Research Paper

Gastrointestinal helminth parasites of the common wallaroo or euro, *Osphranter robustus* (Gould) (Marsupialia: Macropodidae) from Australia

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Abstract

The gastrointestinal helminth parasites of 170 common wallaroos or euros, *Osphranter robustus* (Gould), collected from all mainland states in which the species occurs as well as the Northern Territory, are presented, including previously published data. A total of 65 species of helminths were encountered, including four species of anoplocephalid cestodes found in the bile ducts and small intestine, and 61 species of strongylid nematodes, all but two of which occurring in the stomach, and with the remainder occurring in the terminal ileum, caecum and colon. Among the mainland subspecies of *O. robustus*, 52 species of helminths were encountered in *O. r. robustus*, compared with 30 species in *O. r. woodwardi* and 35 species in *O. r. erubescens*. Of the parasite species encountered, only 17 were specific to *O. robustus*, the remaining being shared with sympatric host species. Host-specific species or species occurring in *O. robustus* at a high prevalence can be classified as follows: widely distributed; restricted to northern Australia; restricted to the northern wallaroo, *O. r. woodwardi*; found only in the euro, *O. r. erubescens*; found essentially along the eastern coast of Australia, primarily in *O. r. robustus*; and species with highly limited regional distributions. The data currently available suggest that the acquisition of a significant number of parasites is due to co-grazing with other macropodids, while subspeciation in wallaroos as well as climatic variables may have influenced the diversification of the parasite fauna.

Introduction

The common wallaroo or euro, *Osphranter robustus* (Gould, 1840) (formerly known as *Macropus robustus* Gould, 1840) is one of the most widely distributed large kangaroos in Australia and is common in all states and the Northern Territory apart from Victoria and Tasmania (Clancy & Croft, 2008). In Victoria, there appears to be a single extant population in east Gippsland close to the border with New South Wales (Menkhorst, 1996), while it is completely absent from Tasmania. In spite of its abundance and distribution, only a single survey of its helminth parasites has been published, based on an examination of 30 wallaroos restricted to central and northern Queensland (Beveridge *et al.*, 1998). Other parasite records from this kangaroo species are based on incidental collection, but *O. robustus* appears to harbour more species of helminth parasites than any other of the large kangaroos belonging to the genera *Macropus* Shaw, 1790 and *Osphranter* Gould, 1842 (Spratt & Beveridge, 2016).

The data presented here, based on the examination of a total of 170 wallaroos (or euros) from across the continent, are intended to contribute to this apparent void in knowledge of the helminth parasites of one of the commonest and most abundant kangaroo species in Australia. An attempt has also been made to determine the extent to which helminth species may be restricted to any of the three major mainland subspecies of *O. robustus* currently recognized, namely the eastern wallaroo, *O. r. robustus* (Gould, 1840) occurring along the Great Dividing Range of eastern Australia, the northern wallaroo, *O. r. woodwardi* (Thomas, 1901) restricted to the Kimberley region of Western Australia and the Top End of the Northern Territory, and the euro, *O. r. erubescens* (Sclater, 1870) occurring across much of the inland areas of Australia (Clancy & Croft, 2008) (fig. 1). In addition, the extent to which wallaroos and euros share their helminth parasites with other sympatric macropodids was investigated.

Materials and methods

Nematodes were collected opportunistically between 1975 and 2018 from fresh road-killed animals, from wallaroos killed by commercial shooters or, in rare cases, wallaroos killed by aboriginal hunters (table 1). A small number of samples were also obtained from animals collected during other unrelated studies (Banks *et al.*, 2006). The oesophagus, stomach, bile
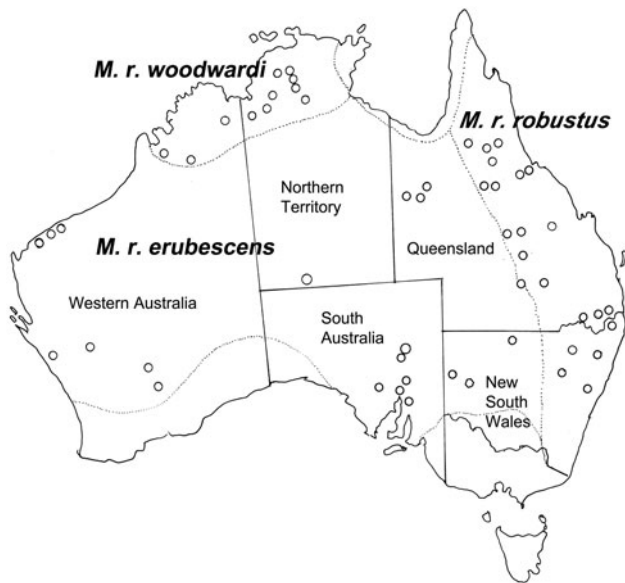
Fig. 1. Sites at which specimens of *Osphranter robustus* were collected for examination of their parasites, together with the presumed distribution of the subspecies of *O. robustus* based on van Dyck & Strahan (2008).

ducts and small and large intestines were examined for helminths. Examination varied depending upon facilities available at collection sites and not all organs were examined in all kangaroos collected either due to trauma in the case of road-killed specimens or inadequate examination of the pylorus and small intestine due to the lack of facilities available at the time of collection.

Various methods of collection were involved, including the preservation of entire gastrointestinal tracts in formalin or the collection of parasites from fresh individual organs and their preservation in either formalin, 70% ethanol or Berland's fluid (Gibson, 1979) for gastric nematodes. Cestodes were relaxed in water before being preserved in 10% formalin or 70% ethanol. As very large numbers of nematodes were invariably present in the stomach, a series of 50–200 nematodes selected at random from the stomach contents were examined. The number of gastric nematodes that needed to be examined in order to reveal all species was investigated by Vendl & Beveridge (2014) for other macropodid host species (50–200) and has been extrapolated to *O. robustus* without explicit validation. Only presence–absence data were recorded. None of the methods used were suitable for the identification of infections with *Strongyloides* sp. Nematodes were cleared in lactophenol for morphological identification, while cestodes were stained in Celestine blue, dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam.

Representative specimens of each species have been deposited in the South Australian Museum, Adelaide (table 2). In the case of parasite species complexes involving cryptic species (the nematodes *Hypodontus macropi* (see Chilton *et al.*, 2012) and *Macroponema comani* (see Tan *et al.*, 2012)) and the cestode *Progamotenia festiva* (see Beveridge & Shamsi, 2009), reference is made only to the genotype(s) present in *O. robustus*. The cestodes *Progamotaenia macropodis* and *Triplotaenia undosa* also constitute complexes with apparently host-specific genetic forms (Hu *et al.*, 2005; Hardman *et al.*, 2012) but have not been investigated morphologically. In the case of *Macropostrongyloides baylisi*, allozyme data suggest that the parasite present in *O. robustus* is genetically distinctive (Beveridge *et al.*, 1993).

Prevalence data are presented using the definition of Bush *et al.* (1997) as the number of infected hosts divided by the number of hosts examined. Diversity was assessed using the reciprocal of Simpson's Index for the species as a whole and for each host subspecies of *O. robustus* separately (Magurran, 1988). The similarity between helminth communities in each of the host subspecies of *O. robustus* was assessed using Sorenson's Index (Magurran, 1988). The bootstrap method of Poulin (1998) estimates the extent to which all parasite species of a given community had been recovered based on prevalence and sample size.

The prevalence data for each organ examined (stomach, small intestine, large intestine, etc.) are based on the number of organs examined rather than the total number of wallaroos collected. In the case of the strongylid genera *Filarinema* Mönnig, 1929 and *Alocostoma* Mawson, 1979 specific identification of females was not possible based on morphological features. For these genera, the occurrence of the species identifiable based on males only has been included. The data presented here include those of Beveridge *et al.* (1998) from northern and central Queensland.

Data on the host specificity of the parasites encountered were derived primarily from Spratt & Beveridge (2016), with additional information in Shuttleworth *et al.* (2016a, b) and Beveridge *et al.* (2018). Each parasite species was categorized as host-specific ('SP' in table 2) if it or a specific genotype of it (or two genotypes in the case of *H. macropi*) was known exclusively from *O. robustus*, or as a shared parasite ('SH' in table 2) if it occurred in additional hosts. In the latter instance, it was often possible to identify a primary host from published prevalence data (Beveridge *et al.*, 1989, 1992, 1998; Beveridge, 1998, 2002, 2016; Aussavy *et al.*, 2011; Spratt *et al.*, 2017), with the parasite occurring at a much higher prevalence in the shared host than in *O. robustus*. Where identifiable, the principal hosts have been indicated in bold in table 2. In some instances, parasites appeared to be generalists from their host ranges and prevalences, and in these instances no principal host is indicated. The rock wallaby genus *Petrogale* Gray, 1837 contains 17 species and they have been treated only at the generic level. Host genera or species which are not sympatric with *O. robustus* (e.g. *Dendrolagus* Müller, 1840, *Thylogale* (Gray, 1837), *Notamacropus eugenii* (Desmarest, 1817)) as well as records from captive animals only (e.g. *Lagorchestes hirsutus* Gould, 1844) were excluded.

The geographical distribution of the species occurring at a prevalence higher than 20% and those occurring primarily in *O. robustus* was plotted on a map. In instances where several wallaroos were examined at localities around a principal town (e.g. Charters Towers, Queensland; Karratha, Western Australia), the data have been combined. Parasite species were categorized as demonstrating either a relatively uniform distribution across the continent ('U' in table 2), those restricted to *O. r. woodwardi* (northern part of the Northern Territory and the Kimberley region of Western Australia; 'Orw' in table 2), those restricted to the northern regions of the continent (northern Western Australia, the Northern Territory, northern Queensland; 'N' in table 2), those restricted to the eastern margin of the country ('E' in table 2) and species with a highly localized distribution. Distribution maps have already been published for *Cloacina atthis*, *C. clymene*, *C. crassicaudata*, *H. macropi*, *Macroponema beveridgei*, *Mac.* cf. *comani* and *P. festiva* (Beveridge & Shamsi, 2009; Chilton *et al.*, 2012; Beveridge *et al.*, 2014, 2018).

Host nomenclature follows Jackson & Groves (2015). Authorities for parasite names are provided in table 2 and are not repeated in the text.

Table 1. Localities and numbers of *Osphranter robustus* examined for gastrointestinal parasites (arranged by state and increasing latitude).

Locality	Coordinates	No. examined
Queensland		**76**
Mount Surprise	18°09′S, 144°19′E	3
Georgetown	18°17′S, 143°33′E	1
Greenvale	18°58′S, 144°56′E	9
Bluewater Springs	19°25′S, 155°39′E	2
Mingela	19°52′S, 146°48′E	2
Charters Towers	20°05′S, 146°16′E	24
Cloncurry	20°42′S, 140°30′E	7
Mount Isa	20°44′S, 139°29′E	4
Hughenden	20°51′S, 144°12′E	2
Prairie	20°52′S, 144°36′E	3
Clermont	22°49′S, 147°38′E	1
Jericho	23°36′S, 146°07′E	3
Barcaldine	23°43′S, 145°08′E	3
Blackwater	23°45′S, 148°49′E	1
Blackall	24°26′S, 145°28′E	4
Augathella	25°48′S, 146°35′E	1
Charleville	26°24′S, 146°15′E	1
Morven	26°25′S, 147°07′E	1
Warwick	28°13′S, 152°02′E	2
Gore	28°17′S, 151°29′E	1
Goondiwindi	28°32′S, 150°18′E	1
Northern Territory		**19**
Mount Smith	13°32′S, 131°17′E	1
Pine Creek	13°49′S, 131°50′E	1
Edith River	14°11′S, 132°02′E	1
Katherine	14°28′S, 132°16′E	7
Mataranka	14°55′S, 133°08′E	1
Victoria River	15°27′S, 129°57′E	1
Timber Creek	15°53′S, 130°31′E	2
Mulga Park Station	25°54′S, 131°40′E	5
New South Wales		**29**
Rivertree	28°37′S, 152°15′E	2
Enngonia	29°19′S, 145°51′E	1
Armidale	30°31′S, 151°40′E	1
Wollomombi	30°31′S, 152°03′E	1
Kingstown	30°30′S, 151°01′E	8
Coonabarabran	31°16′S, 149°17′E	4
Quirindi	31°30′S, 150°41′E	6
Broken Hill	31°58′S, 141°27′E	4
Menindee	32°24′S, 142°25′E	2
Western Australia		**24**

(Continued)

Table 1. (Continued.)

Locality	Coordinates	No. examined
Kununurra	15°47′S, 128°44′E	2
Napier Downs via Derby	17°20′S, 124°48′E	1
Fitzroy Crossing	18°11′S, 125°34′E	1
Roebourne	20°47′S, 117°09′E	2
Karratha	20°53′S, 116°40′E	8
Yalgoo	28°21′S, 116°41′E	3
Northampton	28°21′S, 114°38′E	1
Menzies	29°42′S, 121°02′E	5
Kalgoorlie	30°43′S, 121°28′E	1
South Australia		**22**
Mount Lyndhurst	30°11′S, 138°43′E	1
Leigh Creek	30°32′S, 138°28′E	3
Nonning Station	31°25′S, 136°30′E	3
Hookina	31°48′S, 138°16′E	1
Hawker	31°53′S, 138°25′E	2
Port Augusta	32°30′S, 137°46′E	10
Horrock's Pass	32°38′S, 138°02′E	1
Melrose	32°50′S, 138°11′E	1
Total		**170**

Results

The current study examined the gastrointestinal parasites of 170 *O. robustus* from all mainland states in which the species occurs (apart from Victoria) as well as from the Northern Territory (fig. 1 and table 1) consisting of 87 *O. r. robustus*, 18 *O. r. woodwardi* and 65 *O. r. erubescens*. The sample included 85 males and 30 females; the sex of the remaining animals (usually collected by commercial shooters) was not available. There was a significant bias in the sex ratio towards males among animals for which the sex had been determined ($\chi^2 = 12.6$, $P < 0.005$). All animals examined were adults, although it was not possible to determine ages. Of the various organs examined, stomach nematodes were examined from all 170 animals, the pylorus was examined for *Filarinema* spp. in 152 animals, the small intestine in 116, the large intestine in 150 and the bile ducts in 137.

In total, 65 species of gastrointestinal parasites were encountered, including 61 species of strongylid nematodes, two occurring in the large intestine (Phascolostrongylinae: *Hypodontus* Mönnig, 1929; *Macropostrongyloides* Yamaguti, 1961), 55 in the tubular fore-stomach (Cloacininae) and four (Dromaeostrongylidae: *Filarinema*) in the pyloric antrum, together with four species of anoplocephalid cestodes, one occurring in the bile ducts (*Progamotaenia* Nybelin) and three in the small intestine (*Progamotaenia*, *Triplotaenia* Boas, *Wallabicestus* Schmidt, 1986) (table 2). Allocation of individual hosts to subspecies was based on their geographical distribution (van Dyck & Strahan, 2008) as well as on allozyme and DNA sequence data relating to distribution (Richardson & Sharman, 1976; Eldridge *et al.*, 2014; Richardson, 2019). Among the mainland subspecies of *O. robustus*, 52 helminth

Table 2. Gastrointestinal helminth parasites of *Osphranter robustus*.

Parasite	Site in host	Prevalence (%) (Orr, Orw, Ore)[a]	Specificity (bold indicates principal host(s))	Distribution	SAM reg. no.
Cestodes					
Cyclophyllidea: Anoplocephalidae					
Progamotaenia festiva (Rudolphi, 1817)	Bd	37.2 (31.6, 12.5, 47.8)	SP[b]	U	8167, 8127, 23306, 2944
Progamotaenia macropodis Beveridge, 1976	Si	5.2 (4.9, 9.1, 15.6)	SP[b]	U	28614–28615
Triplotaenia undosa Beveridge, 1976	Si	2.5 (3.3, 0, 1.5)	SP[b]	(Orr, Ore) N	29263
Wallabicestus sp. (undescribed) (Beveridge, 2009)	Si	3.4 (6.6, 0, 0)	SP	E	19751, 20738
Nematodes					
Strongyloidea: Phascolostrongylinae					
Hypodontus macropi Mönnig, 1929	Li	50.7 (69.5, 6.7, 32.7)	SP[b]	U	7899, 8015 33517, 33510
Macropostrongyloides baylisi (Wood, 1931)	Li	41.3 (35.4, 33.3, 50.9)	SP[b]	U	8604, 7899, 33511, 33518
Strongyloidea: Cloacininae					
Zoniolaiminea					
Wallabinema cobbi (Kung, 1958)	St	0.6 (1.1, 0, 0)	SH (**Or**, Mf, Nr)	–	13642
Zoniolaimus latebrosus Huby-Chilton, Beveridge, Gasser & Chilton, 2002	St	0.6 (1.1, 0, 0)	SH (**Or**, Mf, Mg)	–	33964
Zoniolaimus mawsonae Beveridge, 1983	St	1.2 (3.3, 0, 0)	SH (**Or**, Onu)	–	13643, 23187
Labiostrongylinea					
Labiosimplex aridus Smales, 1995	St	1.2 (3.3, 0, 0)	SH (**Or**)	–	32239–32240
Labiosimplex camporum Smales, 2011	St	0.6 (0, 0, 1.5)	SH (**Or**)	–	45798–45799
Labiosimplex longispicularis (Wood, 1929)	St	11.9 (12.6, 0, 12.3)	SH (**Or**, Nr)	–	8626, 9184
Labiosimplex robustus Smales, 1995	St	6.5 (11.5, 0, 1.5)	SP	E	45798–45799
Labiostrongylus grandis Johnston & Mawson, 1938	St	6.5 (8.0, 0, 6.2)	SP	(Orr, Ore) N	11639
Pharyngostrongylinea					
Pharyngostrongylus lambda Mawson, 1965	St	11.9 (17.2, 0, 4.6)	SH (**Or, Mg**, P)	–	31706, 32392
Pharyngostrongylus macropodis Yorke & Maplestone, 1926	St	1.2 (3.3, 0, 0)	SH (**Oa, Na**, Np, Nr, P)	–	13497
Pharyngostrongylus papillatus Beveridge, 1982	St	6.5 (1.1, 55.6, 0)	SH (**Oa**)	Orw	48145
Pharyngostrongylus patriciae Sukee, Jabbar & Beveridge, 2018	St	14.3 (16.0, 61.6, 0)	SH (**Oa, Ob**)	N	48127, 48139
Pharyngostrongylus sharmani Beveridge, 1982	St	2.9 (0, 27.8, 0)	SH (**Ob**)	Orw	32724, 45982
Rugopharynx australis (Mönnig, 1926)	St	15.5 (6.6, 0, 32.3)	SH (Ob, **Or, Mg, Mf**, P, Na, Nd)	–	8020, 8607, 10993, 31927
Woodwardostrongylus obendorfi Mawson, 1976	St	0.6 (1.1, 0, 0)	SH (Na, Np, Nr, W, **P**)	–	6034
Cloacininea					
Cloacina atthis Beveridge, 2014	St	4.8 (0, 0, 12.3)	SP	Ore	35945
Cloacina clymene Beveridge, 1989	St	14.9 (27.6, 0, 1.5)	SP	E	25325, 25322
Cloacina communis Johnston & Mawson, 1938	St	58.3 (56.3, 33.3, 64.6)	SH (**Oa**, Na, Np, Lc, P, W)	U	25307, 31707 32520, 3238
Cloacina crassicaudata Beveridge, 2018	St	11.9 (9.2, 66.7, 0)	SH (**Oa**)	N	25081
Cloacina curta Johnston & Mawson, 1938	St	7.7 (0, 16.7, 15.4)	SH (P)	U	8619, 25309

(*Continued*)

Table 2. (*Continued.*)

Parasite	Site in host	Prevalence (%) (Orr, Orw, Ore)[a]	Specificity (bold indicates principal host(s))	Distribution	SAM reg. no.
Cloacina daveyi Johnston & Mawson, 1938	St	9.5 (0, 0, 24.6)	SH (P)	Ore	7894, 25353
Cloacina dindymene Beveridge, 1989	St	11.3 (11.5, 33.3, 3.1)	SH (**Oa**)	N	25099, 25073
Cloacina dirce Beveridge, 1989	St	10.1 (8.0, 55.6, 0)	SH (**Oa**)	N	25079, 25368
Cloacina dis Beveridge, 1989	St	4.8 (8.0, 0, 0)	SP	Orr	26739–26742
Cloacina echidne Beveridge, 1989	St	43.6 (43.7, 5.6, 53.8)	SH (**Oa**, Lc, P, W)	U	32389, 32512
Cloacina eileithyia Beveridge, 1989	St	5.4 (1.1, 44.4, 0)	SH (**Oa**)	N	27418–27420
Cloacina epona Beveridge, 1989	St	6.0 (0, 0, 15.4)	SP	Ore	26743–26748
Cloacina feronia Beveridge, 1989	St	27.4 (18.4, 0, 44.6)	SH (Mg, Nd, P)	Ore, Orr	8199, 27349
Cloacina frequens Johnston & Mawson, 1938	St	26.8 (20.7, 16.7, 30.8)	SH (**Oa**, P)	U	25240, 32523
Cloacina herceus Beveridge, 1989	St	19.6 (34.5, 0, 4.6)	SH (**Mg**, Mf, Na, Np, Nr)	–	25256, 32525
Cloacina hydriformis Johnston & Mawson, 1938	St	6.5 (6.9, 0, 9.2)	SH (**Or**, Mg, Mf, P, W)	–	8197, 10989
Cloacina ixion Beveridge, 1989	St	24.4 (20.7, 50.0, 21.5)	SH (**Oa**, Np)	N	25335, 32390
Cloacina johnstoni Shuttleworth, Jabbar & Beveridge, 2016	St	10.7 (1.1, 0, 26.1)	SP	U	27260
Cloacina longelabiata Johnston & Mawson, 1938	St	9.5 (0, 0, 24.6)	SH (P)	Ore	25070, 25835
Cloacina longibursata Beveridge, 2018	St	1.8 (0, 16.7, 0)	SH (**Oa**)	Orw	48101–48103
Cloacina macropodis Johnston & Mawson, 1938	St	76.2 (87.4, 22.2, 67.7)	SH (Or, Mf, Np, P)	U	10990, 25266
Cloacina magnipapillata Johnston & Mawson, 1939	St	1.2 (2.3, 0, 1.5)	SH (**Mg, Mf**, Or, Oa)	–	31608, 32571
Cloacina nike Beveridge, 1989	St	0.6 (1.1, 0, 0)	SH (**Lc**, Oa, Np, Onu)	–	–[c]
Cloacina parva Johnston & Mawson, 1938	St	56.5 (47.1, 61.1, 66.2)	SH (**Oa**, P, W)	U	32524, 32395
Cloacina phaethon Beveridge, 1989	St	59.5 (78.2, 11.1, 36.9)	SH (Oa, P)	U	32522, 32388
Cloacina polyxena Beveridge, 1989	St	4.2 (0, 38.9, 0)	SH (**Oa**)	Orw	25075
Cloacina spearei Beveridge, 2018	St	3.0 (0, 27.8, 0)	SH (**Oa**)	Orw	13840, 23831
Cloacina typhon Beveridge, 1989	St	23.2 (43.7, 11.1, 0)	SH (Oa, **Mg**, Lc, Na, Nd, Np)	E	32383, 33839
Cloacina tyro Beveridge, 1989	St	1.2 (0, 16.7, 0)	SP	Orw	27645–27646
Macropostrongylinea					
Alocostoma clelandi Johnston & Mawson, 1939	St	16.1 (28.7, 5.6, 1.5)	SH (**Mf, Mg**, P)	–	7285
Alocostoma propinquum Beveridge, 1986	St	2.4 (2.3, 11.1, 0)	SH (**Oa, Mg**)	–	25440, 33841
Macroponema beveridgei Mawson, 1978	St	28.6 (31.0, 61.1, 15.4)	SH (**Oa**, Na, W)	N	11654–11659, 31708
Macroponema cf. *comani* Mawson, 1978	St	3.0 (0, 27.8, 0)	SP[b]	Orw	32700, 44338–44339
Macropostrongylus macropostrongylus Yorke & Maplestone, 1926	St	0.6 (0, 5.6, 0)	SH (**Na**, Np, P, W)	–	45975
Macropostrongylus spearei Beveridge, 1986	St	14.9 (28.7, 0, 0)	SP	E	7648, 32746

(*Continued*)

Table 2. (Continued.)

Parasite	Site in host	Prevalence (%) (Orr, Orw, Ore)[a]	Specificity (bold indicates principal host(s))	Distribution	SAM reg. no.
Coronostrongylinea					
Coronostrongylus barkeri Beveridge, 2002	St	0.6 (1.1, 0, 0)	SH (**Or**, Onu, P)	–	13645
Papillostrongylus barbatus Chilton, Huby-Chilton, Gasser & Beveridge, 2002	St	4.2 (1.1, 0, 9.2)	SH (**Mf, Mg**, P)	–	10992
Papillostrongylus labiatus Johnston & Mawson, 1939[d]	St	0.6 (1.1, 0, 0)	SH (Ob, Or, **Nd**, Np, Nr, P)	–	48693
Popovastrongylus macropodis Beveridge, 1986	St	3.6 (5.7, 0, 0)	SH (**Or**, Mg, Na, Np)	–	31614
Popovastrongylus pluteus Smales, 2000	St	1.2 (2.3, 0, 0)	SP	E	14546
Trichostrongyloidea: Dromaeostrongylidae					
Filarinema australe (Wood, 1931)	Pa	11.2 (9.5, 11.1, 11.3)	SH (**Or**, Nd, Np, Lc, Onu, P)	–	12033–12035, 43687
Filarinema dissimile (Wood, 1931)	Pa	9.2 (12.2, 0, 9.7)	SH (Or, Mf, Lc, P)	–	16281
Filarinema haycocki Cassone & Baccam, 1985	Pa	2.6 (5.4, 0, 0)	SH (**Mf**)	–	43555
Filarinema mawsonae Cassone & Baccam, 1985	Pa	0.7 (1.4, 0, 0)	SH (Na, **Np**, P, W)	–	10387–10388

St, stomach; Si, small intestine; Li, large intestine; Bd, bile ducts; Pa, pyloric antrum; SP, host-specific; SH, shared; U, widely distributed; N, northern; Orw, in *O. r. woodwardi*; Ore, in *O. r. erubescens*; Orr, in *O. r. robustus*; E, eastern; SAM, South Australian Museum.

Host abbreviations: Lc, *Lagorchestes conspicillatus* Gould; Mf, *Macropus fuliginosus* (Desmarest); Mg, *M. giganteus* Shaw; Na, *Notamacropus agilis* (Gould); Np, *N. parryi* (Bennett); Nr, *N. rufogriseus* (Desmarest); Onu, *Onychogalea unguifera* (Gould); Oa, *Osphranter antilopinus* (Gould); Ob, *O. Bernardus* (Rothschild); Or, *O. rufus* (Desmarest); P, *Petrogale* spp.; W, *Wallabia bicolor* (Desmarest).

[a]Prevalences in *O. r. robustus*, *O. r. woodwardi*, *O. r. erubescens*.
[b]Indicates genotype specific to *O. robustus*.
[c]Cited in Beveridge *et al.* (1989); no voucher located.
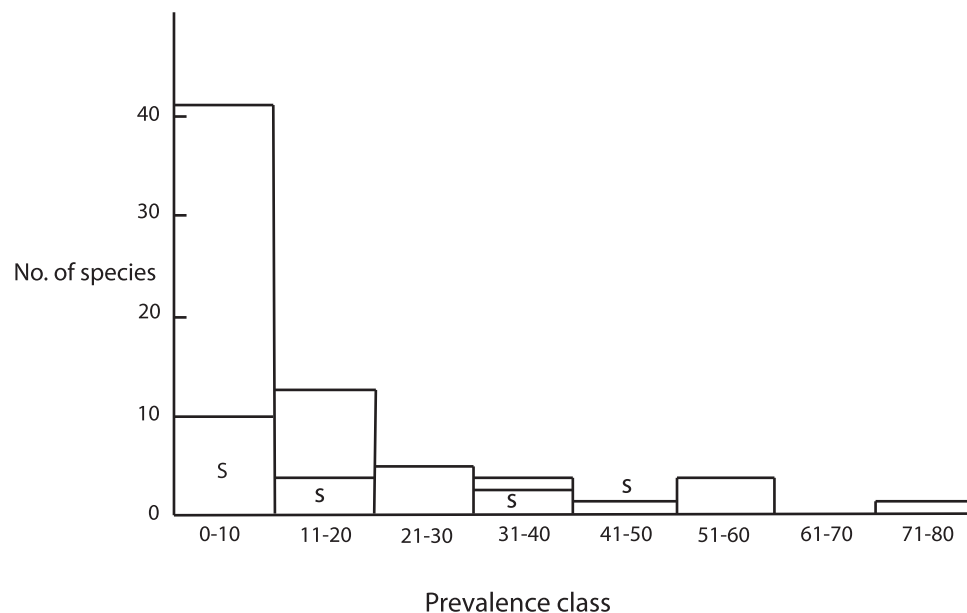[d]Indicates new host record.

Fig. 2. Numbers of species of parasites of *Osphranter robustus* in each 10% prevalence class. 'S' indicates the number of host-specific species.

species were found in *O. r. robustus*, 30 species in *O. r. woodwardi* and 35 species in *O. r. erubescens*.

Using the bootstrap method of Poulin (1998), it was estimated that an additional 4.6 species are likely to be found in *O. robustus* with more extensive sampling. The measure of diversity used, the reciprocal of Simpson's Index, was 24.6 for the host species, 20.7 for *O. r. robustus*, 19.9 for *O. r. woodwardi* and 19.3 for *O. r. erubescens*. Using Sorenson's Index to assess the similarity of the helminth communities in each of the subspecies, the similarity between the community in *O. r. robustus* and *O. r. woodwardi* was 53.7%, between *O. r. woodwardi* and *O. r. erubescens* 55.4%, and between *O. r. robustus* and *O. r. erubescens* 66.7%.

The frequency distribution of prevalences (fig. 2) showed an almost exponential decline from a large number of parasite

Fig. 3. Geographical distribution of *Cloacina parva* in *Osphranter robustus*, representing species with a broad distribution across the continent in all three subspecies of *O. robustus*.

species occurring at a low prevalence to a small number occurring at a high prevalence.

Of the 65 species of parasites present, 17 were specific to *O. robustus*. Others were shared with sympatric macropodid host species: the antilopine wallaroo, *Osphranter antilopinus* (21 species), the black wallaroo, *O. bernardus* (four species), the red kangaroo, *O. rufus* (16 species), the eastern grey kangaroo, *Macropus giganteus* (11 species), the western grey kangaroo, *M. fuliginosus* (11 species), the agile wallaby, *Notamacropus agilis* (ten species), the whiptail wallaby, *N. parryi* (13 species), the black-stripe wallaby, *N. dorsalis* (five species), the red-necked wallaby, *N. rufogriseus* (six species), rock wallabies, *Petrogale* spp. (28 species), the spectacled hare wallaby, *Lagorchestes conspicillatus* (six species), the northern nail-tail wallaby, *Onychogalea unguifera* (four species) and the swamp wallaby, *Wallabia bicolor* (eight species).

In instances where shared parasites occurred at a high prevalence in an alternative host (indicated in bold in table 2), the shared parasites consisted of the following number of species: *O. antilopinus* (17 species), *O. bernardus* (two species), *O. rufus* (12 species), *M. fuliginosus* (four species), *M. giganteus* (eight species), *N. agilis* (two species), *N. dorsalis* (one species), *N. parryi* (one species), *L. conspicillatus* (one species) and *Petrogale* spp. (one species).

Examining the geographical distributions of parasite species occurring at a high prevalence or those that were considered to be primarily parasites of *O. robustus*, several patterns were evident. A series of species occurred across the continent in all three subspecies of *O. robustus*: *Cloacina communis, C. curta, C. echidne, C. frequens, C. johnstoni, C. macropodis, C. parva, C. phaethon, M. baylisi, H. macropi, P. festiva* and *P. macropodis*. The distribution of *C. parva* is shown as an example in fig. 3. A second series was present again in all three subspecies, but in this case restricted to northern Australia; these included: *Cloacina crassicaudata,*

C. dindymene, C. dirce, C. eileithyia, C. ixion, Mac. beveridgei and *Pharyngostrongylus patriciae*. The distribution of *C. dindymene* is shown as an example in fig. 4. A third series of species were restricted to *O. r. woodwardi*: *Cloacina longibursata, C. polyxena, C. spearei, C. tyro, Mac.* cf. *comani, Pharyngostrongylus papillatus* and *P. sharmani*. The distributions of *C. polyxena* and *C. tyro* are shown as examples in fig. 5. Species with a distribution essentially occurring along the Great Dividing Range of eastern Australia and, therefore, primarily parasitic in *O. r. robustus* were: *Cloacina clymene, C. typhon, Labiosimplex robustus, Macropostrongylus spearei* and *Wallabicestus* sp. The distributions of *C. clymene* and *Ma. spearei* are shown as examples in fig. 6. Several species were found only in *O. r. erubescens*, these being *Cloacina daveyi, C. epona* and *C. longelabiata* (fig. 7). Species with apparently localized distributions were: *C. atthis*, restricted to the Pilbara region of Western Australia; *Cloacina dis*, restricted to the Charters Towers region of north Queensland; and *Popovastrongylus pluteus*, restricted to *O. r. robustus* in north-eastern New South Wales (fig. 8). Several species did not fit precisely into any of these categories. *Cloacina feronia* was not found in *M. r. woodwardi* but was present in the remaining subspecies, while *Mac. beveridgei* was absent from Western Australian wallaroos. *Cloacina eileithyia* was prevalent in *O. r. woodwardi* in the Northern Territory but was found in a single wallaroo from the Charters Towers region of north Queensland (table 2). *Triplotaenia undosa* and *Labiostrongylus grandis*, while occurring in both *O. r. robustus* and *O. r. erubescens*, were found only in northern Australia.

Discussion

This is the first study of the gastrointestinal helminth parasites of *O. robustus* across its entire geographical range, the only previous

Fig. 4. Geographical distribution of *Cloacina dindymene* in *Osphranter robustus*, representing species occurring in all three subspecies of *O. robustus*, but restricted to northern Australia.

Fig. 5. Geographical distributions of *Cloacina tyro* (circles) *and C. polyxena* (squares) in *Osphranter robustus*, representing species restricted to *O. r. woodwardi*.

Fig. 6. Geographical distributions of *Cloacina clymene* (circles) and *Macropostrongylus spearei* (triangles) in *Osphranter robustus*, representing parasite species restricted to the east coast of the continent and, therefore, primarily parasitic in *O. r. robustus*.

study being an examination of 30 wallaroos from central and northern Queensland (Beveridge *et al.*, 1998). Consequently, the present study greatly expands the numbers and ranges of parasites encountered, encompassing for the first time the three mainland subspecies of the common wallaroo. Although the collecting of specimens was entirely opportunistic and collections were significantly biased towards northern Queensland, as well as containing an obvious sex bias, they provide novel data on the structure of the helminth community of *O. robustus* as well as a basis for future, more detailed studies.

Three mainland subspecies of the common wallaroo are recognized (Jackson & Groves, 2015) and, in this study, specimens from the northern region of the Northern Territory and the Kimberley region of Western Australia were readily referable to the northern wallaroo, *O. r. woodwardi*, based on their distribution (Clancy & Croft, 2008). Likewise, wallaroos from the remaining regions of Western Australia, from central Australia, South Australia, western New South Wales and western Queensland were readily attributable to the euro, *O. r. erubescens*, again based on geographical distribution (Clancy & Croft, 2008). Wallaroos from south-eastern Queensland and north-eastern New South Wales were attributable to *O. r. robustus* based on both distribution and coat colour (Clancy & Croft, 2008), while animals from the Dividing Range in northern Queensland could potentially have been either *O. r. robustus* or *O. r. erubescens*, as the precise boundary between the two subspecies in this area has not been delineated (Clancy & Croft, 2008). These two subspecies are differentiable based on biochemical grounds (Richardson & Sharman, 1976; Richardson, 2019) and there are limited DNA sequence data for distinguishing between them (Eldridge *et al.*, 2014). Based on the distribution of wallaroos shown in Fig. 1 of

Eldridge *et al.* (2014) and identified using DNA sequence data, as well as data in Richardson (2019) based on allozyme data, it is highly likely that all of the Queensland specimens collected from the Great Dividing Range in this study belong to *O. r. robustus* (fig. 1).

There are several potential biases inherent in this study. First of all, the collecting of specimens was opportunistic rather than structured. There is a clear bias towards male hosts, and the possible effects of host sex on parasites likely to be present in this species are not known. Second, the identification of nematodes from the stomach based on the examination of a relatively small sample of the (potentially) thousands present is likely to overlook the presence of species occurring at low intensities or abundances (Vendl & Beveridge, 2014) and, therefore, the data presented are likely to favour the more abundant species and to potentially overlook rarer species. Thirdly, a survey of this type took no account of seasonal variation in parasite burdens. Previous studies have shown a highly seasonal pattern of parasite infection in *M. giganteus* in the winter rainfall areas of southern Australia (Arundel *et al.*, 1990), while similar studies of the parasites of *O. rufus* in the arid zone of Australia with non-seasonal rainfall found limited seasonal variation in parasite prevalence and abundance (Arundel *et al.*, 1979). One exception in the latter study was *Labiosimplex longispicularis*, which has a highly seasonal annual life cycle (Mykytowycz & Dudzinski, 1965). Comparable data are lacking for congeners occurring in *O. robustus*, and, therefore, some caution is needed in interpreting the current results in the face of a complete lack of seasonal data and the fact that *O. robustus* occurs in arid, non-seasonal areas of rainfall as well as summer-dominant rainfall areas (northern Australia) and temperate non-seasonal rainfall areas (south-eastern Australia).

Fig. 7. Geographical distributions of *Cloacina daveyi* (circles) and *C. epona* (squares) in *Osphranter robustus*, representing species restricted to *O. r. erubescens*.

In the current study, a total of 65 species of gastrointestinal parasites were encountered, compared with the 40 reported by Beveridge *et al.* (1998) from Queensland. This difference is not surprising given the expanded geographical region included in the present study. More helminth species (52) were found in *O. r. robustus*, compared with *O. r. woodwardi* (30) and *O. r. erubescens* (35), but this may reflect sampling intensity rather than true differences between the subspecies. The difference in numbers of helminth species encountered was mirrored in the reciprocal of Simpson's Index for each of the host subspecies. The reciprocal of Simpson's Index of diversity for the entire species (*O. robustus*) (24.6) was similar to that (23.0) reported from Queensland by Beveridge *et al.* (1998). The slight difference may be due to the addition of a significant number of parasite species (25) occurring at low prevalences as Simpson's Index is biased towards prevalent species (Magurran, 1988).

The bootstrap method of Poulin (1998) used to estimate the number of species yet to be described from *O. robustus* suggested that an additional 4.6 species might be found, indicating that the majority of helminth species likely to occur in this host have already been encountered. Based on the data presented here, these additional and as yet unknown species are likely to be host-specific species with an extremely limited geographical range or unusual colonizations from sympatric macropodid hosts.

Sorenson's Index of similarity suggested that the helminth community of *O. r. woodwardi* differed from communities in the remaining host subspecies, a finding considered in more detail below but probably due to a number of helminth species occurring exclusively in this host subspecies.

Of the helminth species encountered, only 17 were specific to *O. robustus*, whilst the remainder of the parasites were shared with sympatric host species. Being able to differentiate shared parasites

on the basis of their prevalences compared with those in *O. robustus* sheds some additional light on the direction of host sharing. For example, in the case of *Petrogale* spp., 23 parasite species were potentially shared with *O. robustus*, yet in all cases except one (*W. obendorfi*) the parasites occurred at very low prevalences in rock wallabies (Beveridge *et al.*, 1989) compared with prevalences in *O. robustus*, suggesting the occasional transfer of most species from *O. robustus* to *Petrogale* spp. By contrast, in species of *Notamacropus*, prevalences of shared parasites were generally much higher than those in *O. robustus* (Beveridge *et al.*, 1998), suggesting, by contrast, the occasional transfer of parasites to *O. robustus* from *Notamacropus* spp. In some instances, high prevalences of the shared parasite also occurred in the shared host, with 21 species of nematodes in *O. antilopinus*, 12 in *O. rufus*, four in *M. fuliginosus* and eight in *M. giganteus*. Smaller numbers of parasite species were shared with sympatric members of the genera *Lagorchestes* and *Onychogalea*. The known life cycles of all of the nematode parasites are terrestrial, with eggs being deposited in faeces, larval development occurring in the external environment and third-stage larvae being ingested by the host while grazing (Smales, 1977a, b; Beveridge & Presidente, 1978; Beveridge, 1979). In the case of the anoplocephalid cestodes, there is a requirement for an intermediate host (most probably an oribatid mite) (Beveridge, 1994), but, again, these are ingested incidentally during grazing. Consequently, there are substantial opportunities for the transfer of parasites between co-grazing macropodid hosts. The extent to which macropodid grazing preferences may influence this transmission has been examined for four sympatric macropodid species in Victoria (Aussavy *et al.*, 2011) and three species in southern New South Wales (Spratt *et al.*, 2017). Thus, in the present study, in the lowest prevalence class (0–10%), fewer than 30% of the parasite species found in

Fig. 8. Geographical distributions of *Cloacina atthis* (triangles), *C. dis* (squares) and *Popovastrongylus pluteus* (circle) in *Osphranter robustus*, representing parasite species with highly localized geographical distributions.

O. robustus were host-specific, while in the higher prevalence classes (>40%), only one of five (20%) of the parasites were host-specific (fig. 2).

The high number of parasite species shared with *O. antilopinus* was not unexpected as these two hosts occur in sympatry across much of northern Australia (Eldridge *et al.*, 2014) and are also closely related phylogenetically (Meredith *et al.*, 2008). Beveridge *et al.* (1998) estimated that the two species shared more than 50% of their parasites in north Queensland. In other areas of Australia, wallaroos occur frequently in sympatry with *O. rufus*, *M. giganteus* and *M. fuliginosus* (van Dyck & Strahan, 2008) and, therefore, it is unsurprising that they share their parasites in these regions, in particular with the congeneric species *O. rufus*. *Osphranter robustus* also shares habitat with various species of *Notamacropus*, *Lagorchestes* and *Petrogale* (van Dyck & Strahan, 2008), thereby explaining the sharing of parasites with these host genera.

The data on numbers of species in each 10% prevalence class mirror that presented by Beveridge *et al.* (1998) for *O. r. robustus*, although based on a much larger sample size. Similar patterns have been reported for additional species of macropodids from north Queensland (Beveridge *et al.*, 1998) and the pattern appears to be a characteristic of the helminth communities of these marsupials with greatest number of species occurring in the low prevalence classes and fewer species in the high prevalence classes.

Recent molecular studies of various cloacinine genera of nematodes occurring in macropodids have suggested that the diversity found among the nematodes may be the result of host colonization (and possibly a limited degree of within-host speciation) rather than coevolution (Chilton *et al.*, 2011, 2016a, b, 2017). The current data support this hypothesis to the extent that

many of the parasites of *O. robustus* are shared with sympatric host species, a prerequisite for the colonization of a new host species and subsequent speciation. However, the details of this mechanism remain to be investigated.

Based on the currently available data, there are several patterns of geographical distribution of the parasites identified herein. A number of species (e.g. *C. parva*, *C. phaethon*, *C. macropodis*) (fig. 3) have a transcontinental distribution occurring in all three host subspecies, and while molecular studies of these nematode species indicate significant levels of genetic differentiation within each species, there is no clear geographical separation of the identified genotypes and, consequently, no obvious association with separate subspecies of *O. robustus* (Shuttleworth *et al.*, 2016b). A number of parasite species are restricted to *O. r. woodwardi*, although they may also occur in the sympatric host *O. antilopinus*, while another series of parasites is restricted to northern Australia, including northern Queensland, thereby being found in *O. r. robustus*, *O. r. erubescens* and *O. r. woodwardi*, again, with some also occurring in *O. antilopinus*. The Carpentaria Gap, a zone of floral and faunal disjunction south of the Gulf of Carpentaria has been invoked to explain the disjunct distribution of plant and animal species between northern Queensland and the Northern Territory, including genetically distinct populations of *O. antilopinus* (Wadley *et al.*, 2016), and while this may facilitate an explanation of the parasite species restricted to *O. r. woodwardi*, it provides no explanation for the species found across northern Australia including Queensland other than a distribution restricted to the monsoonal tropical region of northern Australia. Additional caution is needed in assessing such current distributions of nematode parasites, as *C. eileithyia* is found commonly in *O. r. woodwardi* in the

Northern Territory (Beveridge, 1998), but was found in a single individual of *O. r. robustus* in northern Queensland, suggesting that more intensive sampling may be needed before definitive conclusions can be drawn about nematode distributions.

Apart from helminth species with a broad distribution and those with highly restricted distributions such as *C. dis*, *C. atthis* and *P. pluteus*, groups of species were also identifiable restricted to each of the three subspecies of *O. robustus*. While a significant series of species was identified, which were restricted to *O. r. woodwardi*, a smaller number were restricted to *O. r. erubescens*, with several species occurring primarily within the range of *O. r. robustus* along the east coast of the continent, although the division between subspecies in this region is not clear, as indicated above. Taken together, the data suggest that the process of subspeciation occurring in the wallaroos may have influenced the diversification of their parasites in particular groups of species, as well as the possibility of climatic factors limiting the distribution of other species to the monsoonal tropical regions of northern Australia, irrespective of host subspecies. The observations presented here support the genetic analysis of *H. macropi* by Chilton *et al.* (2012) in which each genotype of the parasite was associated with a particular subspecies of *O. robustus*. However, a more detailed genetic analysis of the host, *O. robustus*, is needed before such hypotheses can be explored further.

In spite of obvious deficiencies in knowledge of the parasites, their distributions and their genetic characteristics, and equally obvious deficiencies in knowledge of the phylogeography of the host *O. robustus*, as well as its close congener *O. antilopinus*, it appears that a more detailed study of this host–parasite system could be useful in understanding the evolution of the complex parasite communities in *O. robustus* and its closely related congeners.

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