

Helminth communities of pademelons, *Thylogale stigmatica* and *T. thetis* from eastern Australia and Papua New Guinea

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Abstract

Gastrointestinal helminths were collected from pademelons of the genus *Thylogale* (Marsupialia: Macropodidae) in eastern Australia and Papua New Guinea. Examined were 12 *Thylogale stigmatica stigmatica* and 13 *T. s. wilcoxi*, the latter subdivided into eight specimens from the northern limit of their distribution and five from southern areas, all from eastern Queensland, Australia, one *T. s. orion* from Papua New Guinea and ten *T. thetis* from southeastern Queensland and northern New South Wales, Australia. Six species of cestodes and 40 species of nematodes were found. The helminth community of *T. s. stigmatica* was similar to that found in northern specimens of *T. s. wilcoxi*, while differences from the helminth community present in southern *T. s. wilcoxi* could be accounted for by parasites acquired from sympatric *T. thetis*. *Thylogale thetis* harboured a community of helminths distinct from but related to that in *T. stigmatica*. The evidence suggests that all subspecies of *T. stigmatica* examined share a common helminth community, but that in areas of sympatry, *T. stigmatica* and *T. thetis* share some of their parasites.

Introduction

Kangaroos and wallabies (family Macropodidae) typically harbour diverse communities of gastro-intestinal helminth parasites. Most communities are dominated numerically by strongyloid nematodes occurring in the sacculated forestomach and in the colon, with smaller numbers of species of trichostrongyloid nematodes in the pyloric antrum and duodenum, oxyuroid nematodes in the colon and anoplocephalid cestodes in the small intestine and bile duct (Beveridge & Spratt, 1996). Comparisons of the helminth communities from different species of macropodid suggest that most hosts harbour a distinctive series of helminth species, sharing relatively few parasites (Beveridge *et al.*, 1992, 1998). The sole exception to this generalization appears to be the rock-wallabies of the *Petrogale penicillata* complex (*P. assimilis*,

P. godmani, *P. herberti*, *P. inornata*, *P. penicillata*, *P. mareeba*, *P. sharmani*), which share a similar suite of parasite species (Beveridge *et al.*, 1989).

However, the general pattern described above is based on observations of a relatively small number of host species. In no instance is the host sub-divided into a range of geographically isolated subspecies. It is possible that such sub-divisions of host range could also provide barriers to the dispersion of parasites and that consequently, different subspecies of macropodid hosts might harbour communities just as distinctive as those found in the host species examined to date. Another possible objection to the general pattern described could be that closely related host species occupying identical habitats might share parasites. Members of the *P. penicillata* complex, while closely related phylogenetically (Flannery, 1989), exhibit a parapatric rather than a sympatric distribution (Briscoe *et al.*, 1982; Eldridge & Close, 1997). By contrast, the related scrub wallabies such as *Macropus agilis*, *M. dorsalis* and *M. parryi*, belonging to the sub-genus *Notamacropus*, are broadly sympatric but exhibit

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habitat specialization which could restrict the exchange of helminths between host species (Beveridge *et al.*, 1998).

These possibilities are examined in the present paper utilizing the helminth communities of two closely related species of pademelons, *Thylogale stigmatica* and *T. thetis*, small wallabies which inhabit rainforests or sclerophyll forests with a dense understorey (Strahan, 1995). *Thylogale stigmatica* is represented by four sub-species in eastern Australia and Papua New Guinea (fig. 1), the separation of the subspecies possibly being a recent phenomenon (Winter, 1997). The helminth community of *T. s. stigmatica* has been studied recently and is highly complex (Beveridge *et al.*, 1992). The sister taxon, *T. thetis*, is restricted to south-eastern Queensland and eastern New South Wales, where it occurs in rain-forest in association with *T. stigmatica* (see Calaby, 1966). The nature of its helminth community has not yet been investigated. This situation therefore provides an opportunity to examine the extent of interchange of

parasites between two host species occupying the same habitat and to examine differences in the helminth communities between geographically separated subspecies of the same host taxon.

Materials and methods

Pademelons were obtained opportunistically as road-kills. Collection localities, with the number of specimens collected in parentheses, were as follows: *T. stigmatica*: Queensland: Lake Barrine (1), Lake Eacham (5), Julatten (4), Tully (1), Ingham (1); *T. stigmatica wilcoxi*: Queensland: Sarina (1), Eungella (2), Mt Julian via Proserpine (2), Mt Lucas via Proserpine (3), Lamington National Park (2), Mt Glorious (3); *T. thetis*: Queensland: Lamington National Park (4), Mt Nebo (1), Emuvale (2), Mt Glorious (2); New South Wales: Dorrigo (1). One specimen of *T. stigmatica oriomo* was collected from Balamuk, Western Province, Papua New Guinea. Carcasses



Fig. 1. Distributions of *Thylogale stigmatica* and *T. thetis* in eastern Australia and Papua New Guinea, showing locations at which specimens were collected.

were frozen at -20°C or in the rare instances in which this was not possible, the entire animal or the entire gastrointestinal tract was preserved in 10% formalin. Frozen animals were thawed and autopsied following methods similar to those of Beveridge *et al.* (1992) and Begg *et al.* (1995). A sample of stomach content (30–40%) was fixed in 10% formalin. The small intestine was examined grossly for cestodes which were washed in water and fixed in alcohol, formalin and acetic acid (AFA) (Pritchard and Kruse, 1982). The entire content of the small and large intestine was preserved in 10% formalin and subsequently washed in water to remove the formalin and examined for helminths using a stereomicroscope.

All parasite material collected has been deposited in the South Australian Museum, Adelaide.

Nematodes were cleared in lactophenol and identified to species using a compound microscope. Cestodes were stained with Celestine blue, dehydrated in ethanol, cleared in clove oil and mounted in Canada balsam for identification.

One *T. stigmatica* and one *T. thetis* were used to determine the sample size of stomach nematodes needed to recover all the species present. Sequential samples of 20 randomly selected nematodes were identified using a compound microscope until no new species were found in three sequential samples. Based on the results, 200 helminths were examined from the stomach contents of each animal examined subsequently.

Specimens of *T. stigmatica* were divided into three groups based on host taxon and location at which they were collected. The population of *T. s. stigmatica* consisted of animals collected between Ingham and the Atherton Tablelands, Queensland. Populations of *T. s. wilcoxi* collected from Sarina, Eungella and Proserpine, Queensland, were designated as the 'northern' population of this subspecies, while the 'southern' population of *T. s. wilcoxi* constituted animals collected from Lamington National Park and Mt Glorious in southeastern Queensland. Specimens of *T. thetis* were obtained from the same localities as *T. s. wilcoxi* in southern Queensland as well as from Warwick, Queensland and Dorrigo, New South Wales.

As host sample sizes were necessarily small, the analysis of the helminth communities is essentially descriptive. The small sample sizes may have underestimated the true parasite species richness in each host population. Therefore, the true species richness was estimated using the bootstrap method of Poulin (1998).

The diversity of helminth communities was expressed as the reciprocal of Simpson's Index ($1/SI$) (Holmes & Podesta, 1968). The overall similarity of helminth communities was compared using Sorenson's Index (Greig-Smith, 1964) and the index of Holmes & Podesta (1968) and the matrices converted to dendrograms using the mean group algorithm (Sneath & Sokal, 1973). The indices were compared with similar data for *T. s. stigmatica* (Beveridge *et al.*, 1992). Host specificity for each helminth was determined from the literature (Spratt *et al.*, 1991; Beveridge *et al.*, 1992; Smales, 1994, 1995; Begg *et al.*, 1995; Beveridge, 1998). The percentage of host population specific, host species specific and host genus specific helminths was calculated for each population, excluding

occurrences of parasites of the Proserpine rock-wallaby, *Petrogale persephone*, which shares its habitat with *T. stigmatica* in the Proserpine region of Queensland (Begg *et al.*, 1995).

Host-switching was deemed to have occurred in instances in which helminths occurred at a prevalence of 10% or less in one population and a prevalence of 40% or greater in the other, or, alternatively, exhibited a prevalence difference of greater than or equal to 50% in the sympatric population. The first criterion ($< 10\%$) follows Bush *et al.* (1990). The second criterion was applied in instances where there were fewer than ten animals in a group and prevalences of 10% or less were not encountered. A second similarity matrix was calculated with helminth species identified as host-switches removed, using Sorenson's Index.

An alternative approach used to determine host switches was the core-satellite species hypothesis (Hanski, 1982; Bush & Holmes, 1986a,b). The number of helminth species occurring in each 10 or 20% prevalence class was determined for each pademelon population. The combined data for all four populations were plotted and a division into core, secondary and satellite species made based on the modes exhibited (Bush & Holmes, 1986a,b). The proportion of core and satellite species in each population of pademelons was calculated.

Results

Six species of cestodes and 40 species of nematodes were recovered from the Australian pademelons examined (table 1). New host records are indicated (table 1) by an asterisk. Species of helminths found in the single specimen of *T. s. orion* from Papua New Guinea were: Cestodes: *Progamotaenia queenslandensis*, *Calostaurus macropus*; Nematodes: *Amphicephaloides thylogale*, *Cloacina cloelia*, *C. cybele*, *C. dahli*, *Coronostrongylus coronatus*, *Foliostoma macropodis*, *Macropoxyuris* sp., *Monilonema lacunosum*, *Pharyngostongylus iota*, *P. setosus*, *Popovastrongylus thylogale*, *Rugopharynx sigma*, *Sutarostrongylus* sp., *Thallostonema lichtenfelsi*, *Trigonostonema trigonostoma*, *Thylonema barkeri*, *T. arundeli* and *T. thylonema*.

Observed helminth species richness in pademelon populations ranged from 24 to 33 (table 2). Estimates of true species richness (Poulin, 1998) suggested that between one and five additional species of helminths might have been found in each host population (table 2).

Comparable numbers of helminth species and comparable indices of diversity were evident in each of the four populations of pademelons examined (table 2). The population specificity of helminths in *Thylogale stigmatica* was low (table 2), while *T. stigmatica* harboured a higher proportion of species-specific nematodes than *T. thetis*. All populations were parasitized by helminths which were highly specific at the host genus level.

Overall similarities between helminth communities, as indicated by Sorenson's index (fig. 2) indicated a high similarity between the communities of *T. s. stigmatica* and the northern population of *T. s. wilcoxi* (92.3%), with a slightly lower similarity between that of *T. s. stigmatica* and the southern population of *T. s. wilcoxi*. (72.1%). The community of helminths in *T. thetis* was most similar to

Table 1. Prevalence (%) of helminth parasites in populations of *Thylogale stigmatica* and *T. thetis* in eastern Australia.

	<i>T. thetis</i>	<i>T. s. wilcoxi</i>		<i>T. s. stigmatica</i>
		'southern'	'northern'	
Number of animals examined	10	5	8	12
CESTODA				
Anoplocephalidae				
<i>Progamotaenia queenslandensis</i> Beveridge, 1985	0	0	88	58
<i>Progamotaenia sparei</i> Beveridge, 1980	0	0	50	42
<i>Progamotaenia thylogale</i> Beveridge & Thompson, 1979	20	0	0	0
<i>Progamotaenia zschokkei</i> (Janicki, 1905)	10*	20	25	75
<i>Calostaurus macropus</i> (Ortlepp, 1922)	10*	40	75	67
Taeniidae				
<i>Echinococcus granulosus</i> (Batsch, 1786)	0	0	25	0
NEMATODA				
Strongyloidea: Cloacinidae				
Macropostrongyloidinae				
<i>Hypodontus macropi</i> (Mönnig, 1929)	50	20*	0	0
Cloacininae: Cloacininae				
<i>Cloacina cloelia</i> Beveridge, 1998	30*	100	100	83
<i>Cloacina cybele</i> Beveridge, 1998	10*	60	88	33
<i>Cloacina dahli</i> (Linstow, 1898)	0	0	88	58
Cloacininae: Coronostromylinea				
<i>Corollonema thylogale</i> Beveridge & Chilton, 1998	20	60	0	0
<i>Popovastrongylus thylogale</i> Beveridge, 1987	40	60	50	92
<i>Popovastrongylus wallabiae</i> (Johnston & Mawson, 1939)	30*	20*	0	0
<i>Thylonema arundeli</i> Beveridge, 1981	0	80	75	33
<i>Thylonema barkeri</i> Beveridge, 1981	0	80	100	100
<i>Thylonema thylonema</i> Beveridge, 1981	0	80	88	58
<i>Thylonema woodalli</i> Griffith, 1999	0	20	0	0
<i>Thylonema clelandae</i> Griffith, 1999	0	20	0	0
Cloacininae: Macropostrongylinea				
<i>Monilonema lacunosum</i> Beveridge & Johnson, 1981	10*	40	75	50
<i>Foliostoma macropodis</i> Beveridge & Johnson, 1981	10*	80	88	58
<i>Thallostonema kirkpatricki</i> Beveridge, 1983	20	20	0	0
<i>Thallostonema lichtenfelsi</i> Beveridge, 1983	10*	20	75	67
<i>Thallostonema thylogalarum</i> Beveridge, 1983	40	0	0	0
<i>Trigonostonema longibursatum</i> Beveridge, 1981	10*	0	63	17
<i>Trigonostonema trigonostoma</i> Beveridge, 1981	20*	80	63	58
Cloacininae: Labiostrongylinea				
<i>Labiostrongylus thetidis</i> Smales, 1995	90	20	25	17
<i>Labiostrongylus thylogale</i> Smales, 1995	0	0	25	8
<i>Labiostrongylus flanneryi</i> Smales, 1995	0	0	0	8
Cloacininae: Pharyngostrongylinea				
<i>Pharyngostrongylus iota</i> Johnston & Mawson, 1939	70	20	0	17
<i>Pharyngostrongylus setosus</i> Beveridge, 1982	0	60	75	67
<i>Rugopharynx tau</i> Beveridge & Chilton, 1999	80	20*	0	0
<i>Rugopharynx sigma</i> Beveridge, Chilton & Andrews, 1994	100	100	100	100
<i>Rugopharynx zeta</i> Johnston & Mawson, 1939	20	0	0	0
<i>Thylostrongylus parvus</i> Beveridge, 1982	40	0	0	0
<i>Thylostrongylus tasmaniensis</i> Beveridge, 1982	10*	20*	0	0
<i>Thylostrongylus franklinae</i> Griffith, 1999	10	60	0	0
Cloacininae: Zoniolaiminae				
<i>Cassunema exiguum</i> Beveridge & Johnson, 1981	10	80	25	42
<i>Tethystrongylus coronatus</i> Beveridge, 1983	20	0	0	0
<i>Wallabinema gallardi</i> (Johnston & Mawson, 1939)	60*	60*	0	0
<i>Wallabinema parvispiculare</i> Beveridge, 1983	10	80	75	50
<i>Wallabinema thylogale</i> Beveridge, 1983	90	40	0	0
Trichostrongyloidea: Herpetostrongylidae				
<i>Amphicephaloides thylogale</i> Beveridge, 1979	70	60	88	100
<i>Sutarostrongylus kirkpatricki</i> Beveridge & Durette-Desset, 1986	50	0	0	0
<i>Sutarostrongylus</i> sp. of Beveridge & Durette-Desset, 1986	0	20	0	17
Spiuroidea: Spirocercidae				
<i>Physocephalus sexualatus</i> (Molin, 1860)	0	40	0	8
Oxyuroidea: Oxyuridae				
<i>Macropoxyuris</i> sp.	10*	20*	38*	8*

*New host record.

Table 2. Characteristics of the helminth communities in populations of *Thylogale stigmatica* and *T. thetis* from eastern Australia.

	<i>T. thetis</i>	<i>T. s. wilcoxi</i>		<i>T. stigmatica</i>
		'southern'	'northern'	
Total no. of helminth species observed	32	33	24	28
True species richness (estimated)	37	38	25	30
Reciprocal of Simpson's Index	22.2	25.2	21.1	21.8
% of helminths population specific	15.6	6.1	4.0	7.1
% of helminths species specific	15.6	33.3	44.0	39.3
% of helminths genus specific	93.8	90.1	92.0	89.3
% of satellite species	66.0	40.0	20.0	29.0
% of core species	13.0	27.0	48.0	21.0

that in the southern population of *T. s. wilcoxi* (76.5%). Indices calculated following the removal of identifiable host switches were very similar to those derived using the index of Holmes & Podesta (1968) and therefore only the latter data are shown (fig. 2). In this analysis, the community present in *T. s. stigmatica* was most similar to that found in the northern population of *T. s. wilcoxi* (83.1%) compared with a similarity of 65.3% with the southern population of *T. s. wilcoxi*. Similarities between the community present in *T. thetis* and those in *T. stigmatica* populations were lower than those obtained using Sorenson's index but exhibited a similar pattern, with the community in *T. thetis* most similar to that present in the southern population of *T. s. wilcoxi*.

Plotting the number of helminths in each prevalence class (fig. 3) resulted in a histogram with a relatively uniform distribution of prevalence class frequencies. There was a weak mode in the 20% prevalence class, potentially identifying satellite species according to the classification of Hanski (1982). A weak mode in the 60% prevalence class was taken to indicate the existence of secondary species (Bush & Holmes, 1986a,b) while the

mode in the 80% prevalence class was taken to indicate core species (Hanski, 1982). Based on this pattern, helminths were designated as satellite species if they occurred at a prevalence of 30% or less and core species if they occurred at a prevalence of greater than 71%. Relative proportions of satellite species within each pademelon population differed little whether the limit for the class was set at 20%, 30% or 40%. Using 30% prevalence as the upper limit of the satellite class, *T. thetis* and the southern population of *T. s. wilcoxi* harboured a higher proportion of satellite species than the remaining populations. *Thylogale thetis* harboured a smaller proportion of core species than the other populations.

Discussion

All four populations of pademelons examined harboured a diverse fauna of helminth parasites, as expected from a prior study of the parasites of *T. s. stigmatica* by

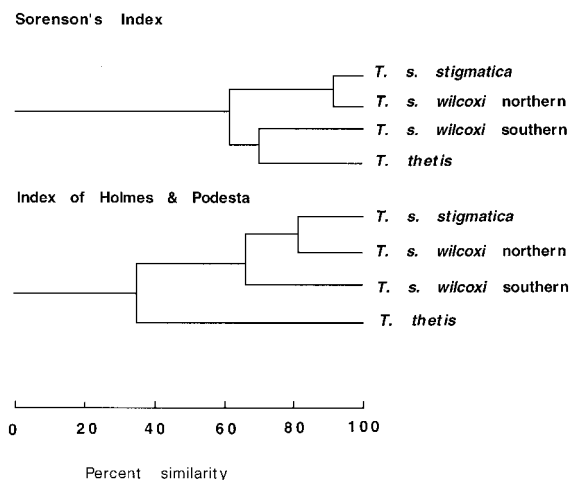


Fig. 2. Similarities between the helminth communities of populations of *Thylogale stigmatica* and *T. thetis* using Sorenson's index (upper figure) or the similarity index of Holmes & Podesta (1968) (lower figure).

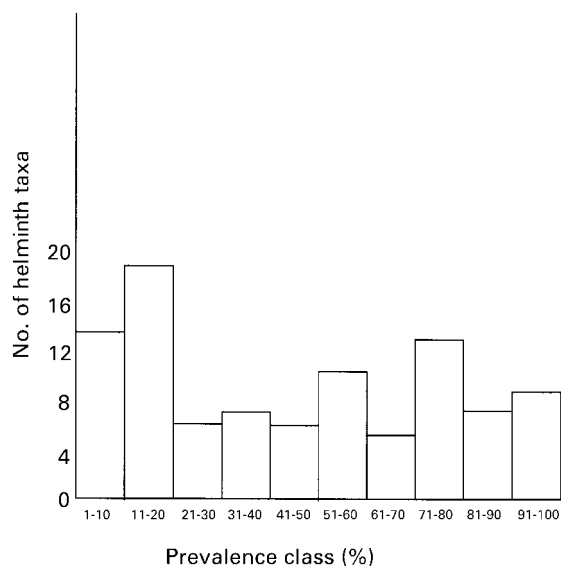


Fig. 3. Prevalence class distribution of the helminth species found in four populations of *Thylogale stigmatica* and *T. thetis* in eastern Australia.

Beveridge *et al.* (1992). In each population of hosts, the helminth community was dominated by strongyloid nematodes in the stomach, with small numbers of trichostrongyloid nematodes, anoplocephalid and davainid cestodes in the small intestine, and oxyuroid and strongyloid nematodes in the colon (table 1), conforming with the general pattern described hitherto in other macropodoid marsupials (Beveridge & Spratt, 1996). In addition, the specificity of parasites at the host genus level was high (table 2), supporting the suggestion of Beveridge & Spratt (1996) that pademelons harbour a distinctive series of helminth species when compared with other macropodid hosts.

In determining the specificity of helminths at the host genus level, the status of two nematode species warrants comment. Both *Pharyngostromylus iota* and *Wallabinema gallardi* were originally described from 'red-necked wallabies' (*Macropus rufogriseus*) from Ourimbah, New South Wales (Beveridge, 1982, 1983). However, neither has since been found in *M. rufogriseus* (see Spratt *et al.*, 1991) although both are common in 'red-necked pademelons' (*T. thetis*). It seems likely therefore that the host from which the original specimens were collected was in fact a 'red-necked pademelon' rather than a 'red-necked wallaby' as both species occur in the vicinity of Ourimbah (Strahan, 1995). For this reason both have been treated as parasites specific to *Thylogale* spp.

The range of helminth species encountered in *T. s. stigmatica* in this study was comparable with that reported previously (Beveridge *et al.*, 1992), minor differences being due primarily to the fact that in the present study only gastrointestinal parasites were examined. Psilostomatid digeneans and the nematodes *Coronostrongylus coronatus* Johnston & Mawson, 1939 and *Filarinema* sp. (undescribed), reported by Beveridge *et al.* (1992) were not encountered in Australian hosts in this study, while three species of *Labiostrongylus* were found, compared with a single undescribed species reported by Beveridge *et al.* (1992). In addition, oxyurid nematodes, not previously reported from pademelons, were found in this study. In spite of minor differences, the range of helminths encountered in the present study was similar to that reported previously.

The range of parasites present in the northern population of *T. s. wilcoxi* was virtually identical with that found in *T. s. stigmatica*, differing only in the absence of *Sutarostromylus* sp. (undescribed), which occurred at a low prevalence in *T. s. stigmatica* (see Beveridge *et al.* 1992) and *Physocephalus sexalatus*, a parasite of feral pigs in Australia (Mackerras, 1958) which appears to occur opportunistically in macropodids collected from habitats in which feral pigs are common (Beveridge *et al.*, 1989, 1992, 1998).

By contrast, the helminth communities of *T. thetis* and the southern population of *T. s. wilcoxi* differed substantially from those of their northern counterparts. The helminth community of *T. thetis* is defined here for the first time. While similar in many respects to that found in *T. s. stigmatica*, particularly in the high proportion of helminths which are specific to the genus *Thylogale*, there are significant differences. Several helminth species (*Progamotaenia thylogale*, *Thallostemonema thylogalarum*, *Rugopharynx zeta*, *Thylostrongylus parvus*,

Tethystrongylus coronatus, *Sutarostromylus kirkpatricki*) occur exclusively in *Thylogale thetis*, while other species (*Hypodontus macropi*, *Corollonema thylogale*, *Popovastrongylus wallabiae*, *Thallostemonema kirkpatricki*, *Rugopharynx tau*, *Thylostrongylus tasmaniensis*, *T. franklinae*, *Wallabinema gallardi* and *W. thylogale*) occurred in *T. thetis* and the southern population of *T. s. wilcoxi* but were absent from the northern population of *T. s. wilcoxi* and from *T. s. stigmatica*. Only two helminth taxa (*Thylonema woodalli* and *T. clelandae*) occurred exclusively in *Thylogale stigmatica wilcoxi*, although a single record of *Thylonema woodalli* in *Thylogale stigmatica stigmatica* exists from examinations of pademelons not included in this study (Griffith, 1999). Only five specimens of the southern population of *T. s. wilcoxi* were examined, however, it was estimated, using the bootstrap method advocated by Poulin (1998) that 87% of the helminth species likely to be found were in fact recovered in this sample. The conclusions drawn from the sample are therefore considered reasonable, but clearly need to be interpreted in a conservative fashion due to the small sample sizes.

The possible origins of the helminths occurring only in *T. thetis* and the southern population of *T. s. wilcoxi* were investigated using a comparison of the similarities of communities which takes into account the prevalence of individual parasite species (Holmes & Podesta, 1968) and by removing identifiable instances of host switching. Both analyses produced identical results, thereby providing support for the somewhat subjective designation of 'host-switches' in the second analysis. These results were supported by the analysis of proportions of core and satellite species in each population. Although some deficiencies in the application of these methods to the parasites of macropodids have been identified (Beveridge *et al.*, 1989, 1992, 1998), and the current analysis is limited by a lack of clear modes in the frequency distribution, a higher proportion of satellite species in *T. thetis* and the southern population of *T. s. wilcoxi* was identified, a result which is consistent with the hypothesis of frequent host switching between the two populations. The results therefore suggest that *T. thetis* harbours a community of helminths similar to but distinct from that found in *T. s. stigmatica* and that in south-eastern Queensland and north-eastern New South Wales where the two host species are sympatric, there is some exchange, in both directions, of helminth parasites.

That *T. stigmatica* harbours a well-defined community of helminths is confirmed by the occurrence in southern Papua New Guinea of precisely the same sequence of helminth parasites. Although only a single specimen of *T. s. oriomo* was available for examination, analyses suggest that even a single host specimen of pademelons harbours at least 50% of the helminth taxa likely to be encountered. Given the practical difficulties associated with collecting *T. s. oriomo* as well as the Cape York subspecies, *T. s. coxeni*, current results suggest that they are unlikely to harbour parasites distinctive to those already encountered. Therefore, it is concluded that, apart from the acquisition of parasites from sympatric *T. thetis* in the southern part of its distribution, *T. stigmatica* harbours a distinctive series of parasites throughout its geographic range.

The subspecies of *T. stigmatica* are based primarily

on geographic subdivisions of their range and to date there are no studies of the genetic differences between populations. In addition, the actual distribution of *T. s. wilcoxi* is highly fragmented compared with the generalized distribution of the sub-species presented by Strahan (1995) and in fact correspond more closely with the four 'rainforest refugia' areas designated in eastern Australia by Maynes (1989). Winter (1997) suggested that *T. stigmatica* originated in southern Queensland, reaching the 'wet tropics' of northern Queensland 6000–7500 years ago. The species probably crossed the Torres Strait 5000 years ago to reach southern Papua New Guinea (Maynes, 1989). According to these hypotheses, subspeciation in *T. stigmatica* is a very recent phenomenon and it might be expected therefore that the helminth communities of *T. stigmatica* would be quite similar in spite of substantial geographical separation, a hypothesis supported by the data presented in this paper.

The conclusions of this study are that the closely related pademelon species *T. stigmatica* and *T. thetis* harbour very similar yet distinctive helminth parasite faunas and that in south-eastern Queensland and north-eastern New South Wales, where the two species coexist, there is exchange of helminth parasites between them.

The three geographically separated subspecies of *T. stigmatica* examined harbour essentially the same suite of parasites and the short period of separation of these subspecies (5000–7500 years) has probably not been sufficient to allow for diversification of the helminth community, based on morphological analyses of the parasites present.

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