs (typical strongyle, *Strongyloides*-like, *Potoroxyuris* sp., *Trichuris* sp. and *Linstowinema* sp.), a single type of cestode egg (undescribed species), coccidian oocysts (including *Eimeria woyliei*), and first stage (metastrongyloid) lungworm larvae were identified (Table 2, Appendix Fig. 4). *Eimeria woyliei* was identified in cases where sporulated oocysts were present and distinguishing morphological characteristics were observed (see Northover *et al.* 2019*c*); coccidian oocyst counts (Table 2) include *E. woyliei*. Unidentified nematode eggs/larvae were also found and may represent either infective nematode larvae or free-living nematodes.

Overall, 90.8% of samples contained at least one type of gastrointestinal parasite (including unidentified nematode eggs/larvae). Prevalence of infection among individuals was 95.2%. Excluding unidentified nematode eggs/larvae, strongyle eggs were most prevalent, with other parasite taxa detected less frequently (Table 2). Of the samples that were negative, the majority (92.1%) were from Dryandra. Except for cestode eggs, which were only detected in hosts from Dryandra, the prevalence and diversity of gastrointestinal parasite taxa was lowest within this site (Appendix Table 4). *Linstowinema* sp. eggs were found in just two hosts, while strongyle eggs, *Strongyloides*-like eggs and coccidian oocysts were ubiquitous across all sites. *Potoroxyuris* sp., *Trichuris* sp. eggs and lungworm larvae were only identified in hosts within or originating from Perup Sanctuary.

Trichosurus vulpecula hypoleucus

We examined 234 faecal samples from 112 hosts and detected four distinct types of nematode eggs (typical strongyle, *Parastrongyloides* sp., *Protospirura* sp. and oxyurid), a single type of anoplocephalid egg (*Bertiella* sp.), coccidian oocysts and unidentified nematode eggs/larvae (Table 2, Appendix Fig. 5). Distinctive, large gravid nematodes (approximately 200 µm in length) were also frequently observed (Appendix Fig. 5); we suspect these are free-living spp. based on their reproductive anatomy (Chitwood and Chitwood 1937). Overall, gastrointestinal parasites were identified in 74.4% of samples, and strongyle eggs were the most prevalent taxon detected (Table 2). Prevalence of infection among individuals was 92.0%. Species diversity was similar across all sites, with prevalences generally lower in Dryandra, except for coccidian oocysts and *Bertiella* sp. (Appendix Table 5). *Parastrongyloides* eggs were only found in hosts from the UWR, whereas strongyle eggs and coccidian oocysts were detected in all sites (Appendix Table 5).

Dasyurus geoffroii

We examined 112 faecal samples collected from 80 individuals and identified typical strongyle eggs, oxyurid eggs, spiruroid eggs (including *Physaloptera* sp.), two distinct anoplocephalid eggs [i.e. an unidentified sp. (Anoplocephalid egg) and *Bertiella* sp.], a *Capillaria* sp. egg, coccidian oocysts

Table 2. The gastrointestinal parasite taxa (in alphabetical order) detected in faeces from marsupials during this study [no. infected/no. samples tested (% infected); 95% CI].

Parasite taxa	*B. penicillata*	*T. v. hypoleucus*	*D. geoffroii*	*I. fusciventer*
Overall prevalence	**859/946 (90.8%)**	**174/234 (74.4%)**	**99/112 (88.4%)**	**12/12 (100%)**
	88.8–92.5%	**68.4–79.5%**	**81.0–93.2%**	**69.9–100%**
Anoplocephalid egg	0/946 (0%)	0/234 (0%)	**4/112 (3.6%)**	0/12 (0%)
	0.0–0.5%	0.0–2.0%	**1.1–9.2%**	0.0–30.1%
Australiformis sp. egg	0/946 (0%)	0/234 (0%)	0/112 (0%)	**1/12 (8.3%)**
	0.0–0.5%	0.0–2.0%	0.0–4.1%	**0.4–40.2%**
Bertiella sp. egg	0/946 (0%)	**10/234 (4.3%)**	**3/112 (2.7%)**	0/12 (0%)
	0.0–0.5%	**2.3–7.8%**	**0.6–8.0%**	0.0–30.1%
Capillaria sp. egg	0/946 (0%)	0/234 (0%)	**1/112 (0.9%)**	0/12 (0%)
	0.0–0.5%	0.0–2.0%	**0.0–5.5%**	0.0–30.1%
Cestode egg	**21/946 (2.2%)**	0/234 (0%)	0/112 (0%)	0/12 (0%)
	1.4–3.4%	0.0–2.0%	0.0–4.1%	0.0–30.1%
Coccidian oocysts	**141/946 (14.9%)**	**34/234 (14.5%)**	**12/112 (10.7%)**	**6/12 (50.0%)**
	12.8–17.3%	**10.6–19.7%**	**6.1–18.0%**	**25.4–74.6%**
Gravid (free-living) nematodes	0/946 (0%)	**36/234 (15.4%)**	0/112 (0%)	0/12 (0%)
	0.0–0.5%	**11.3–20.6%**	0.0–4.1%	0.0–30.1%
Labiobulura sp. egg	0/946 (0%)	0/234 (0%)	0/112 (0%)	**4/12 (33.3%)**
	0.0–0.5%	0.0–2.0%	0.0–4.1%	**11.3–64.6%**
Linstowinema sp. egg	**2/946 (0.2%)**	0/234 (0%)	0/112 (0%)	**4/12 (33.3%)**
	0.0–0.8%	0.0–2.0%	0.0–4.1%	**11.3–64.6%**
Lungworm larvae	**13/946 (1.4%)**	0/234 (0%)	0/112 (0%)	**3/12 (25.0%)**
	0.8–2.4%	0.0–2.0%	0.0–4.1%	**6.7–57.2%**
Megastrongyle egg	0/946 (0%)	0/234 (0%)	**9/112 (8.0%)**	0/12 (0%)
	0.0–0.5%	0.0–2.0%	**4.2–14.8%**	0.0–30.1%
Oxyurid egg	0/946 (0%)	**1/234 (0.4%)**	**10/112 (8.9%)**	0/12 (0%)
	0.0–0.5%	**0.0–2.7%**	**4.8–15.9%**	0.0–30.1%
Parastrongyloides egg	0/946 (0%)	**33/234 (14.1%)**	0/112 (0%)	0/12 (0%)
	0.0–0.5%	**10.2–19.2%**	0.0–4.1%	0.0–30.1%
Physaloptera sp. egg	0/946 (0%)	0/234 (0%)	**1/112 (0.9%)**	0/12 (0%)
	0.0–0.5%	0.0–2.0%	**0.0–5.5%**	0.0–30.1%
Potorolepis sp. egg	0/946 (0%)	0/234 (0%)	0/112 (0%)	**3/12 (25.0%)**
	0.0–0.5%	0.0–2.0%	0.0–4.1%	**6.7–57.2%**
Potoroxyuris sp. egg	**18/946 (1.9%)**	0/234 (0%)	0/112 (0%)	0/12 (0%)
	1.2–3.0%	0.0–2.0%	0.0–4.1%	0.0–30.1%
Protospirura sp. egg	0/946 (0%)	**12/234 (5.1%)**	0/112 (0%)	0/12 (0%)
	0.0–0.5%	**2.9–8.9%**	0.0–4.1%	0.0–30.1%
Spiruroid egg	0/946 (0%)	0/234 (0%)	**3/112 (2.7%)**	0/12 (0%)
	0.0–0.5%	0.0–2.0%	**0.6–8.0%**	0.0–30.1%
Strongyle egg	**712/946 (75.3%)**	**157/234 (67.1%)**	**92/112 (82.1%)**	**10/12 (83.3%)**
	72.4–77.9%	**60.8–72.8%**	**73.9–88.2%**	**50.9–97.1%**
Strongyloides-like egg	**449/946 (47.5%)**	0/234 (0%)	0/112 (0%)	**2/12 (16.7%)**
	44.3–50.6%	0.0–2.0%	0.0–4.1%	**2.9–49.1%**
Trichuris egg	**4/946 (0.4%)**	0/234 (0%)	0/112 (0%)	**4/12 (33.3%)**
	0.1–1.1%	0.0–2.0%	0.0–4.1%	**11.3–64.6%**
Unidentified nematode eggs/larvae	**715/946 (75.6%)**	**48/234 (20.5%)**	**22/112 (19.6%)**	**7/12 (58.3%)**
	72.7–78.2%	**15.8–26.2%**	**13.3–28.2%**	**28.6–83.5%**

Positive results are highlighted in bold.

and unidentified nematode eggs/larvae (Table 2, Appendix Fig. 6). We also found a distinct morphotype of strongylid nematode egg (unidentified species referred to as 'megastrongyle' egg), which was much larger (approximately 150 μm × 75 μm) than typical strongyle eggs (Appendix Fig. 6). Overall, gastrointestinal parasites were present in 88.4% of samples, with strongyle eggs detected in 82.1% of samples (Table 2). Prevalence of infection among individuals was 90.0%. Species diversity was lowest in Walcott, with prevalences generally lower in Dryandra, except for *Bertiella* sp. (Appendix Table 6). Strongyle eggs, 'megastrongyle' eggs and coccidian oocysts were ubiquitous across all sites (Appendix Table 6).

Other species

Twelve faecal samples from *I. fusciventer* were screened for gastrointestinal parasites. Typical strongyle eggs, coccidian oocysts, *Strongyloides*-like eggs, lungworm (L1) larvae, *Trichuris* sp. eggs, *Linstowinema* sp. eggs, *Labiobulura* sp. eggs, *Potorolepis* sp. eggs, an *Australiformis* sp. egg and unidentified nematode eggs/larvae were observed (Table 2, Appendix Fig. 7). All 12 samples were positive for parasites, with strongyle eggs detected in all but two samples; coccidia were detected in 50% of samples. Two faecal samples from *P. t. wambenger* (Walcott origin) were also examined; both were positive for strongyle eggs; a *Linstowinema* sp. egg was detected in the faeces from one host and unidentified nematode larvae were present in the other (Appendix Fig. 8). Faecal samples from *T. rugosa* were not examined.

Ectoparasites

Bettongia penicillata

In total, 923 samples collected from 404 individuals were morphologically identified. Five species of tick (*Amblyomma triguttatum, Ixodes australiensis*, *Ixodes myrmecobii*, *Ixodes tasmani* and *Ixodes woyliei*), seven species of flea (*Acidesta chera*, *Choristopsylla ochi*, *Echidnophaga myrmecobii, Echidnophaga perilis*, *Pygiopsylla hilli*, *Pygiopsylla tunneyi* and *Stephanocircus dasyuri*), two species of louse (*Boopia uncinata* and *Paraheterodoxus calcaratus*), and four species of mite (*Androlaelaps fahrenholzi, Haemolaelaps hattanae*, *Haemolaelaps marsupialis* and *Haemolaelaps quartus*) were identified (Table 3). Larval/nymph stages of ticks and mites were also frequently encountered, but in most instances could not be identified to species. Trombiculid mites (Acari: Trombiculidae) were detected (based on their distinctive macroscopic appearance; Fig. 4*a*) on five hosts [Dryandra (origin UWR) $n = 1$; Perup Sanctuary $n = 4$] but were not collected for morphological identification.

Of the 1314 *B. penicillata* (641 individuals) that were examined for the presence of ectoparasites in the field, 95.2% (95% CI: 93.9–96.2%) were positive for at least one ectoparasite taxon. Prevalence of infection among individuals was 98.0%. Fleas were recorded on only six hosts from Dryandra (one translocated, five resident); however, specimens were not collected for identification. Of the four ectoparasite taxonomic groups (ticks, fleas, lice and mites), ticks were most common (Appendix Table 7). From these groups, *I. australiensis*, *P. tunneyi*, *P. calcaratus* and *H. hattanae* were most prevalent, respectively; however, site differences were apparent (Appendix Table 8). For example, *I. australiensis* was not detected in Dryandra, despite this tick being the most prevalent species overall. In contrast, the prevalence of *I. woyliei* and *Amblyomma* spp. ticks was highest within Dryandra (Appendix Table 8), despite this site having the lowest overall prevalence of ticks (Appendix Table 7).

Trichosurus vulpecula hypoleucus

We morphologically identified 194 ectoparasite samples from 138 individuals. Seven species of tick (*Amblyomma* sp., *Haemaphysalis bancrofti*, *Haemaphysalis bremneri*, *Haemaphysalis humerosa*, *I. australiensis*, *I. myrmecobii* and *I. tasmani*), four species of flea (*C. ochi*, *E. myrmecobii, P. tunneyi* and *S. dasyuri*), one species of louse (*P. calcaratus*), and six mite taxa (*H. hattanae*, *H. marsupialis*, *Liponyssoides lukoschusi*, *Ornithonyssus praedo*, trombiculid mites and *Ulyxes penelope*) were identified (Table 3). Unidentified larval/nymph stages of ticks and mites were also common. 'Stick-fast' fleas were identified in the field based on their characteristic appearance embedded in the skin on seven hosts from Perup Sanctuary (Fig. 4*b*; confirmed as *E. myrmecobii* in five hosts).

Of the 323 *T. v. hypoleucus* (230 individuals) that were assessed for the presence of ectoparasites in the field, 81.1% (95% CI: 76.5–85.0%) were host to at least one ectoparasite taxon. Prevalence of infection among individuals was 88.7%. Of the three major ectoparasite taxonomic groups found on *T. v. hypoleucus* (ticks, fleas and mites), ticks were most common (Appendix Table 9). From these groups, *I. tasmani*, *C. ochi*, and trombiculid mites were most prevalent, respectively, though site differences were evident (Appendix Table 10).

Dasyurus geoffroii

Eighty-four ectoparasite samples collected from 80 individuals were morphologically identified. All four ectoparasite taxa were present on *D. geoffroii*, including three species of tick (*I. australiensis*, *Ixodes fecialis* and *I. tasmani*), six species of flea (*A. chera*, *C. ochi*, *E. myrmecobii*, *E. perilis*, *P. tunneyi* and *S. dasyuri*), two species of louse (*B. uncinata* and *P. calcaratus*), and four mite taxa (*H. hattanae*, *H. marsupialis*, *Ornithonyssus dasyuri* and trombiculid mites) (Table 3); unidentified larval/nymph stages of ticks and mites were also present.

Of the 120 *D. geoffroii* (99 individuals) that were examined for the presence of ectoparasites, at least one ectoparasite taxon was detected in 74.2% (95% CI: 65.6–81.2%) of cases. Prevalence of infection among individuals was 84.8%. Of the four major ectoparasite taxonomic groups, mites were the most common (Appendix Table 11). From these groups,

Table 3. Summary of the ectoparasites (in alphabetical order by taxonomic group) identified from marsupials during this study [no. infected/no. samples tested (% infected); 95% CI].

	Parasite taxa	*B. penicillata*	*T. v. hypoleucus*	*D. geoffroii*
Ticks	*Amblyomma* spp.	**81/923 (8.8%)**	**21/194 (10.8%)**	0/84 (0%)
		7.1–10.8%	**7.2–16.1%**	0.0–5.4%
	Amblyomma triguttatum	**2/923 (0.2%)**	0/194 (0%)	0/84 (0%)
		0.00–0.8%	0.0–2.4%	0.0–5.4%
	Ixodes australiensis	**210/923 (22.8%)**	**7/194 (3.6%)**	**17/84 (20.2%)**
		20.2–25.6%	**1.6–7.4%**	**13.0–30.2%**
	Ixodes fecialis	0/923 (0%)	0/194 (0%)	**11/84 (13.1%)**
		0.0–0.5%	0.0–2.4%	**7.4–22.2%**
	Ixodes myrmecobii	**60/923 (6.5%)**	**9/194 (4.6%)**	0/84 (0%)
		5.1–8.3%	**2.4–8.7%**	0.0–5.4%
	Ixodes tasmani	**1/923 (0.1%)**	**69/194 (35.6%)**	**7/84 (8.3%)**
		0.00–0.7%	**29.2–42.5%**	**3.9–16.6%**
	Ixodes woyliei	**89/923 (9.6%)**	0/194 (0%)	0/84 (0%)
		7.9–11.7%	0.0–2.4%	0.0–5.4%
	Haemaphysalis bancrofti	0/923 (0%)	**2/194 (1.0%)**	0/84 (0%)
		0.0–0.5%	**0.1–4.0%**	0.0–5.4%
	Haemaphysalis bremneri	0/923 (0%)	**1/194 (0.5%)**	0/84 (0%)
		0.0–0.5%	**0.0–3.2%**	0.0–5.4%
	Haemaphysalis humerosa	0/923 (0%)	**2/194 (1.0%)**	0/84 (0%)
		0.0–0.5%	**0.1–4.0%**	0.0–5.4%
	Unidentified larval/nymph stages	**576/923 (62.4%)**	**76/194 (39.2%)**	**34/84 (40.5%)**
		59.2–65.5%	**32.6–46.2%**	**30.6–51.2%**
	Unknown	**17/923 (1.8%)**	0/194 (0%)	0/84 (0%)
		1.1–3.0%	0.0–2.4%	0.0–5.4%
Fleas	*Acidesta chera*	**1/923 (0.1%)**	0/194 (0%)	**13/84 (15.5%)**
		0.00–0.7%	0.0–2.4%	**9.2–24.9%**
	Choristopsylla ochi	**1/923 (0.1%)**	**71/194 (36.6%)**	**1/84 (1.2%)**
		0.00–0.7%	**30.1–43.6%**	**0.0–7.2%**
	Echidnophaga myrmecobii	**2/923 (0.2%)**	**5/194 (2.6%)**	**11/84 (13.1%)**
		0.00–0.8%	**1.0–6.1%**	**7.4–22.2%**
	Echidnophaga perilis	**1/923 (0.1%)**	0/194 (0%)	**3/84 (3.6%)**
		0.00–0.7%	0.0–2.4%	**0.8–10.5%**
	Pygiopsylla hilli	**82/923 (8.9%)**	0/194 (0%)	0/84 (0%)
		7.2–10.9%	0.0–2.4%	0.0–5.4%
	Pygiopsylla tunneyi	**148/923 (16.0%)**	**12/194 (6.2%)**	**29/84 (34.5%)**
		13.8–18.6%	**3.5–10.6%**	**25.2–45.2%**
	Stephanocircus dasyuri	**120/923 (13.0%)**	**1/194 (0.5%)**	**18/84 (21.4%)**
		11.0–15.3%	**0.0–3.2%**	**14.0–31.5%**
	Unknown	0/923 (0%)	**2/194 (1.0%)**	0/84 (0%)
		0.0–0.5%	**0.1–4.0%**	0.0–5.4%
Lice	*Boopia uncinata*	**1/923 (0.1%)**	0/194 (0%)	**9/84 (10.7%)**
		0.00–0.7%	0.0–2.4%	**5.6–19.4%**

(*Continued on next page*)

Table 3. (*Continued*).

	Parasite taxa	*B. penicillata*	*T. v. hypoleucus*	*D. geoffroii*
	Paraheterodoxus calcaratus	**624/923 (67.6%)**	**2/194 (1.0%)**	**3/84 (3.6%)**
		64.5–70.5%	**0.1–4.0%**	**0.8–10.5%**
	Unidentified nymph stages	**6/923 (0.7%)**	0/194 (0%)	0/84 (0%)
		0.3–1.5%	0.0–2.4%	0.0–5.4%
	Unknown	**8/923 (0.9%)**	0/194 (0%)	**1/84 (1.2%)**
		0.4–1.7%	0.0–2.4%	**0.0–7.2%**
Mites	*Androlaelaps fahrenholzi*	**1/923 (0.1%)**	0/194 (0%)	0/84 (0%)
		0.00–0.7%	0.0–2.4%	0.0–5.4%
	Haemolaelaps hattanae	**305/923 (33.0%)**	**4/194 (2.1%)**	**2/84 (2.4%)**
		30.1–36.1%	**0.6–5.4%**	**0.2–8.9%**
	Haemolaelaps marsupialis	**1/923 (0.1%)**	**2/194 (1.0%)**	**4/84 (4.8%)**
		0.00–0.7%	**0.1–4.0%**	**1.6–12.1%**
	Haemolaelaps quartus	**146/923 (15.8%)**	0/194 (0%)	0/84 (0%)
		13.6–18.3%	0.0–2.4%	0.0–5.4%
	Liponyssoides lukoschusi	0/923 (0%)	**6/194 (3.1%)**	0/84 (0%)
		0.0–0.5%	**1.3–6.8%**	0.0–5.4%
	Ornithonyssus dasyuri	0/923 (0%)	0/194 (0%)	**1/84 (1.2%)**
		0.0–0.5%	0.0–2.4%	**0.0–7.2%**
	Ornithonyssus praedo	0/923 (0%)	**1/194 (0.5%)**	0/84 (0%)
		0.0–0.5%	**0.0–3.2%**	0.0–5.4%
	Trombiculid mite	**Present**	**51/194 (26.3%)**	**39/84 (46.4%)**
			20.6–32.9%	**36.2–57.0%**
	Ulyxes penelope	0/923 (0%)	**1/194 (0.5%)**	0/84 (0%)
		0.0–0.5%	**0.0–3.2%**	0.0–5.4%
	Unidentified larval/nymph stages	**11/923 (1.2%)**	**16/194 (8.2%)**	**22/84 (26.2%)**
		0.6–2.2%	**5.1–13.1%**	**18.0–36.6%**
	Unknown	**9/923 (1.0%)**	**9/194 (4.6%)**	0/84 (0%)
		0.5–1.9%	**2.4–8.7%**	0.0–5.4%

Positive results are highlighted in bold.

Fig. 4. Trombiculid mites on a woylie (*Bettongia penicillata*) (*a*; black arrow), 'stick-fast' fleas (*Echidnophaga myrmecobii*) on a brush-tailed possum (*Trichosurus vulpecula hypoleucus*) (*b*), and trombiculid mites on a chuditch (*Dasyurus geoffroii*) (*c*).

I. australiensis, *P. tunneyi*, *B. uncinata* and trombiculid mites (Fig. 4*c*) were most prevalent, respectively (Appendix Table 12). Overall, the prevalence and diversity of ectoparasites was lowest in Dryandra (Appendix Tables 11 and 12).

Other species

Ticks were collected from seven *T. rugosa* and morphologically identified as *Amblyomma albolimbatum* in six hosts, and *Amblyomma* sp. in the other host. Fleas, lice and mites were not observed on *T. rugosa*. The fleas *S. dasyuri* and *P. tunneyi* were present on three *I. fusciventer* (origin Perup, Walcott and Warrup East); mites and ticks were also recorded as present on one of these hosts (Walcott) but were not collected for morphological identification. *Amblyomma* sp., *I. australiensis* and *Ixodes* sp. ticks were isolated from a *P. t. wambenger*.

Discussion

This study identified a diverse parasite community including nine haemoparasite taxa, 21 gastrointestinal parasite taxa and 27 ectoparasite taxa (Fig. 5) in free-ranging terrestrial wildlife from Australia's south-west. Parasite diversity is likely to be grossly underestimated, given that species-level identification was not achieved for many taxa, particularly gastrointestinal parasites and larval/nymph stages of ectoparasites. To the best of our knowledge this is the first report of *Hepatozoon* spp. infection in *T. v. hypoleucus*, and *T. noyesi* in *T. rugosa*. Several new host–ectoparasite associations were also identified, including *A. fahrenholzi* and trombiculid mites on *B. penicillata*; *L. lukoschusi* on *T. v. hypoleucus*; *I. australiensis* and *I. tasmani* on *D. geoffroii*; and *I. australiensis* and *Amblyomma* sp. ticks on *P. t. wambenger*. Representative ectoparasite specimens, where available, have been deposited at the Western Australian Museum (reference numbers WAM E117331-E117336; T163145-T163157). We also report novel host–gastrointestinal parasite associations including the presence of *Trichuris* sp. and *Linstowinema* sp. eggs in *B. penicillata*, and *Physaloptera* sp. and *Capillaria* sp. eggs in *D. geoffroii*.

Differences in parasite species diversity and composition among sites and host species were apparent. Although some parasites were host-specific (e.g. *E. woyliei*, *P. hilli* and *I. woyliei*), many were generalists (e.g. *Trypanosoma* spp. and most ticks), though species-level identification could not be achieved for all parasite taxa. With increasing recognition of the intrinsic biodiversity value of parasites (Colwell *et al.* 2012; Thompson *et al.* 2018), the potential loss of parasite taxa should be a serious consideration when planning fauna translocations, particularly for host-specific parasites that are likely to be endangered themselves (Colwell *et al.* 2012). For *I. woyliei*, a tick with a high predilection for its critically endangered host (Ash *et al.* 2017), the risk of extinction following translocation is likely to be higher than for generalist ectoparasites with multiple host species (e.g. *Amblyomma* spp. ticks: Waudby *et al.* 2007). Loss of specialist parasites may also lead to biotic homogenisation of parasite communities, enhancing the risk of disease emergence (Dharmarajan *et al.* 2021).

For all host species and parasite groups (i.e. blood-borne, gastrointestinal and ectoparasite taxa), prevalence at the individual level was higher than prevalence at the sample level, indicating some level of sampling bias. As each host is exposed to a variety of parasites over time, resulting in fluctuations in both infection status (as shown by repeat sampling) and our ability to detect infection (e.g. measurable parasitaemia: Northover *et al.* 2019*a*), we would expect individual prevalence to be higher than sample prevalence during long-term parasite monitoring. As the purpose of this study was to document the parasite diversity of marsupials from different sites, we did not evaluate parasite prevalence at the individual level beyond these broad parasite groupings. To better inform disease risk and the need for management intervention during translocations, more research is needed to evaluate temporal parasite dynamics (e.g. the effect of season, host/vector density or diversity) including the biological significance of parasites on individuals and host populations. The incorporation of molecular techniques (e.g. Davey *et al.* 2021) will also help to improve parasite detection rates and more accurately characterise polyparasitism within a host/population.

Haemoparasites

Host–haemoparasite associations not previously reported (Paparini *et al.* 2011; Botero *et al.* 2013; Thompson *et al.* 2014*b*; Cooper *et al.* 2018; Northover *et al.* 2019*a*) include *Hepatozoon* spp. and piroplasm infection in *T. v. hypoleucus*, and *T. noyesi* in *T. rugosa*. During this study, elongate intraerythrocytic *Hepatozoon* gamont's were detected in red blood cells from three *T. v. hypoleucus* in Dryandra: the first record of *Hepatozoon* infection in *Trichosurus vulpecula* within Australia. Organisms were not observed 'free' in the plasma or within leucocytes. All three hosts were coinfected with trypanosomes and *I. tasmani* ticks were present on two hosts. In WA, *Hepatozoon* sp. have been identified from other native Australian marsupials, including *Isoodon obesulus* (Wicks *et al.* 2006), with similar descriptions of intraerythrocytic gamont's attributed to *Hepatozoon peramelis*. Like reports in other marsupial species (Wicks *et al.* 2006; Barbosa 2017), there was no evidence of clinical disease associated with *Hepatozoon* infection in *T. v. hypoleucus* during this study. Molecular sequencing methods developed for *Hepatozoon* spp. (e.g. amplification of *18S* rRNA gene fragments: Barbosa 2017) are recommended to confirm the species identity.

Unidentified piroplasms were also detected within erythrocytes from *T. v. hypoleucus* during this study. This is the first report of piroplasm infection in *T. vulpecula* from WA, although piroplasms, including *Babesia* and *Theileria* spp., have been reported from several other marsupials in WA (Clark and Spencer 2007; Paparini *et al.* 2012; Rong *et al.* 2012; Northover *et al.* 2019*a*). *Babesia lohae*-like sequences have been identified from *T. vulpecula* in Sydney and New South Wales (NSW) (Egan *et al.* 2021) and also from *Ixodes*

Fig. 5. Summary of parasites identified from woylies (*Bettongia penicillata*), brush-tailed possums (*Trichosurus vulpecula hypoleucus*) and chuditch (*Dasyurus geoffroii*) in Western Australia (Photographs © John Lawson) (Baylis 1934; Inglis 1968; von Kéler 1971; Haigh *et al.* 1994; Burmej *et al.* 2008; Beveridge and Durette-Desset 2009; Clark 2011; Hillman 2016; Ash *et al.* 2017; Cooper *et al.* 2018; Thompson *et al.* 2018; Northover *et al.* 2019*c*; Egan *et al.* 2021; Krige *et al.* 2021*b*). Note: blue text, previously documented host–parasite associations; underlined text, new host–parasite associations; asterisk, query accidental (spurious) infection.

holocyclus and *I. tasmani* ticks parasitising *T. vulpecula* in NSW and Queensland (Qld) (Loh *et al.* 2018). As above, the incorporation of molecular techniques (e.g. Flaherty *et al.* 2021) would help to determine the species of piroplasm infecting *T. v. hypoleucus* in the current study.

Detection of *T. noyesi* infecting *T. rugosa* is the first record of a trypanosome isolated from a native reptile in WA. Other *Trypanosoma* spp. have been documented in reptiles from SA, NSW and Qld (Johnston 1907; Mackerras 1961; Jakes *et al.* 2001), but reptilian taxa are highly underrepresented in parasitological studies (Cooper *et al.* 2017). Although knowledge of the transmission of Australian trypanosomes is limited (Thompson *et al.* 2014*b*), ticks have been implicated as vectors in mammals (McInnes *et al.* 2009; Austen *et al.* 2011;

McInnes *et al*. 2011; Barbosa *et al*. 2017; Krige *et al*. 2021*a*) and *T. noyesi* DNA has been detected within several (*Amblyomma* and *Ixodes*) species of questing tick (Krige *et al*. 2021*b*). *Amblyomma albolimbatum* ticks were present on one of the *T. noyesi*-infected *T. rugosa* during this study. Although *A. albolimbatum* ticks are generally considered host specific, more generalist species such as *A. triguttatum*, the ornate kangaroo tick, and ixodid ticks were present on marsupials infected with trypanosomes, though several *Haemaphysalis* spp. ticks were also present on *Trypanosoma*-positive *T. v. hypoleucus*.

The very low seroprevalence of *T. gondii* in *B. penicillata* (1.8%) is consistent with previous studies that used similar diagnostic methods (e.g. Parameswaran 2008; Skogvold *et al*. 2017). Antemortem diagnosis of *T. gondii*, however, is difficult, given the often acute-onset and short-lived serological response to disease (Portas 2019). Studies that used more sensitive and specific diagnostic methods to analyse tissue samples from deceased specimens (e.g. PCR: Parameswaran *et al*. 2010) have reported a much higher prevalence of infection (50.0%) in *B. penicillata*. Clinical disease was not evident in *T. gondii*-infected hosts during this study.

For all marsupial species, *Trypanosoma* species diversity was greatest within the UWR and lowest within Dryandra. Interestingly, a much higher prevalence of *Trypanosoma* spp. infection was detected in *T. v. hypoleucus* (82.6% overall) compared to other species (54.0% *B. penicillata*; 11.8% *D. geoffroii*). Within Warrup East, at least one *Trypanosoma* spp. was detected in every *T. v. hypoleucus* sampled ($n = 41$). In contrast, trypanosome infections were comparatively rare in *D. geoffroii*: only one of the 54 samples from Dryandra was *Trypanosoma*-positive. The prevalence of coinfection, however, was highest in *D. geoffroii* (46.2%) compared to *T. v. hypoleucus* (26.0%) or *B. penicillata* (23.1%). Species differences were also apparent, with *T. copemani* most prevalent in *T. v. hypoleucus*, and *T. vegrandis* most prevalent in *B. penicillata*. Both *T. copemani* and *T. noyesi* were equally most prevalent in *D. geoffroii*. Species differences may reflect different modes, and vectors, by which trypanosomes are transmitted.

Gastrointestinal parasites

To the author's knowledge this is the first published record of *Trichuris* sp. (Nematoda: Trichuridae) and *Linstowinema* sp. (Nematoda: Seuratidae) in *B. penicillata*, and anoplocephalid (including *Bertiella* sp.) (Platyhelminthes: Anoplocephalidae), *Capillaria* sp. (Nematoda: Capillariidae) and *Physaloptera* sp. (Nematoda: Physalopteridae) in *D. geoffroii*. For *B. penicillata*, the low prevalence of these parasites warrants caution. For example, *Linstowinema* spp. are known to infect other sympatric marsupials (e.g. *I. obesulus*: Hillman 2016) in WA, which may have been captured during the same trapping session; thus, sample contamination cannot be ruled out. While it is important to interpret the results of faecal flotation with caution in carnivorous species such as *D. geoffroii*, as parasite eggs/oocysts from prey may not represent a true parasite infection, the morphological similarity of anoplocephalid eggs from multiple hosts in this study *may* represent a true/real primary infection. However, as there is no record of Anoplocephalidae (or Oxyuridae) infection in carnivorous hosts (Spratt and Beveridge 2016), pseudoinfection from the ingestion of infected prey is most probable. The presence of a *Physaloptera* sp. egg and *Capillaria* sp. egg in a single *D. geoffroii* from Warrup East and Walcott, respectively, is more difficult to interpret. Northern (*Dasyurus hallucatus*) and spotted-tailed (*Dasyurus maculatus*) quolls are known hosts of *Physaloptera* sp. nematodes (Spratt and Beveridge 2016); however, no *Physaloptera* sp. have been documented in *D. geoffroii* (western quoll) until now. Likewise, there are no published records of *Capillaria* sp. in *D. geoffroii*, though *Capillaria ornamentata* is known to infect other dasyurids (Spratt 2006) and a *Eucoleus* sp. was isolated from *D. hallucatus* (Oakwood and Spratt 2000).

An undescribed species of cestode egg was isolated from *B. penicillata* in Dryandra only. To date, *Rodentolepsis fraterna* (Spratt and Beveridge 2016) is the only species of cestode (Platyhelminthes: Hymenolepididae) formally described in *B. penicillata*, and the eggs of *R. fraterna* are morphologically different from those observed here. Work is being undertaken to characterise this putative new species, which has been isolated from the faeces of *B. penicillata* (Northover *et al*. 2019*b*) and *T. v. hypoleucus* (A. Elliot pers. comm.) previously. The absence of cestode eggs from all other sites suggests that the intermediate host for this parasite may be endemic to Dryandra.

Overall, all host species had a high prevalence of infection (*B. penicillata* 90.8%; *D. geoffroii* 88.4%; *T. v. hypoleucus* 74.4%). All *I. fusciventer* samples were positive for at least one type of parasite; though sample size was small ($n = 12$) and biased to the UWR. Nematodes, particularly strongyle eggs, were most prevalent, followed by coccidia; both were ubiquitous across target host species and site. The overall prevalence of coccidia infection in wild *I. fusciventer* (50.0%, $n = 12$) was considerably lower than has been reported in urban *I. obesulus* (96.7%, $n = 123$: Hillman 2016), though it is difficult to compare free-ranging and urbanised populations due to small sample size here.

Strongyle eggs (Nematoda: Strongylidae) likely represent several nematode species; however, we have limited information regarding the species of nematode infecting marsupials in WA (Spratt and Beveridge 2016) as few have been formally described (Baylis 1934; Johnston and Mawson 1939; Inglis 1968; Mawson 1973; Smales 2005; Beveridge and Durette-Desset 2009; Hobbs and Elliot 2016). Currently, *Potorostrongylus woyliei* (Smales 2005) and *Paraustrostrongylus bettongia* (Mawson 1973) have been documented in *B. penicillata*. *Mackerrastrongylus mawsonae* is the only strongylid nematode described in *I. obesulus* from WA

(Inglis 1968). Four species of trichostrongylid nematode [*Sprattellus waringi*, *Woolleya cathiae*, *Mackerrastrongylus mawsonae* (Inglis 1968) and *Copemania darwini* (Beveridge and Durette-Desset 2009)] have been reported in *D. geoffroii*.

Based on current published data, the *Strongyloides*-like and *Trichuris* sp. eggs isolated from *I. fusciventer* may be those of *Parastrongyloides australis* and *Trichuris peramelis*, respectively, though neither species has been documented from *I. obesulus* in WA (Mawson 1960). *Protospirura* (Nematoda: Spiruridae), *Parastrongyloides* (Nematoda: Strongyloididae) and *Bertiella* spp. eggs have been detected in *T. vulpecula* from WA (Clark 2011); however, *Protospirura marsupialis*, *Parastrongyloides trichosuri* and *Bertiella trichosuri* are the only formally described species from *T. vulpecula* outside of WA (Mackerras 1959; Viggers and Spratt 1995; Spratt 2018). The majority of unsporulated coccidian oocysts isolated from *T. v. hypoleucus* were morphologically consistent with *Eimeria trichosuri* (O'Callaghan and O'Donoghue 2001; Power *et al.* 2009). The *Potoroxyuris* sp. eggs isolated from *B. penicillata* are most likely *Potoroxyuris keninupensis* (Nematoda: Oxiuridae) given their UWR origin, size, and characteristic mammilated outer shell covering (Hobbs and Elliot 2016). The incorporation of molecular techniques (e.g. sequencing of DNA extracted from faeces: Davey *et al.* 2021) would help to develop/refine existing DNA barcode libraries and provide a more detailed understanding (i.e. species level identification) of the gastrointestinal parasite taxa present.

As described for haemoparasites, a lower prevalence and diversity of gastrointestinal parasite taxa were present in samples from Dryandra, which may reflect host (e.g. density) and/or environmental (e.g. climate) differences. Strongyle eggs, for example, were detected in 32.2–69.2% of samples from Dryandra compared with 91.3–100% of samples from the UWR. In *T. v. hypoleucus*, *Parastrongyloides* eggs were not detected in Dryandra (n = 172), despite their high prevalence elsewhere. Higher rainfall within the UWR may facilitate the persistence of eggs within the environment and thus the completion of helminth life-cycles. In contrast, the prevalence of coccidia in *T. v. hypoleucus* was highest in Dryandra, which may be related to host density [*T. v. hypoleucus* capture rates = 0.17 Dryandra; 0.10 Warrup East; and 0.04 Walcott]; though differences in the timing of sampling also may have influenced these results [i.e. additional trapping conducted during winter (June and August) in Dryandra].

Ectoparasites

Bettongia penicillata

Host–ectoparasite associations not previously reported in *B. penicillata* (von Kéler 1971; Dunnet and Mardon 1974; Domrow 1987; Kaewmongkol *et al.* 2011; Ash *et al.* 2017; Thompson *et al.* 2018; Krige *et al.* 2021*a*) include *A. chera*, *C. ochi*, *B. uncinata*, *H. marsupialis*, *A. fahrenholzi* and trombiculid mites. *Pygiopsylla tunneyi* was the most common flea species identified on *B. penicillata* during this study. In contrast, *B. penicillata* may be an accidental host for *A. chera*, *C. ochi* and *H. marsupialis* as the nominal host [*I. obesulus* for *A. chera* (Dunnet and Mardon 1974) and *H. marsupialis* (Domrow 1987); and *T. vulpecula* for *C. ochi* (Dunnet and Mardon 1974)] was captured beforehand, making bag contamination a possibility. The presence of *A. fahrenholzi* on a single host from Warrup East is intriguing, as birds or their nests are the only known hosts within (south-eastern) Australia (Domrow 1987). Outside of Australia *A. fahrenholzi* is known to parasitise a wide range of hosts, in particular rodents (Silva-de la Fuente *et al.* 2020), but there is no record of this parasite in WA until now. *Dasyurus* species are the predominant host of *B. uncinata* (von Kéler 1971); however, we did not detect *B. uncinata* on *D. geoffroii* in Dryandra, and only *B. penicillata* were captured on the day *B. uncinata* was detected. While this is the first published record of trombiculid (larval stage) mites on *B. penicillata*, specimens were not obtained to confirm the species.

Stark site variation in parasite type and prevalence were also apparent. For example, *I. australiensis* and *P. tunneyi* were not detected on *B. penicillata* from Dryandra, despite these species being the most prevalent overall within their respective taxon groups. *Ixodes australiensis* was not found on sympatric species within Dryandra either, and *P. tunneyi* was only detected on a single host (*T. v. hypoleucus*) from Dryandra. In contrast, the host-specific tick *I. woyliei* was most prevalent within Dryandra, which is unexpected given the lack of *I. australiensis* and low prevalence of *I. tasmani* (n = 1), as these three species are considered sympatric, sharing the same geographical region, habitat and host (Ash *et al.* 2017). Fleas were also extremely rare (excluding *C. ochi* on *T. v. hypoleucus* and *E. myrmecobii* on *D. geoffroii*) within Dryandra. Encouragingly, the threatened host-specific flea, *P. hilli* (Kwak 2018), is persisting in all UWR sites. The critically endangered status and current reliance of *B. penicillata* upon periodic translocations, however, places this density dependent and site-specific coendangered parasite at risk of extinction.

Trichosurus vulpecula hypoleucus

Host–ectoparasite associations not previously reported in *T. vulpecula* (Roberts 1970; Dunnet and Mardon 1974; Viggers and Spratt 1995; Burmej *et al.* 2008; Clark 2011; Hillman 2016; Krige *et al.* 2021*a*) include *P. calcaratus*, *H. hattanae*, *H. marsupialis*, *O. praedo* and *U. penelope*. Additionally, this is the first report of *P. tunneyi*, *H. bancrofti*, *H. bremneri*, *H. humerosa*, *L. lukoschusi* and trombiculid mites on *T. v. hypoleucus* from south-western WA.) While *H. bremneri* (and another *Haemaphysalis* spp. tick) have been isolated from a *T. vulpecula* in the greater Perth region (Hillman 2016), *H. humerosa* and *H. bancrofti* have not been identified on *T. vulpecula* from WA (Roberts 1970). We identified *H. humerosa* on two hosts from Warrup East,

one of which had two specimens. Previous studies (Roberts 1963) suggest that bandicoots are the primary host species for *H. humerosa*. Although the host with two *H. humerosa* ticks was captured after an *I. fusciventer*, the other host was not. We also found *H. bancrofti* (and *H. bremneri*) on *T. v. hypoleucus* from Dryandra. *Haemaphysalis bancrofti* has been reported from *T. vulpecula* in eastern Australia (Roberts 1963, 1970; Viggers and Spratt 1995; Laan *et al.* 2011), but this is the first report in WA.

The presence of *P. calcaratus* on *T. v. hypoleucus* ($n = 2$) from Walcott is unusual, as no lice have been recorded on *T. vulpecula* (Johnson and Hemsley 2008). While it is likely that *T. v. hypoleucus* is an accidental host (i.e. *P. calcaratus*-positive *B. penicillata* captured beforehand in one instance), we cannot rule out *T. v. hypoleucus* being an alternative host; particularly when lice (unidentified species) were recorded on a further six hosts in the field (Appendix Table 9).

The presence of six mite taxa is noteworthy. *Haemolaelaps hattanae* was found on four hosts (from all sites), though its presence could be attributed to bag contamination in two cases. The presence of two *Haemolaelaps* mite species and *U. penelope* (previously *Haemolaelaps penelope*; Shaw 2014), however, may indicate that *T. v. hypoleucus* is an alternative host. *Haemolaelaps sisyphus* has been recorded from *T. vulpecula* in NSW and Qld (Viggers and Spratt 1995). *Ornithonyssus praedo* has only been documented on other marsupials (Domrow 1987), and birds are the recognised host of *L. lukoschusi* (Domrow 1987). As we identified *L. lukoschusi* on six hosts from Dryandra, and Hillman *et al.* (2018) found a *Liponyssoides* sp. mite on *T. vulpecula* ($n = 1$) from the greater Perth region, *T. v. hypoleucus* may be an alternative host, though its arboreal nature may expose it to such parasites. The presence of *O. praedo* on a single host is more difficult to interpret, though no known hosts (i.e. *P. tapoatafa*: Domrow 1987) were captured during this trapping session.

As for *B. penicillata*, site differences in ectoparasite prevalence and diversity were evident. The prevalence of *Ixodes* spp. ticks was lowest within Dryandra; neither *I. australiensis* nor *I. myrmecobii* were detected on *T. v. hypoleucus* within this site. In contrast, *L. lukoschusi*, *H. bancrofti* and *H. bremneri* were detected only on *T. v. hypoleucus* within Dryandra, and the prevalence of *C. ochi*, trombiculid mites and *Amblyomma* spp. ticks was highest within this site. The majority of *Haemolaelaps* spp. mites (5/7) were isolated from *T. v. hypoleucus* in Walcott (as was *S. dasyuri*), whereas *O. praedo* was found only in Warrup East. *Amblyomma* spp. ticks, *I. tasmani*, *C. ochi*, *P. tunneyi* and *H. hattanae* were ubiquitous across sites.

Dasyurus geoffroii

Host–ectoparasite associations not previously reported in *D. geoffroii* (von Kéler 1971; Haigh 1994; Burmej *et al.* 2008; Thomasz 2014) include *I. australiensis*, *I. tasmani*, *C. ochi*, *P. calcaratus*, *H. hattanae*, *H. marsupialis* and *O. dasyuri*. *Ixodes australiensis* was detected on 17 animals and had the highest prevalence of any tick species, indicating that *D. geoffroii* is a true host. Likewise, the presence of *I. tasmani* on *D. geoffroii* across all sites suggests a legitimate host–parasite association. In contrast, the presence of *C. ochi* in a single host from Warrup East is questionable. *Choristopsylla ochi* is commonly found in arboreal species such as *T. vulpecula* (Dunnet and Mardon 1974) and although *D. geoffroii* may be an accidental host, its semiarboreal nature may expose it to such parasites. *Bettongia penicillata* was the only other animal captured before this host (using the same handling bag) on that day. *Paraheterodoxus calcaratus* has not been recorded in *D. geoffroii*. We believe *D. geoffroii* is an accidental host of *P. calcaratus* as two of the three hosts detected with *P. calcaratus* were captured immediately after *B. penicillata* infected with *P. calcaratus* using the same handling bag. The presence of four mite species was surprising. Although we detected a low prevalence of *H. hattanae*, *H. marsupialis* and *O. dasyuri*, *O. dasyuri* has been found on the eastern quoll (*Dasyurus viverrinus*) (Domrow 1987) and both *Haemolaelaps* spp. were found on *D. geoffroii* at multiple (UWR) sites. Trombiculid mites had the highest prevalence of all mite taxa and were observed on *D. geoffroii* at all sites during this study.

As for other host species, site variation in parasite prevalence and diversity was identified. For instance, nine parasite taxa that were present on *D. geoffroii* from Warrup East and Walcott were not detected on *D. geoffroii* within Dryandra. This includes *I. australiensis*, *P. tunneyi* and *B. uncinata*, which were the most prevalent species identified within their respective ectoparasite taxa groups. The opposite trend was observed for trombiculid mites and *E. myrmecobii*, which had the highest prevalence within Dryandra; *O. dasyuri* ($n = 1$) was detected only within this site. In comparison to *B. penicillata* and *T. v. hypoleucus*, in which ticks were the most prevalent ectoparasite found, mites were most prevalent on *D. geoffroii*.

Other species

Ticks collected from *T. rugosa* were identified as *A. albolimbatum* on six hosts, and *Amblyomma* sp. in the other host. *Tiliqua rugosa* is the primary host of *A. albolimbatum* (Sharrad and King 1981; Barker and Walker 2014). The two flea species found on *I. fusciventer* (*S. dasyuri* and *P. tunneyi*) have been previously documented on *I. obesulus* from WA (Dunnet and Mardon 1974; Hillman 2016). In contrast, this is the first report of *I. australiensis* and *Amblyomma* sp. ticks from *P. t. wambenger*. *Phascogale tapoatafa wambenger* is a known host of other *Ixodes* spp. ticks (Roberts 1970) and *Amblyomma* spp. ticks have a wide host range, including domestic animals and humans (Roberts 1970; Waudby *et al.* 2007). As we only collected a larval *Amblyomma* specimen from this host, we were unable to identify the species.

For all host species, many of the ectoparasites collected were larval stages of ticks and mites, which could not be

identified to species using morphological keys. Unidentified ticks had the highest prevalence within their taxonomic group. Molecular techniques could be used in future to determine the species of ectoparasite and provide more accurate prevalence data. Introducing measures to reduce the risk of cross contamination will also help to reduce the likelihood of spurious host–ectoparasite associations. For example, single use handling bags or providing handling bags and equipment for each species.

Conclusion

We identified a diverse parasite community within WA's native fauna including several new host–parasite records. This study improves our knowledge of parasites infecting terrestrial wildlife within Australia's south-west and highlights the importance of monitoring both target and sympatric species when compiling baseline data of parasite fauna present within translocation sites. Further research to identify differences between host species over space and time, and factors driving these patterns/differences is recommended. A better understanding of the life cycle, transmission and potential effects of parasite infection on host health and populations (including the need for antiparasitic drugs), will help to provide an informed framework for the management of threatened species and their parasite taxa to minimise disease risk and improve translocation outcomes. Host-dependent threatened parasites, in particular, require careful deliberation in terms of their disease risk (if any) and benefits of preservation. Sampling in a manner that minimises contamination will help to reduce anthropogenic cross infections and improve confidence of host–parasite associations. Likewise, the incorporation of molecular sequencing techniques will help to evaluate parasite species diversity more accurately (e.g. identifying larval stages of ectoparasites or gastrointestinal species). Screening of other host species that serve as potential disease reservoirs (e.g. introduced species and livestock) and the inclusion of other parasite taxa (e.g. viruses) should also be considered.

Supplementary material

Supplementary material is available online.

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Data availability. Data will be shared upon reasonable request to the corresponding author with permission from the Department of Biodiversity, Conservation and Attractions.

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