IJP: Parasites and Wildlife 10 (2019) 13–22

Contents lists available at ScienceDirect

IJP: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Altered parasite community structure in an endangered marsupial following translocation

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ARTICLE INFO

Keywords:
Bettongia penicillata
Host-parasite relationship
Ivermectin
Polyparasitism
Wildlife
Woylie

ABSTRACT

Fauna translocations play an integral role in the management of threatened wildlife, though we are limited by our understanding of how the host-parasite community changes during translocation. During this longitudinal field-based study, we monitored gastrointestinal, blood-borne and ectoparasite taxa infecting woylies (*Bettongia penicillata*) for up to 12 months following two fauna translocations to supplement existing wild woylie populations in three different sites (Dryandra, Walcott and Warrup East) within the south-west of Western Australia. We aimed to (a) identify changes in parasite community structure of both translocated and resident woylies following translocation; and (b) evaluate the efficacy of ivermectin treatment in translocated hosts. Destination site and time since translocation had the strongest effects on parasite prevalence and mean faecal egg counts following translocation. Ivermectin treatment did not significantly reduce parasite prevalence or mean faecal egg counts in treated hosts. Prior to translocation, parasite community composition differed significantly between woylies selected for translocation and resident woylies within each release site. Following translocation, the parasite communities of translocated and resident hosts converged to become more similar over time, with loss of parasite taxa and novel host-parasite associations emerging. This is the first study to examine changes to the broader parasite community in translocated and resident animals following translocation. The dominant site-specific response of parasites following translocation reinforces the importance of incorporating parasite studies to enhance our fundamental understanding of perturbations in host-parasite systems during translocation, in particular the site-level drivers of parasite dynamics.

1. Introduction

Parasites are an essential component of biodiversity, providing crucial ecosystem services and driving host evolution (Hudson et al., 2006; Hatcher et al., 2012; Gomez et al., 2012). Parasites are also capable of compromising host health and have been implicated in some species declines (Viggers et al., 1993; Daszak et al., 2000; Tompkins et al., 2015; Spratt and Beveridge, 2019). Despite polyparasitism (co-infection, concomitant infection or multiparasitism) being the norm in wild animal populations (Keusch and Migasena, 1982; Graham, 2008), we often know little about the parasite communities of wildlife or how these communities will be affected by management practices, such as translocation.

Fauna translocations play a pivotal role in sustaining genetic diversity, population health and species survival, but the process of translocating a host from one ecosystem to another will inevitably disrupt pre-existing host-parasite relationships. This will impact both the host and their infracommunity of parasites (Telfer et al., 2010; Moir et al., 2012), with the potential to significantly affect host health and population dynamics (Thompson et al., 2010). Of particular concern during translocations, is the threat of alien or invasive disease, which may impact translocated hosts, resident conspecifics or cohabiting species (e.g. Vadlejch et al., 2017). Fauna translocations may also be a significant stressor capable of inducing immunosuppression (Hing et al., 2017), thus enhancing susceptibility to parasitic disease (Dickens et al., 2009) or stimulating recrudescence of latent infection (Adkesson

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https://doi.org/10.1016/j.ijppaw.2019.07.001
Received 9 April 2019; Received in revised form 27 June 2019; Accepted 2 July 2019

et al., 2007). For parasites with density-dependent transmission, translocation-induced changes to population density and host connectivity may enhance parasite transfer among hosts and increase disease prevalence within a population (Aiello et al., 2014). For rare host-specific parasites, fauna translocation may promote parasite extinction and loss of biodiversity (Moir et al., 2012; Dougherty et al., 2015; Thompson et al., 2018).

Regrettably, translocation protocols rarely encompass host-parasite studies, thus the impact of fauna translocation on host-parasite dynamics is poorly understood, as are the consequences of such perturbations on translocation outcomes (Northover et al., 2018). In addition, wildlife are often administered antiparasitic drugs prior to translocation, which will disrupt parasite community structure within a host. While this practice may be justified in some species (e.g. McGill et al., 2010), antiparasitic drugs are often used with no clear rationale, or without any effort to determine the efficacy of treatment following translocation (Pedersen and Fenton, 2015).

The woylie or brush-tailed bettong *Bettongia penicillata* is a critically endangered macropodid marsupial confined to three remaining wild indigenous populations within south-western Australia. Following unexpected and abrupt population declines between 1999 and 2006, periodic fauna supplementations continue to play a pertinent role in the conservation management of this species (Wayne et al., 2015). Although the spatio-temporal pattern of population declines suggests the involvement of an infectious disease agent (Thompson et al., 2014; Wayne et al., 2015; Godfrey et al., 2018), no study has examined the long-term changes to the broader parasite community (i.e. gastrointestinal, blood-borne and ectoparasite taxa) in translocated and resident woylies following translocation or in response to ivermectin treatment.

In this longitudinal field-based study, we examined the dynamics of the parasite community of woylies for up to 12 months following two translocations to supplement existing wild woylie populations at three different sites. Specifically, we aimed to (a) investigate changes in parasite community structure (i.e. parasite prevalence, infracommunity richness and infracommunity composition) of translocated and resident woylies following translocation; and (b) evaluate how ivermectin treatment impacts the prevalence of different parasite taxa, and parasite infracommunity structure within a host. Given that parasite loss following fauna reintroductions typically occurs (Torchin et al., 2003; MacLeod et al., 2010) and ivermectin should theoretically reduce the burden of target parasites (nematodes and arthropods), we predicted that parasite prevalence would decrease following translocation.

2. Material and methods

2.1. Translocations and trapping regime

Two translocations were undertaken in south-western Australia in collaboration with the Department of Biodiversity, Conservation and Attractions (DBCA) under DBCA Scientific License's (Regulation 4: written notice of lawful authority; and 17: licence to take fauna for scientific purposes) and with approval of the Murdoch University Animal Ethics Committee (RW2659/14). The first translocation was carried out in June 2014, where 182 woylies were translocated from Perup Sanctuary (a fenced reserve; 34.2506°S, 116.1425°E) to supplement two unfenced wild sites, Walcott ($n = 92$) and Warrup East ($n = 90$), located within the Upper Warren region approximately 15 km west and 20 km north-west of Perup Sanctuary, respectively (Fig. 1). Woylies within Perup Sanctuary are considered wild as they receive no interventional management (e.g. supplementary food, routine parasite treatment or vaccines). With a Mediterranean-style climate, the Upper Warren region is characterised by warm, dry summers and cool, wet winters. Average annual rainfall varies across the area from around 650–900 mm (Wayne, 2005). The dry sclerophyll forests are dominated by jarrah (*Eucalyptus marginate*), marri (*Corymbia calophylla*) and wandoo (*Eucalyptus wandoo*) (Wayne et al., 2015). The second translocation was carried out in June 2015, during which 69 woylies were translocated from six unfenced wild sites within the Upper Warren, into an unfenced wild site within Dryandra woodland (32.8027°S, 116.8854°E). Dryandra is located about 250 km north-east of the Upper Warren region (Fig. 1). The semi-arid woodland of Dryandra experiences a Mediterranean climate, with warm to hot, dry summers and mild, wet winters (McArthur et al., 1977). Rainfall is on average 500–600 mm per annum (DWMP, 2011). The open-canopy woodlands comprise predominantly wandoo, powderbark wandoo (*Eucalyptus accedens*), brown mallet (*Eucalyptus astringens*) and occasionally marri (McArthur et al., 1977). Within Dryandra, resident woylie density is estimated to be lower than both Upper Warren sites, especially Walcott (Northover et al., 2019).

Each woylie was identified with two uniquely numbered ear-tags. Prior to translocation, half of the translocated woylies (Dryandra $n = 35$, Walcott $n = 47$, Warrup East $n = 46$) were administered a single subcutaneous injection of ivermectin (Ivomec® 0.2 mg/kg).

2.2. Parasite sampling

Samples were collected from woylies at each (re)capture. For resident woylies, this includes all time points prior to (April and May 2014, Walcott and Warrup East; June 2015, Dryandra), and following, translocation (one, three, six, ten and eleven months after translocation, Walcott and Warrup East; one, two, three, six, nine and twelve months after translocation, Dryandra). For translocated woylies, this includes the point of translocation (i.e. prior to translocation/release) and all time points thereafter (as above); see Northover et al. (2019) for further details of the trapping regimes. As for resident woylies, translocated hosts are referred to by their destination site. Blood and ectoparasite samples were not collected from Warrup East resident woylies in July 2014 due to logistical constraints. Given time limitations and the large number of samples that were collected during the first translocation (June 2014), a randomly selected subset of faecal samples were analysed from translocated hosts destined for translocation into each site.

Newspaper was placed beneath each trap to collect faeces, which were stored in 10 per cent buffered formalin at 4 °C until processing. Faecal samples were examined for the presence of gastrointestinal parasite eggs, oocysts and larvae, using faecal flotation with sodium nitrate (specific gravity 1.37), as described by Northover et al. (2017). Strongyle and *Strongyloides*-like nematode eggs were counted (quantified as eggs per gram of faeces) to estimate gastrointestinal nematode burden; non-invasive methods such as this are often used in threatened species where parasite burden cannot be directly quantified (e.g. via post-mortem; Lynsdale et al., 2015). Coccidian oocysts, cestode eggs (undescribed sp.), *Potoroxyuris* sp. eggs and first stage (metastrongyloid) lungworm larvae were recorded as present or absent. Only one faecal sample from each individual per trapping session was included in our analyses.

Each woylie was examined for the presence of ectoparasites in a systematic manner (i.e. visual inspection and standardised coat combing) and was recorded as positive or negative for the presence of ticks, lice and/or louse eggs, fleas and mites, including larval and nymph stages for ticks and mites.

Blood was collected from the lateral tail vein into EDTA MiniCollect® tubes (Greiner Bio-One, Germany) for the detection of trypanosomes and frozen at −20 °C prior to processing. Genomic DNA was extracted from 200 µl aliquots of whole blood using the QIAmp 96 DNA blood kit in accordance with the Qiagen handbook (Qiagen, Hilden, Germany), with a final elution volume of 60 µl. A negative control was included in the extraction process. A nested polymerase chain reaction (PCR), targeting the second fragment of the conserved 18S rDNA gene region, was carried out using generic trypanosome primers as described by Maslov et al. (1996) and McInnes et al. (2011). All PCR reactions were performed as described by Cooper et al. (2018),

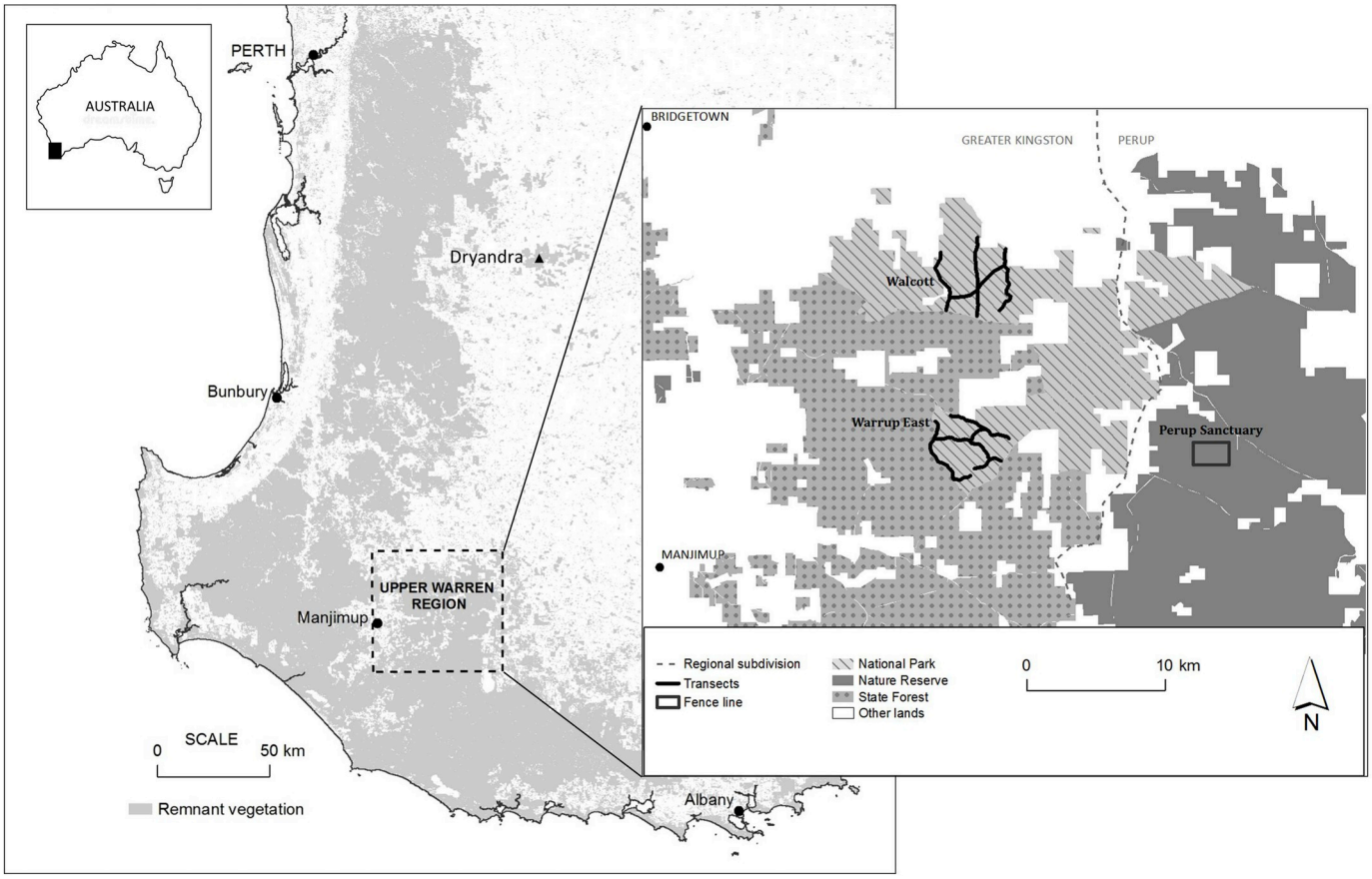

Fig. 1. Map (from Northover et al., 2019) illustrating the study sites within south-western Australia, including Walcott and Warrup East in relation to Perup Sanctuary (box, right), and Dryandra, situated roughly 250 km north-east of the Upper Warren region.

with the exception that 2 µl of DNA was added to a 24 µl master mix.

2.3. Data analysis

For each parasite taxon, prevalence of infection was calculated as the proportion of infected individuals with Jeffrey's 95% confidence intervals calculated assuming a binomial distribution. Where faecal egg counts (FEC) were obtained (i.e. strongyle and *Strongyloides*-like nematodes), means are also reported. Parasite infracommunity richness (polyparasitism) was described by the number of parasite taxa within or on an individual host, without regard to intensity of infection.

To evaluate the effect of destination site (Dryandra, Walcott and Warrup East), time since translocation (TST) and ivermectin treatment (translocated woylies only), and their interactions, on the presence of each parasite taxon, and on parasite infracommunity richness, we used generalised linear mixed-effects models (packages *lme4*, Bates et al., 2015; *glmmADMB*, Skaug et al., 2016) in R (version 6.1.15; R Core Team, 2015). All analyses were conducted separately for translocated and resident woylies. For each of our models, we tested for collinearity between predictor variables using variance inflation factors, and residuals were checked for normality/outliers to ensure model validity. Both strongyle and *Strongyloides*-like egg counts were modelled as a negative binomial distribution with a log link function. Presence/absence data for all other parasites were modelled as binomial distributions with a logit link function. For translocated woylies, Walcott was omitted from the tick model, because tick prevalence was 100% following translocation. We could not run these models for cestode eggs, *Potoroxyuris* sp. eggs or lungworm larvae due to the low prevalence of these parasites ($n = 21$, $n = 3$ and $n = 13$ positive samples, respectively). Parasite community richness was modelled as a Poisson distribution with a log link function and we only included woylies that were sampled for all parasite taxa at each capture. In all models, we included woylie ID as a random effect to account for repeated measures of individuals following translocation. In order to control for multiple corrections after significance testing, the *P*-value threshold for significance was adjusted for each family of tests (here, we define a family as each parameter in our model set, corresponding to a particular question/hypothesis) using the Hochberg (1988) method.

We evaluated differences in parasite community composition between translocated and resident woylies twice for each site; pre-translocation and six months following translocation. Differences in parasite community composition among translocated and resident hosts were estimated from presence/absence data with the Bray-Curtis coefficient for each site at each time point and visualised with non-metric multidimensional scaling plots. The effect of host group (translocated or resident) and time (pre-translocation or six months after translocation) on community composition were tested using a permutational analysis of variance (PERMANOVA + for PRIMER v. 6.0; Anderson et al., 2008) in a repeated measures design, with host group and time as fixed factors, and ID nested within host group as a random factor. Pairwise differences in community composition between translocated and resident woylies for each time point in each locality were tested by one-way ANOSIM (implemented in PRIMER v. 6.0; Clarke and Gorley, 2006), with the Hochberg correction applied for multiple testing. Using the SIMPER procedure in PRIMER, the contribution of individual parasite taxa to differences in composition among host groups was calculated by averaging the Bray-Curtis coefficients for each taxon over all pairwise host combinations.

Table 1
Results from Generalised Linear Mixed Model analysis of factors influencing parasite faecal egg counts (strongyle and *Strongyloides*-like eggs), prevalence (all other parasite taxa) and parasite infracommunity richness in woylies. Significant results following Hochberg adjustment are highlighted in bold; TST: time since translocation.

	Strongyle eggs			*Strongyloides*-like eggs			Coccidia		
	X^2	*df*	*P*	X^2	*df*	*P*	X^2	*df*	*P*
Translocated									
Site	7.3	2	0.026	21.4	2	< **0.001**	11.2	2	**0.004**
TST	75.1	1	< **0.001**	4.7	1	0.030	15.7	1	< **0.001**
Ivermectin	2.7	1	0.103	0.1	1	0.719	0.0	1	0.990
Site:TST	26.4	2	< **0.001**	5.0	2	0.082	2.5	2	0.284
Site:Ivermectin	0.2	2	0.884	2.0	2	0.372	4.1	2	0.128
TST:Ivermectin	0.2	1	0.636	0.2	1	0.657	0.4	1	0.542
Site:TST:Ivermectin	3.7	2	0.157	1.7	2	0.420	0.2	2	0.910
Resident									
Site	134.4	2	< **0.001**	73.5	2	< **0.001**	16.0	2	< **0.001**
TST	4.8	1	0.029	8.2	1	**0.004**	2.6	1	0.104
Site:TST	5.6	2	0.062	9.7	2	0.008	0.9	2	0.639

	Ticks			Mites			Lice		
	X^2	*df*	*P*	X^2	*df*	*P*	X^2	*df*	*P*
Translocated									
Site	0.2	1	0.692	42.7	2	< **0.001**	0.4	2	0.812
TST	9.5	1	**0.002**	0.0	1	0.897	4.2	1	0.039
Ivermectin	0.4	1	0.553	0.1	1	0.738	0.7	1	0.406
Site:TST	0.8	1	0.372	8.1	2	0.017	0.0	2	0.998
Site:Ivermectin	0.0	1	0.922	2.2	2	0.336	0.7	2	0.700
TST:Ivermectin	0.0	1	0.944	0.0	1	0.983	0.4	1	0.522
Site:TST:Ivermectin	1.0	1	0.327	3.8	2	0.152	0.4	2	0.816
Resident									
Site	47.8	2	< **0.001**	132.8	2	< **0.001**	0.1	2	0.947
TST	0.8	1	0.364	1.3	1	0.247	0.9	1	0.336
Site:TST	18.0	2	< **0.001**	24.0	2	< **0.001**	4.9	2	0.085

	Fleas			Trypanosomes			Parasite richness		
	X^2	*df*	*P*	X^2	*df*	*P*	X^2	*df*	*P*
Translocated									
Site	3.5	1	0.061	17.4	2	< **0.001**	17.9	2	< **0.001**
TST	0.0	1	0.880	10.9	1	**0.001**	4.0	1	0.045
Ivermectin	0.2	1	0.666	0.0	1	0.852	0.2	1	0.658
Site:TST	9.2	1	**0.002**	7.5	2	0.023	3.7	2	0.159
Site:Ivermectin	0.1	1	0.712	7.5	2	0.024	1.6	2	0.457
TST:Ivermectin	1.7	1	0.198	0.2	1	0.649	0.2	1	0.625
Site:TST:Ivermectin	0.3	1	0.585	2.9	2	0.233	0.0	2	0.998
Resident									
Site	88.7	2	< **0.001**	59.4	2	< **0.001**	257.1	2	< **0.001**
TST	2.8	1	0.093	0.3	1	0.585	3.3	1	0.127
Site:TST	4.6	2	0.101	4.9	2	0.086	1.2	2	0.556

3. Results

Overall, we analysed 872 faecal samples, 1211 blood samples and assessed 1277 woylies for the presence of ectoparasites; this included recaptures from 627 individuals (250 translocated, 377 resident).

3.1. Effect of site

3.1.1. Translocated woylies

Strongyloides-like egg counts and the prevalence of coccidia, mites and trypanosomes varied significantly between sites (Table 1); though Walcott (100% tick prevalence) was excluded from our analyses. Parasite prevalence/mean FEC were on average highest within Walcott and lowest within Dryandra (Fig. 2A; Supplementary data, Tables S1–3). Trypanosome prevalence, which was highest within Dryandra, was a notable exception to this trend (Fig. 2A).

3.1.2. Resident woylies

All parasite taxa except for lice varied significantly between sites (Table 1). Parasite prevalence/mean FEC were highest within the Upper Warren (Walcott and Warrup East) (Fig. 2B; Supplementary data, Tables S1–3). Strongyle eggs were ubiquitous within all Upper Warren sites but were not detected in Dryandra resident woylies prior to translocation. Cestode eggs were only found in Dryandra resident woylies before translocation, while lungworm larvae and *Potoroxyuris* sp. eggs were only identified in woylies originating from Perup Sanctuary (Supplementary data, Tables S1–3).

3.2. Effect of time since translocation

3.2.1. Translocated woylies

Major changes to the parasite community occurred within the immediate post-translocation period (i.e. 1–3 months following translocation). Strongyle egg counts, and the prevalence of coccidia and ticks

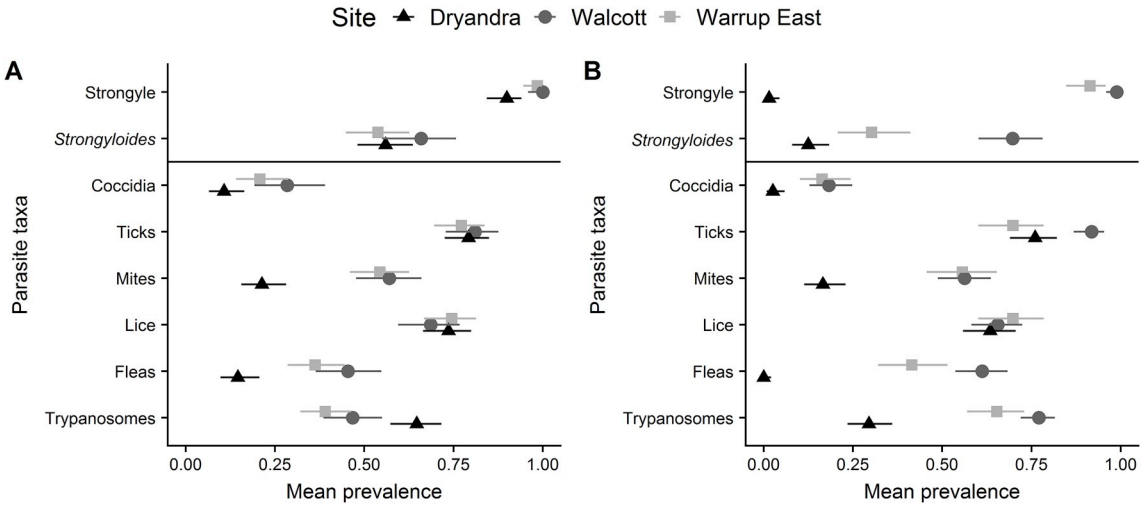

Fig. 2. The overall effect of site on mean faecal egg counts (above solid line) and parasite prevalence (below solid horizontal line) for each parasite taxon in (A) translocated and (B) resident woylies. Error bars represent 95% CI.

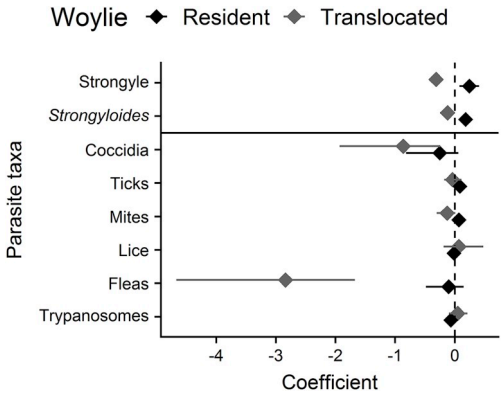

Fig. 3. The effect of time since translocation (model coefficients for all sites combined) on mean faecal egg counts (above solid horizontal line) and parasite prevalence (below solid horizontal line) for each parasite taxon in translocated and resident woylies. Left of the dashed vertical line indicates a negative effect, right of the line indicates a positive effect; Error bars represent 95% CI.

(Walcott excluded), declined with TST, while trypanosome prevalence increased with TST (Table 1; Fig. 3). We also detected a significant interaction between TST and site for strongyle egg counts and fleas (Table 1). Within Dryandra, mean strongyle egg counts decreased considerably between June and September and continued to decrease thereafter (Fig. 4A). Flea prevalence also abruptly declined between June (53.6%) and July (0.0%) in Dryandra (Fig. 4B), after which we only found fleas (low burden) in a single translocated host in August.

3.2.2. Resident woylies

Strongyloides-like egg counts increased with TST (Table 1; Fig. 3). A significant interaction between TST and site was also identified for ticks and mites (Table 1). Within Dryandra, tick prevalence markedly decreased between June (95.2%) and July (57.1%). Mite prevalence increased almost three-fold between May (34.5%) and September (91.7%) within Warrup East.

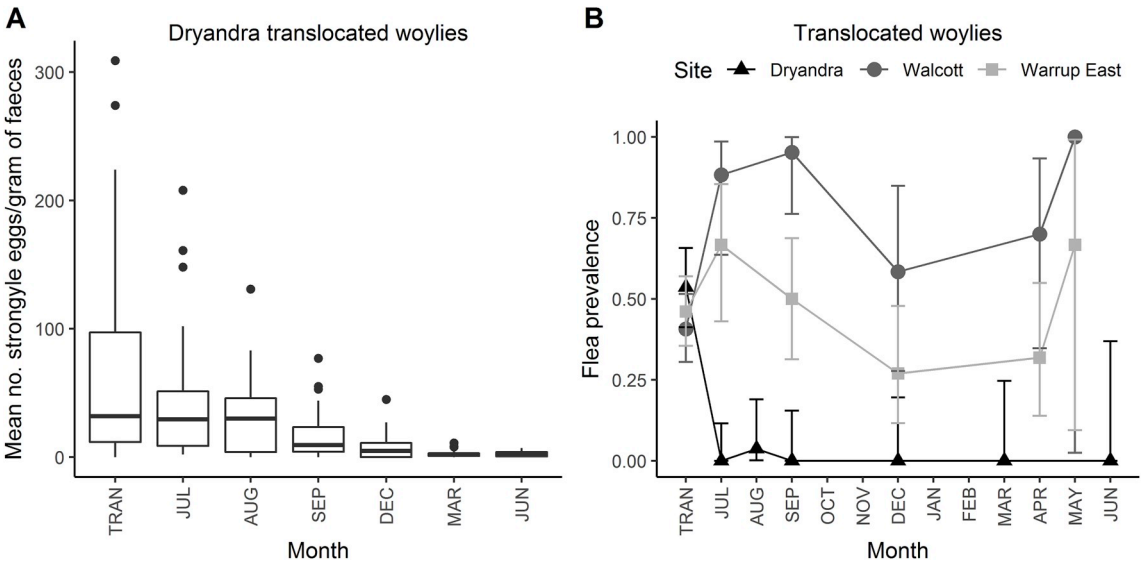

Fig. 4. Significant changes to mean strongyle egg counts (A) and flea prevalence (B) over time. TRAN: time of translocation; Boxplots (A) are delimited by the first (lower) and third (upper) quartile with the median represented by the thick horizontal line; whiskers represent the 1.5 interquartile range; solid black dots represent outliers; Error bars (B) represent 95% CI.

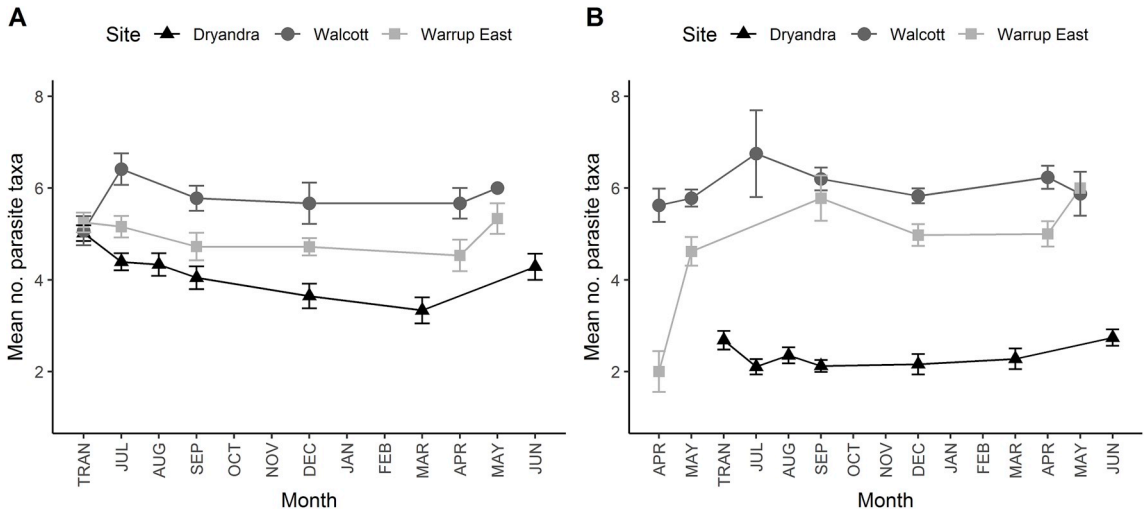

Fig. 5. Overall parasite infracommunity richness in (A) translocated and (B) resident woylies over time. TRAN: time of translocation; Error bars represent one standard error.

3.3. Effect of ivermectin treatment

Ivermectin treatment did not have a significant effect on any parasites in translocated animals, though dead lice were observed on treated woylies following translocation.

3.4. Parasite community structure in translocated and resident woylies

In translocated and resident woylies, parasite infracommunity richness differed significantly between sites (Table 1). Overall, parasite richness was highest within Walcott and lowest within Dryandra (Fig. 5). The maximum number of parasite taxa identified from a single host was nine (Walcott translocated woylie), with up to eight parasite taxa readily identified in woylies originating from the Upper Warren, compared to a maximum of five in the Dryandra resident woylie population. Dryandra was the only site in which we found woylies without any parasites ($n = 4$ residents).

In all three sites, parasite infracommunity composition was significantly influenced by both host group (Dryandra, Pseudo-$F = 22.0$, $P = 0.001$; Walcott, Pseudo-$F = 5.7$, $P = 0.001$; Warrup East, Pseudo-$F = 4.6$, $P = 0.008$) and time (Dryandra, Pseudo-$F = 13.8$, $P = 0.001$; Walcott, Pseudo-$F = 3.9$, $P = 0.02$; Warrup East, Pseudo-$F = 8.0$, $P = 0.004$), with a significant interaction between these factors (Dryandra, Pseudo-$F = 9.4$, $P = 0.002$; Walcott, Pseudo-$F = 11.2$, $P = 0.001$; Warrup East, Pseudo-$F = 6.5$, $P = 0.001$). The significant interaction was due to increasing similarity in parasite infracommunity composition between translocated and resident hosts over time (Fig. 6). Prior to translocation, parasite community composition differed significantly ($P < 0.001$) between translocated and resident woylies in all three sites, particularly Dryandra (Dryandra $R = 0.658$; Walcott $R = 0.254$; Warrup East $R = 0.237$); with *Strongyloides*-like nematodes (15.9%), trypanosomes (15.5%), fleas (15.0%) and mites (14.3%) contributing the most towards this dissimilarity. Six months after translocation, there was no significant difference in community composition between translocated and resident woylies in Dryandra ($R = 0.131$, $P > 0.05$), Walcott ($R = -0.066$, $P > 0.05$) or Warrup East ($R = -0.032$, $P > 0.05$) (Fig. 6). Within Dryandra, coccidia and fleas were not detected in translocated woylies within a few months of translocation, and novel host-parasite associations were identified. Cestode eggs were identified in two translocated woylies twelve months after translocation when they hadn't been detected in this group previously. Strongyle eggs were also detected in three resident woylies following translocation ($n = 1$, December 2015; $n = 2$, March 2016) and they had not been detected within the Dryandra resident population prior to this. Translocated woylies within Dryandra, however, maintained a significantly higher prevalence of trypanosome infection compared to resident woylies (Fig. 7).

4. Discussion

One of the notable results from this study was that the response of parasites following translocation differed significantly between sites. Changes in host population size and connectivity are two core concepts of disease ecology that underpin disease dynamics during translocation (Aiello et al., 2014). Host density may explain the particularly high prevalence of parasites (and parasite species richness) observed within Walcott; in our study, capture rates of woylies were twice as high in Walcott as the other two sites, and capture rates have been found to closely correlate with population density in woylies (Wayne et al., 2013). Low host density may explain the abrupt decline in mean strongyle egg counts and flea prevalence observed in translocated hosts within Dryandra (which had the lowest capture rates) following translocation. Alternatively, the spatially independent nature of Dryandra, in which environmental conditions differ from the Upper Warren (McArthur et al., 1977; Wayne, 2005), may be unfavourable for the completion of certain parasite life-cycles or the persistence of eggs within the environment. In addition, the way in which woylies utilse the landscape, or come into contact with cohabiting species that share the same parasites, may also differ between the open-canopy woodland of Dryandra and the comparatively taller and denser forests and woodlands of the Upper Warren. All of these factors may contribute to the site-specific differences we observed in the response of the host-parasite community following translocation.

Parasite community composition in resident and translocated woylies generally converged to become more similar over time, and changes to parasite community structure were most pronounced during the first few months following translocation. In Walcott, where resident woylie density and parasite prevalence/mean FEC were highest, the prevalence of most ectoparasites and trypanosomes increased in translocated hosts. Tick prevalence for instance, increased from 70.7% to 100% following translocation, closely resembling the high prevalence observed in resident woylies. In Dryandra, where woylie density and the number of parasites infecting residents were lower, we observed decreasing parasite prevalence and apparent loss of parasite taxa (see below) in translocated woylies following translocation. Our prediction that parasite prevalence would decrease after translocation was therefore site dependent. Variability between different sites makes it difficult to predict what will happen to the parasite community within a host

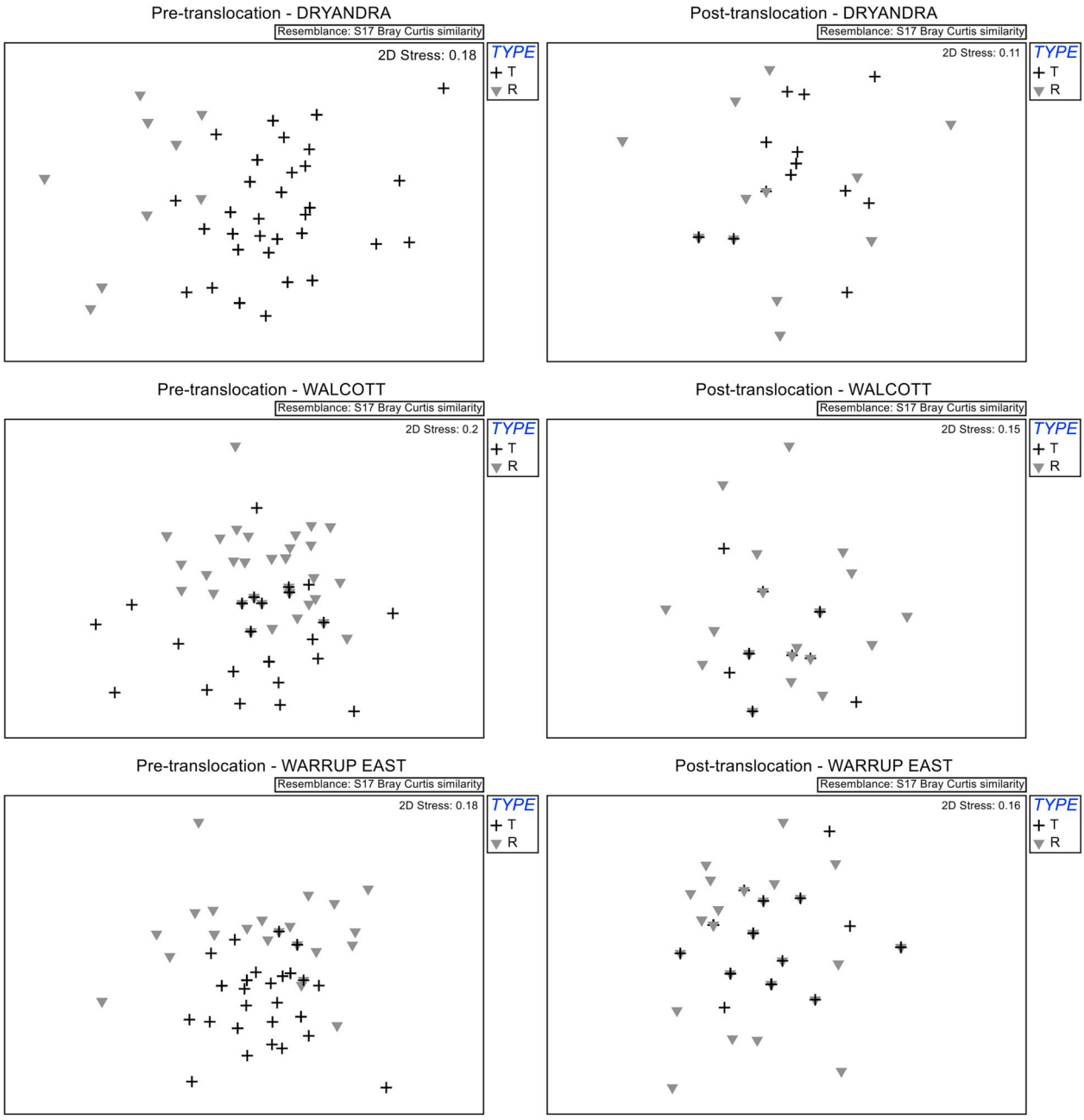

Fig. 6. Non-metric multidimensional scaling plots showing convergence of parasite community composition in translocated (TYPE T) and resident (TYPE R) woylie groups following translocation. Boxes on the left depict both groups at all time points prior to and including the point of translocation; boxes on the right depict both groups six months after translocation.

following translocation.

In this study, novel host-parasite associations with strongyles and cestodes were detected following translocation. We hypothesise that translocated woylies originating from the Upper Warren, in which strongyle infection was ubiquitous, may have introduced strongylid nematodes into the Dryandra resident woylie population. Similarly, we suspect woylies translocated into Dryandra likely acquired cestode infection within this site. The absence of cestode eggs from over 730 woylie faecal samples collected within the Upper Warren region (Northover et al., unpublished data) suggests that the intermediate host for this parasite is specific to the Dryandra region. The presence of lungworm larvae and *Potoroxyuris* sp. eggs in only translocated hosts originating from Perup Sanctuary also suggests site specificity, although this may be a function of the low prevalence of these parasites. The apparent occurrence of reciprocal parasite transmission highlights one of the risks associated with translocating wildlife and the importance of host-parasite studies. The rapid response of most parasites following translocation indicates that the immediate post-translocation period is an important time to conduct follow-up sampling. The delayed response of novel host-parasite associations however, also highlights the value of long-term parasite sampling. As for most threatened species, more field studies are needed to build a comprehensive database of the parasite species endemic within each population, and should include cohabiting host species that may impact parasite prevalence within a population.

Given the link between translocation, stress and coccidial disease (Sainsbury and Vaughan-Higgins, 2012) the observation that coccidia prevalence in translocated woylies decreased over time may coincide with woylie acclimation and recovery from translocation-associated stress (e.g. Franceschini et al., 2008). Alternatively, this may reflect the presence of fewer individuals within the destination site (e.g. following

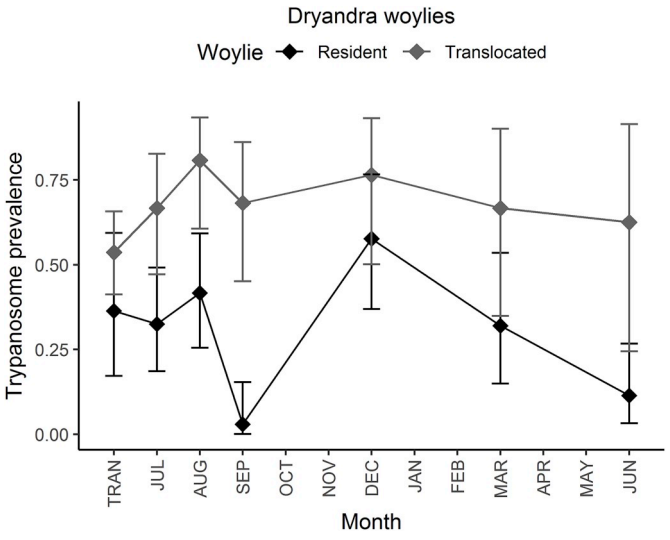

Fig. 7. Mean trypanosome prevalence over time (with 95% CI) in translocated and resident woylies within Dryandra. TRAN: time of translocation.

dispersal or predation). Seasonal variation may also explain the reduced prevalence of coccidia over summer; however prevalence would be expected to increase again during late autumn when wet conditions are optimum for oocyst development (Barker et al., 1972). For all parasite taxa, it is important to acknowledge that seasonal and annual variation in parasite prevalence/mean FECs were confounded with translocation in our study. The inclusion of a control site, which monitors hosts in the absence of translocation, would be ideal for identifying 'normal' parasite trends over time; although this is not always feasible when working with threatened species such as the woylie, where wild populations are periodically supplemented with translocated animals.

As observed in other fauna reintroduction studies (e.g. Torchin et al., 2003; MacLeod et al., 2010; Fairfield et al., 2016), specific parasite taxa were not detected in translocated hosts following translocation, although this effect was site-dependent. The absence of coccidia within Dryandra translocated woylies after September suggests that this parasite may not have survived following translocation. We did not detect coccidia in Dryandra resident woylies prior to translocation, although oocyst shedding is intermittent and the absence of oocysts in faeces does not rule out the presence of infection (Vogelnest and Portas, 2008). For gastrointestinal parasite taxa, limitations associated with the use of faecal flotation for estimating parasite burden (see Bordes and Morand, 2011) must also be considered, particularly when parasite prevalence is low. Likewise, variables such as faecal preservation method and type of flotation solution will impact the ability to recover different parasite taxa (Hu et al., 2016).

Fleas were rare within the Dryandra resident woylie population and their absence in translocated hosts after August suggests that they may have failed to persist. Given the increased recent interest in conserving parasites, as well as their hosts, as integral components of biodiversity, the loss of parasite species during translocations represents an important risk that needs consideration in translocation protocols. Thompson et al. (2018) provided a comprehensive list of woylie parasites and identified six species that appear to be host-specific and are in danger of extinction. Given that we identified three of these six species (*Ixodes woyliei*, *Eimeria woyliei* and *Potoroxyuris keninupensis*) plus a novel undescribed species of cestode during this study (Northover et al., unpublished data) and woylies are the most commonly translocated species in Australia (Morris et al., 2015), the consequences of host-specific parasite extinction require careful deliberation. Likewise, the link between parasite presence and host health needs to be investigated. If specific parasite taxa are associated with poor health in woylies, then translocation protocols could potentially be adapted to control for these parasites (e.g. targeted antiparasitic drug treatment or utilizing next generation sequencing to identify potentially harmful *Trypanosoma* genotypes infecting specific populations; see below). On the other hand, if there is no evidence to suggest that known parasite taxa adversely impact host health, parasite conservation should be a key consideration, particularly for rare host-specific parasites.

Within Dryandra, there remained a persistently high prevalence of trypanosome infection in translocated compared to resident woylies, despite a general convergence in parasite infracommunity structure over time. As detectable parasitaemia associated with the active acute phase of infection is typically short-lived (Campos et al., 2010), trypanosome prevalence would be expected to decrease over time in a site where trypanosome prevalence is low. The fact that trypanosome prevalence remained high suggests that another process is responsible for maintenance of parasitaemia in the absence of reinfection. For example, translocated woylies may be infected with *Trypanosoma copemani* genotype 2, which has the proposed ability to invade tissues, replicate and re-enter the peripheral blood (Botero et al., 2013, 2016; Thompson et al., 2013). Molecular evaluation of specific *Trypanosma* species infecting woylies during the same translocation (Northover et al., 2019) attributed this pattern of divergence to the presence of *T. copemani*, however the specific genotype remains unknown.

Unexpectedly, ivermectin treatment did not significantly reduce parasite prevalence or mean FEC in target parasites during this study. It is important to note that the lack of a significant effect in target parasites does not necessarily indicate that ivermectin is ineffective. No clinical studies have evaluated the efficacy of ivermectin in woylies, thus the dose or dosage regime may have been suboptimal. The dose administered to woylies during this study was at the lower end of the suggested reference range for macropods (Vogelnest and Portas, 2008) and was selected based on its apparent safe use in the closely related eastern bettong *Bettongia gaimardi* (Portas et al., 2014). The absence of an effect in target parasites may indicate that woylies require a higher dose or repeat dosing. Furthermore, different parasite species are likely to vary in their susceptibility to ivermectin.

5. Conclusions

This is the first study to evaluate how the broader parasite community changes following fauna translocation in translocated and resident hosts. The response of most parasites following translocation occurred rapidly but varied significantly among sites. These findings have several important implications for fauna translocations. First, given the innate ability of parasites to impact host health and translocation outcomes, and the large degree of unpredictability associated with translocating wildlife, translocation protocols should incorporate long-term parasite monitoring to better understand (a) how the parasite community within a host changes following translocation; and (b) the biological implications of these changes on individuals (e.g. reproductive fitness, survivorship), host populations (e.g. population health, growth rates) and ultimately translocation success. For woylies, more research is needed to understand the site-level drivers of parasite dynamics. Second, with increasing recognition of the intrinsic biodiversity value of parasites (Colwell et al., 2012; Thompson et al., 2018), the potential loss of host-parasite associations should be a serious consideration when planning fauna translocations. Finally, antiparasitic drugs should be applied prior to translocation only where there is a clear rationale for their use; field studies that examine the response of parasites following experimental manipulation are required to provide such justification.

Acknowledgements

This project was primarily funded by the Australian Research Council (LP130101073) and has been assisted by grants from the

Holsworth Wildlife Research Endowment (HOLSW2015-1-F149) and the Ecological Society of Australia, The Royal Zoological Society of New South Wales (Paddy Pallin Grant) and the Australian Wildlife Society. We would like to thank Marika Maxwell, Colin Ward, Chris Vellios, Julia Wayne, Peter Wnuk, Malcolm Ovans, Brian Macmahon and other DBCA staff for their assistance in the field, and all of our dedicated volunteers for their support with fieldwork, sample collection and processing. The woylie image (graphical abstract) has been provided courtesy of John Lawson.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2019.07.001.

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