Gastrointestinal helminths from the common warthog, *Phacochoerus africanus* (Gmelin) (Suidae), in KwaZulu-Natal Province, South Africa, with comments on helminths of Suidae and Tayassuidae worldwide

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Running title:

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Key Findings:

- Warthogs harboured nine species of gastrointestinal helminths
- Host age had a significant effect on abundance of *Murshidia* spp.
- Host sex had a significant effect on abundance of *Trichostrongylus thomasi*
- Helminth communities of three genera of wild suids in Africa differ from each other
- Limited overlap between helminth faunae of Suidae and Tayassuidae worldwide

Abstract

Thirty warthogs, *Phacochoerus africanus*, were collected in the Pongola Game Reserve, South Africa and examined for helminths. Gastrointestinal helminth assemblages comprised *Gastrodiscus aegyptiacus*, the cestode genus *Moniezia* and seven species of nematodes. A single warthog harboured a metacestode of *Taenia hydatigena* in the mesenteries. No helminths were found in the heart, lungs or liver of the warthogs. *Probstmayria vivipara* and *Murshidia* spp. were the most prevalent as well as abundant helminth species, followed by *Physocephalus sexalatus*. The incidence of *Moniezia* did not differ between hosts of different sex or age. Numbers of *Murshidia* spp. were not affected by host sex, but were higher in adults than in juveniles. Conversely, burdens of *Trichostrongylus thomasi* were not affected by host age, but were higher in males than in females. While not highly significant, helminth assemblages in male warthogs were more species rich than in females. Helminth communities in the three genera of wild sub-Saharan suids are largely unique, but *Ph. africanus* and *Hylochoerus meinertzhageni* share more worm species with each other than with *Potamochorus larvatus*, possibly because the former two are more closely related. Overlap between helminth communities of African wild suids and those of other suids and Tayassuidae worldwide is limited.

Key words:

helminth communities; host range; geographic distribution; warthogs; Suidae; Tayassuidae

Introduction

The Suidae is a family within the Cetartiodactyla and comprises 17 species belonging to six genera. Originating in the Old World approximately 20 million years ago, they have successfully colonised the African and Eurasian continents (Frantz *et al.*, 2016). Their counterparts in the New World are the pig-like peccaries, Tayassuidae, who diverged from the common ancestry during the late Eocene/early Oligocene (Frantz *et al.*, 2016).

On the African continent, three genera of the Suidae are indigenous and listed on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species as of the least concern: *Phacochoerus* F. Cuvier, containing *Ph. africanus* (Gmelin) and *Ph. aethiopicus* (Pallas) (de Jong *et al*., 2016a, b), *Potamochoerus* Gray, comprising *Po. larvatus* (F. Cuvier) (Seydack, 2016) and *Po. porcus* (Linnaeus) (Reyna *et al*., 2016), and *Hylochoerus* Thomas, represented by *H. meinertzhageni* Thomas (d'Huart and Reyna, 2016). Of these, only the geographic range of *Ph. africanus* and *Po. larvatus* extends into South Africa (Skinner and Chimimba, 2005; Seydack, 2016). For most of the 20th century, *Ph. africanus* was commonly considered a subspecies of *Ph. aethiopicus* and is usually recorded as such in studies pertaining to its ecology, habits and/or parasites. Nowadays, the validity of the two species of warthogs is again recognised. In South Africa, *Ph. a. aethiopicus* became extinct in the 1870s, and since then only *Ph. africanus* remains (Skinner and Chimimba, 2005; Wilson and Reeder, 2005; Grubb and d'Huart, 2010; de Jong *et al*., 2016a, b). However, the two species are sympatric in parts of north Somalia, as well as in parts of central, east, and southeast Kenya (de Jong *et al*., 2016a, b).

Of all the Suidae, *Sus* Linnaeus is the genus with an almost cosmopolitan distribution. This is not surprising, since the native range of *S. scrofa* Linnaeus covers vast areas of Eurasia and some North African countries, while humans have introduced the species in countries worldwide, including the Americas, Australia and Africa (Oliver and Leus, 2008; Frantz *et al*., 2016). The remaining species of the genus *Sus* inhabit various parts of Asia, all being listed on the IUCN Red List of Threatened Species as near threatened to critically endangered (Frantz *et al*., 2016). The second genus of the Suidae in Asia is monotypic, with *Porcula salvania* (Hodgson) considered extinct, except in a few areas in Assam (Narayan *et al*., 2008; Frantz *et al*., 2016), whereas representatives of the third genus, *Babyrousa* Perry, are categorised as vulnerable and their geographic range is limited to Indonesia (Mcdonald *et al*., 2008, 2016; Leus *et al*., 2016).

In the Americas, the family Tayassuidae is represented by three extant species in three genera, *Pecari tajacu* (Linnaeus), listed as of the least concern on the IUCN Red List of Threatened Species, *Tayassu pecari* (Link), listed as vulnerable, and *Catagonus wagneri* (Rusconi), considered endangered (Gongora *et al*., 2011a, b; Keuroghlian *et al*., 2013; Altrichter *et al*., 2015).

Although the influence of parasites on host fitness as well as the population dynamics of their hosts is well documented (Hudson and Greenman, 1998; Torchin *et al*., 2001; Hudson *et al*., 2002), and the critical conservation status of many species of the Suidae and Tayassuidae is known, knowledge about their helminth parasites is scant.

Given that *Ph. africanus* is one of the most iconic suids on the African continent, surprisingly little work has been done on its helminth parasites, with most works focusing on taxonomy (Leroux, 1940; Ortlepp, 1964; Round, 1968; Troncy *et al*., 1973; Boomker, 1990; Beveridge, 2014), and only a few studies describing the composition of helminth assemblages. The latter were conducted in mostly southern Africa and include surveys in Namibia as well as the Mpumalanga and Limpopo Provinces in South Africa (Horak *et al*., 1983, 1988; Boomker *et al*., 1991a; van Wyk and Boomker, 2011), while Ortlepp (1964) examined material obtained from *Ph. africanus* from Mozambique and South African game reserves in Zululand, now part of KwaZulu-Natal Province. Boomker *et al*. (1991a) provide a host parasite list for this host comprising 31 species of helminths: trematodes (n = 2), cestodes (n = 6) and nematodes (n = 23).

Even less is known about the helminth fauna of the remaining species of African wild suids, and, as for *Ph. africanus*, the majority of papers are taxonomic works or based on incidental findings (e.g. van den Berghe, 1943; Inglis, 1958; Ortlepp, 1964; Round, 1968; Troncy *et al*., 1973; Iori and Lanfranchi, 1996).

Likely the best studied of the suids is *S. scrofa*, which may not be unexpected considering its wide geographic range and economic importance. Most of these studies were done on wild boars in Europe (see Järvis *et al*., 2007 and references cited therein), with fewer studies conducted in Africa, Asia, the Middle East and the Americas (e.g. Ajayi *et al*., 1988; Pence *et al*., 1988; McKenzie and Davidson, 1989; Esrony *et al*., 1997; Solaymani-Mohammadi *et al*., 2003; da Silva and Müller, 2013a, b; Ahn *et al*., 2015; Mansouri *et al*., 2016; Chaisiri *et al*., 2017).

The helminths of both barbirusas and peccaries are poorly studied (Schwartz and Alicata, 1933; Samuel and Low, 1970; Corn *et al*., 1985; Munro *et al*., 1990; Romero-Castañón *et al*., 2008; Widyarsi, 2011).

The common warthog, *Ph. africanus*, is found in Grassland, Shrubland and Savanna habitats in sub-Saharan Africa. Warthogs are diurnal and spend much of the day grazing on short grass, preferring fresh and new shoots, sedges, herbs and wild fruits. Nights are spend holed up, typically in repossessed aardvark [*Orycteropus afer* (Pallas)] burrows that are changed frequently, possibly to avoid high parasite burdens (Somers *et al*., 1994; Skinner and Chimimba, 2005). Socially, *Ph. africanus* is organised in the following categories: solitary males; bachelor groups containing 2–3 males more than one year old; matriarchal groups consisting of adult females with juveniles and/or yearlings; or yearling groups. Yearling groups comprising males and females break up as the females farrow and yearling males either move off as solitary adult males or remain part of bachelor groups (Somers *et al*., 1995; Skinner and Chimimba, 2005).

In this paper, we describe the helminth community of *Ph. africanus* in a game reserve in the KwaZulu-Natal Province, South Africa, a region for which currently only scant information on this particular host-parasite system is available, and assess the influence of host age and sex on the composition and abundance of these helminth assemblages. We expected males to carry higher helminth burdens than females as is the case with many mammal species (Folstad and Karter, 1992; Poulin, 1996; Arneberg *et al*., 2002; Moore and Wilson, 2002; Wirsing *et al*., 2007). With regard to the effect of age, we proposed two alternative predictions, namely that yearlings will be (a) more heavily infected than adults because of their not yet fully-developed immune system (Reinecke, 1983; Anderson, 1987; MacIntosh *et al*., 2010) or (b) less infected than adults due to the accumulation of helminth individuals and/or species in older animals (Behnke *et al*., 1999).

We further compare our findings to earlier studies on the helminth parasites of warthogs in South Africa and compare similarities between helminth communities in warthogs and other species of the Suidae and Tayassuidae worldwide.

Materials and methods

Survey area

In March 2015, 31 free-roaming common warthogs were culled in the Pongola Game Reserve (PGR; 27° 22′ 09.26″ S, 31° 50′ 42.16″ E), KwaZulu-Natal Province, South Africa. The PGR is situated in the Savanna biome and forms part of the Zululand Lowveld. This bioregion is typically characterised by summer rainfall, although some rains might fall in winter, with mean annual precipitation ranging from 500–900 mm. Summers are warm to hot, and the mild winters remain frost-free (Mucina and Rutherford, 2006). The Pongola River, which flows through the reserve, is perennial and provides water throughout the year, together with the Pongolapoort Dam, which it enters within the boundaries of the reserve (http://www.pongolagamereserve.co.za). Altitude within the reserve varies from approximately 140–600 m above sea level (http://en-za.topographic-map.com/places/Pongola-Nature-Reserve-9257351/).

Survey animals and parasite collection

Warthogs were culled over a period of five days at different sites within the PGR, using single shot bolt action rifles during daylight (ethical clearance number: 11LV_HOF02) and within a radius of approximately 1 km from the water. The animals were shot as part of a project evaluating quality characteristics of warthog meat from different sex (males, females) and age classes [adults (> 24 months), yearlings (12–24 months)] (see Rudman *et al*., 2018 for further details on age classification and processing of animals). Except for the fact that specific sex and age classes were targeted, warthogs were shot randomly and belonged to different groups. Of the 31 warthogs that were culled, 30 (eight adult females, eight adult males, eight juvenile females and six juvenile males) could be examined for gastrointestinal helminths.

Carcasses were transported to the government accredited slaughter facility within the PGR, skinned and eviscerated. The gastrointestinal tract (GIT) was divided into stomach, small intestine and large intestine and these sections were placed into individual trays and cut open. Macroscopically visible parasites were removed and preserved in 70% ethanol. Aliquots of the ingesta from the different GIT sections were prepared and helminths collected from them as described by Boomker *et al*. (1991a). The heart was opened and examined macroscopically for parasites. Longitudinal incisions, approximately 10 mm apart, were made in the lungs and liver and the exposed surfaces scanned macroscopically for parasites. All helminths collected were stored in 70% ethanol. Except for *Probstmayria vivipara* (Probstmayr, 1865) (see below), nematodes were identified and counted as temporary mounts in lactophenol under a compound light microscope. Cestodes and digeneans were cleared in Hoyer’s medium for identification. Cestode counts reflect the number of scoleces present. We

Table 1. Prevalence and mean abundance (MA±SE) of gastrointestinal helminth parasites collected from 30 common warthogs in the Pongola Game Reserve, South Africa

Species	Site in host	Life cycle	Infected hosts (N)	Prevalence (%)	Total count	MA(±SE)	MA range
Trematodes							
Gastrodiscus aegyptiacus (Cobbold, 1876) Leuckart in Cobbold, 1877	Large intestine	Indirect	4	13.3	380	12.67 ± 10.36	0–310
Cestodes							
Moniezia sp.	Small intestine	Indirect	13	43.3	59	1.97 ± 0.55	0–13
Nematodes							
Ascaris phacochoeri Gedoelst, 1916	Stomach	Direct	5	16.7	6	0.20 ± 0.09	0–2
Impalaia tuberculata Mönnig, 1923	Small intestine	Direct	4	13.3	18	0.60 ± 0.34	0–9
Murshidia hamata Daubney, 1923	Large intestine	Direct	30	100	458440	15281.33 ± 2564.25	2850–58110
Murshidia pugnicaudata (Leiper, 1909) Yorke and Maplestone, 1926	Large intestine	Direct	30	100	41450	1381.67 ± 273.97	80–6070
Physocephalus sexalatus (Molin, 1860) Diesing, 1861	Stomach	Indirect	27	90	1106	36.87 ± 9.49	0–200
Probstmayria vivipara (Probstmayr, 1865) Ransom, 1907	Large intestine	Direct	30	100	Numerous*	ND	ND
Trichostrongylus thomasi Mönnig, 1932	Stomach	Direct	23	76.7	784	26.13±7.98	0–167

*This species was too abundant to obtain individual counts. ND = Not determined.

were not able to identify cestodes of the genus *Moniezia* Blanchard, 1891 to species level and list them here as *Moniezia* sp. However, Beveridge (2014) confirmed the presence of two species of *Moniezia* in warthogs. Identifications were based on descriptions and redescriptions of the various genera and species recovered; authorities of the species identified are listed in Table 1. Voucher material was deposited in the National Collection of Animal Helminths, Agricultural Research Council-Onderstepoort Veterinary Institute, South Africa (accession numbers S/2019/11-17).

Data analysis

Three of nine helminth species recorded in this study (*Ascaris phacochoeri*, *Impalaia tuberculata* and *Gastrodiscus aegyptiacus*) demonstrated very low prevalence (13.3–16.7%), whereas the numbers of *P. vivipara* could not be established due to the extremely high infection intensity of this parasite. For the analyses of the effects of host sex and age on the number of helminths of a given species they harboured, we, therefore, selected the five remaining species (*Moniezia* sp., *Murshidia hamata*, *M. pugnicaudata*, *Physocephalus sexalatus* and *Trichostrongylus thomasi*). Of them, *Moniezia* sp. was the least prevalent (43.3%), resulting in a large number of zeroes in the dataset for this species. In addition, the number of *Moniezia* sp. varied weakly among infected animals (on average, 1.96±0.5 worms per animal). Consequently, we chose to analyse the effect of host sex and age on incidence (i.e., whether a parasite occurs in a host individual or not; Stanko *et al.*, 2015) rather than numbers of this species. The response variable for *Moniezia* sp. was thus dichotomous and took a value of either 1 or 0 if an individual was either infected with at least one helminth or not, respectively. We analysed the response variable using generalized linear models with the binomial error distribution and logit-link function. Categorical independent variables were host sex and host age as well as interaction between these factors, whereas we included host body mass as a continuous covariate. The effects of host sex and age and their interactions on the number of *M. hamata*, *M. pugnicaudata*, *P. sexalatus* and *T. thomasi* (separately) were analysed using generalized linear models with the gaussian error distribution and identity-link function. The values of the response variables were log+1-transformed prior to analyses. Host body mass was included in the model as a covariate. In addition, we calculated the number of helminth species recorded in each individual host and analysed the effect of host sex and age on this number in a similar way as we did for number of helminth individuals, except that we did not transform the values of the response variable. All analyses were done using R Statistical Environment (R Core Team, 2018). After the initial running of each model, we selected the best model based on the Akaike Information Criterion (AIC), using the function “dredge” from the R package ‘MuMIn’ (Barton, 2018) implemented in R, and ran the best model again (in cases, when the best model was not the intercept-only model).

Results

Overall GIT helminth prevalence in common warthogs from the PGR was 100%. Cestodes and trematodes were represented by one species each, whereas the majority of helminths were nematodes, represented by seven species belonging to six genera (Table 1). Except for *A. phacochoeri* and *I. tuberculata,* both of which had a low prevalence as well as abundance, all nematodes species were highly prevalent. *Probstmayria vivipara* was the most abundant helminth in all hosts examined, followed by *M. hamata* which ranged from 2850– 58110 individuals per host. *Murshidia pugnicaudata* was the third most abundant species, although it occurred in distinctly lower numbers (80–6070) than its congener. Mean species richness of GIT helminths was six, ranging from 4–7 species per individual host. In a single warthog, a metacestode of *Taenia hydatigena* Pallas, 1766 was collected from the mesenteries. No helminths were found in the heart, lungs and liver of the hosts examined.

No effect of either host sex or age or their interaction was found for the incidence of *Moniezia* sp. (z-values of coefficients varied from -0.12 for intercept to 0.70 for the sex x age interaction; p > 0.48 for all). The best model for the incidence of *Moniezia* sp. was the intercept only model (log-likelihood = -20.53, AICcorrected = 43.2, ΔAIC = 0.00, AICweight = 0.37).

Numbers of *M. hamata* and *M. pugnicaudata* were similar in male and female warthogs, but were significantly higher in adults than in yearlings (Table 2, Fig. 1). No effect of either sex or age of a host on the number of *P. sexalatus* was found (Table 2). Numbers of *T. thomasi* were significantly higher in male than in female warthogs (Table 2, Fig. 2), but did not depend on host age (Table 2). Finally, male warthogs tended to harbour richer helminth assemblages than female warthogs, although this difference was only marginally significant (Table 2, Fig. 3).

Table 2. Summary of best models of the effect of warthogs' age and sex and their interactions on the number of four helminths species and helminth species richness. Body mass of a host individual was included in the full models as a covariate. LL – log-likelihood, AICc – Aikaike Information Criterion corrected for sample size, ΔAIC – delta AIC, AICw – AIC weight. Reference levels of explanatory variables were female for sex and adult for age

Helminth	Factor	Coefficient			LL	AICc	ΔAIC	AICw
		Value±SE	*t*	*p*				
Murshidia hamata	Intercept	4.18 ± 0.09	48.44	>0.001	-9.65	26.20	0.00	0.30
	Age	-0.35 ± 0.12	-2.76	0.01				
Murshidia pugnicaudata	Intercept	3.06 ± 0.12	25.26	>0.001	-19.78	46.50	0.00	0.32
	Age	-0.37 ± 0.18	-2.08	0.047				
Physocephalus sexalatus	Intercept	-0.15 ± 1.05	-0.14	0.89	-31.27	67.00	0.00	0.43
Trichostrongylus thomasi	Intercept	0.63 ± 0.17	3.72	>0.001	-30.09	67.10	0.00	0.33
	Sex	0.57 ± 0.25	2.89	0.03				
Species richness	Intercept	0.51 ± 0.18	28.9	>0.001	-32.32	71.60	0.00	0.37
	Sex	0.54 ± 0.27	2.02	0.05				

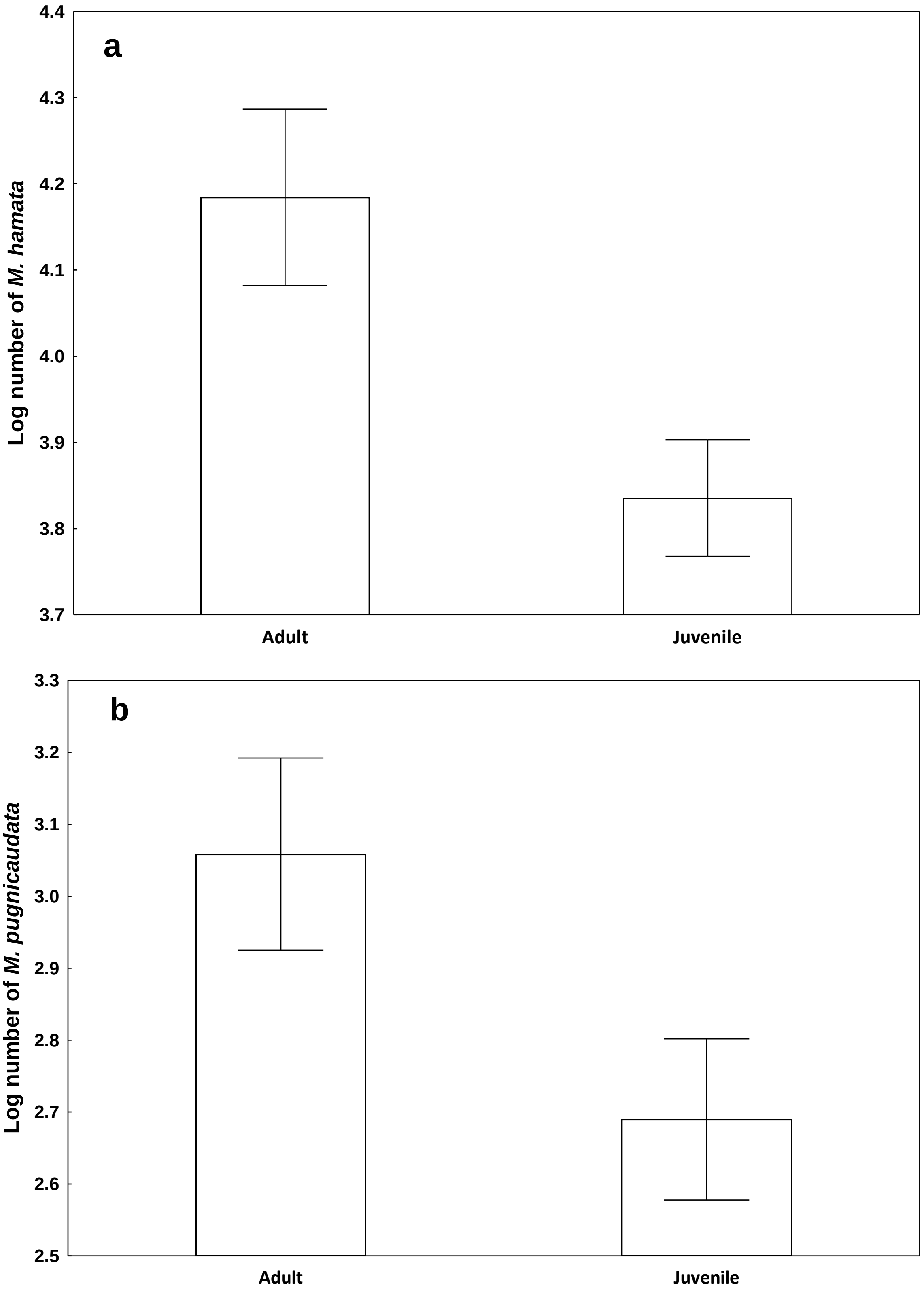

Fig. 1. Mean (±SE) numbers of *Murshidia hamata* (a) and *M. pugnicaudata* (b) in adult and juvenile warthogs.

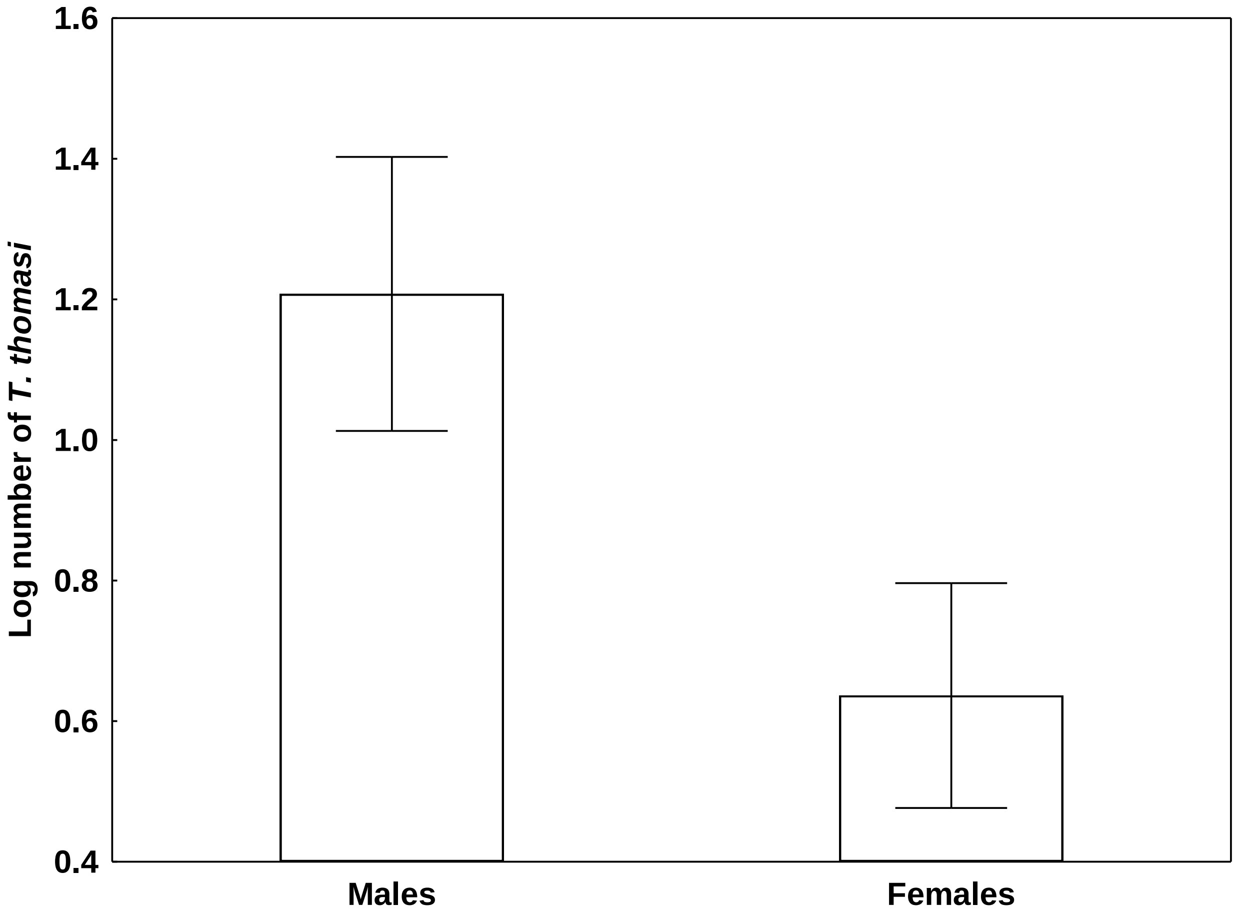

Fig. 2. Mean (±SE) numbers of *Trichostrongylus thomasi* in male and female warthogs.

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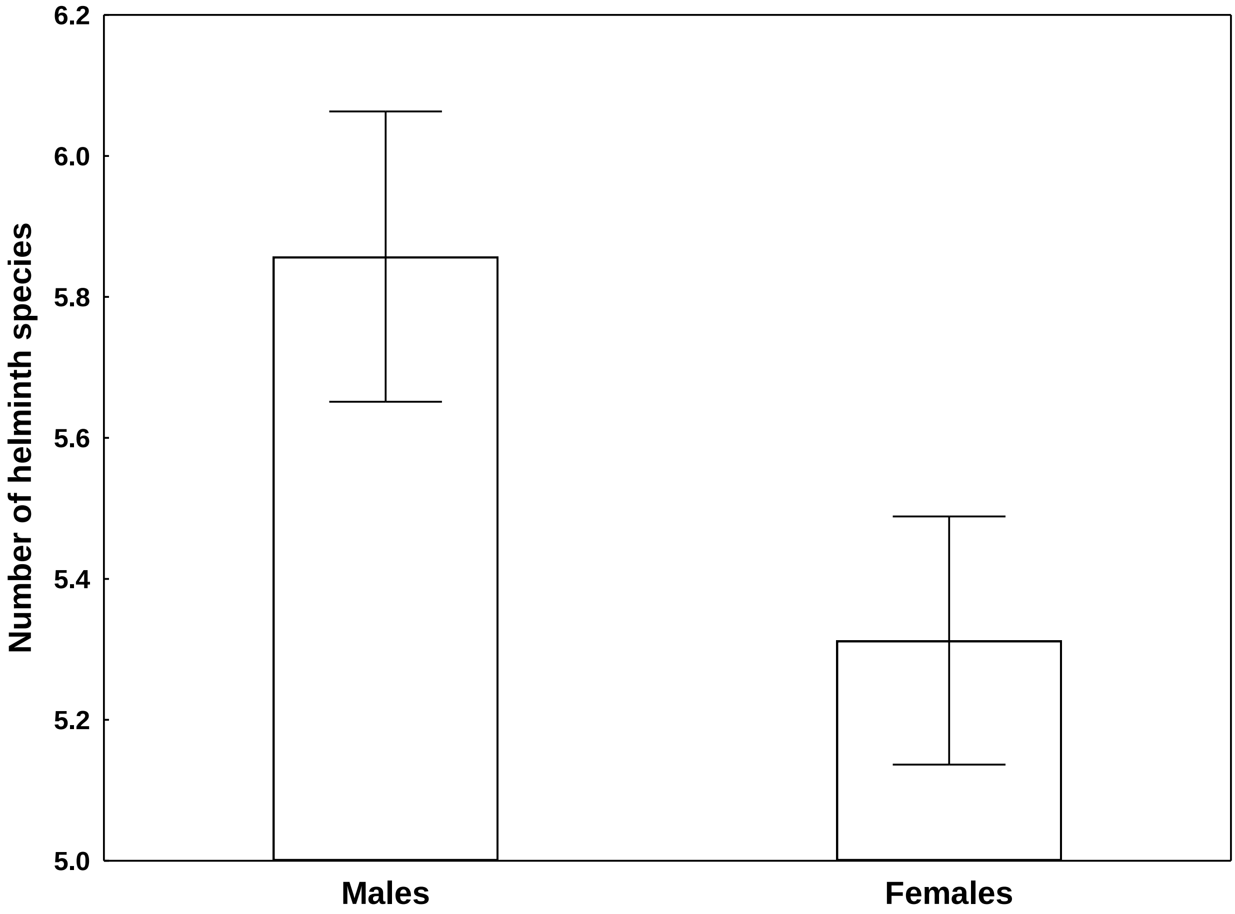

Fig. 3. Mean (±SE) number of helminth species harboured by male and female warthogs

Discussion

The prevalence of helminth infections in warthogs from the PGR was high and each animal that was examined harboured GIT helminths.

All nine species recovered had previously been recorded from *Ph. africanus* in South Africa and its neighbouring country Namibia (Ortlepp, 1964; Horak *et al*., 1983, 1988; van Wyk and Boomker, 2011), and are considered typical parasites of this host. Interestingly, while the number of species recorded from the GIT of warthogs from the PGR and Namibia was similar (9 *vs* 11), warthogs in Namibia did not harbour any *Murshidia* spp., but were instead host to *Daubneyia* spp. (as *Oesophagostomum mpwapwae* Duthy, 1948, *O. mwanzae* Daubney, 1924 and *O. roubaudi* Daubney, 1926). In addition, the genus *Impalaia* Mönnig, 1923 was represented by *I. nudicollis* Mönnig, 1931 , while *I. tuberculata* was not found (Horak *et al*., 1983). Species richness of helminth assemblages in game and nature reserves in the Limpopo and Mpumalanga Provinces was usually higher than that in the PGR, and helminth assemblages in these two provinces contained both *Murshidia* spp. as well as *Daubneyia* spp. (as *O. mocambiquei* Ortlepp, 1964 and *O. mwanzae*) (Horak *et al*., 1988; Boomker *et al*., 1991a). It is noteworthy that Ortlepp (1964) reported a similar separation of these two oesophagostomine genera in warthogs from Mozambique and KwaZulu-Natal, with the former harbouring only *Daubneyia* spp. while the latter were parasitised by only *Murshidia* spp. Little is known about the life cycle of either genus, but oesophagostomines in general have a direct life cycle and eggs as well as first- to third-stage larvae occur free in the environment (Anderson, 2000). A possible explanation for the observed differences in the geographic distribution pattern of the two genera might be a difference in their tolerance towards environmental factors. A number of species of the Strongylida, including *Oesophagostomum* spp. and *Trichostrongylus* spp., have been shown to differ in the ability of their eggs to develop at different faecal moisture contents and their susceptibility to moisture and hot and cold temperatures (Rossanigo and Gruner, 1995; Anderson, 2000; O'Connor *et al*., 2006).

In areas where *Murshidia* spp. occur, both species have a more or less equally high prevalence (Horak *et al*., 1988; Boomker *et al*., 1991a; this paper), which somewhat contradicts speculation by Troncy *et al*. (1973) that *H. meinertzhageni* and not *Ph. africanus* is the true host of this parasite. However, we consistently found higher numbers of *M. hamata* than *M. pugnicaudata*. Similar results have been reported previously (Horak *et al*., 1988; Boomker *et al*., 1991a), and this might suggest certain variability in the suitability of warthogs as hosts for these two species.

Trichostrongylus thomasi had a high prevalence in the present study and, following *Murshidia* spp. and *P. sexalatus*, had the fourth highest mean abundance of all helminths found in warthogs in the PGR. It had a similarly high prevalence in warthogs in the Kruger National Park (KNP) (Horak *et al*., 1988) and the Hoedspruit Nature Reserve (HNR) (Boomker *et al*., 1991a), but was absent in warthogs examined in Limpopo Province by van Wyk and Boomker (2011), and by Horak *et al*. (1983) in Namibia, where *T. colubriformis* (Giles, 1892) was found instead, with low prevalence and abundance. Only a few *Trichostrongylus* spp. females were found in warthogs at a military base situated within the HNR, but separated from it by a number of fences (Boomker *et al*., 1991a). The latter authors pointed out that *T. thomasi* was typically a parasite of a number of antelope species and considered its presence in warthogs an accidental infection. Warthogs in the KNP, which supports a large diversity of antelopes, were parasitised by a number of *Trichostrongylus* spp. (Horak *et al*., 1988), and it is possible that the *Trichostrongylus* Looss, 1905 fauna of warthogs at a given locality reflects the helminth fauna of co-occurring antelopes. The same might be true for species of *Impalaia*, which parasitise a vast number of antelope hosts (Boomker, 1977; Gibbons *et al*., 1977). Unfortunately, there are no data on the helminth assemblages of antelope species in the PGR to confirm these assumptions.

Compared to other nematode species with a direct life cycle, the prevalence of *A. phacochoeri* (*Ascaris* sp. in Namibia) in warthogs in southern Africa is relatively low (2.6–46%) (Horak *et al*., 1983, 1988; van Wyk and Boomker, 2011; this study), and the highest mean abundance, recorded in warthogs from HNR, was 4.07 (Boomker *et al*., 1991a). Contrary to *Impalaia* spp., *Murshidia* spp. and *Trichostrongylus* spp., in which developing larvae hatch from the eggs and the phototropic infective third-stage larvae climb to the top of grasses, larvae of *Ascaris* spp. remain in the egg during their development, and it is the embryonated egg on the ground that has to be ingested by the host (Anderson, 2000). The former might be a more effective mode of transmission in herbivorous warthogs.

Although typically a parasite of equines and highly abundant in zebra in southern Africa (Ransom, 1907; Scialdo-Krecek, 1983; Scialdo-Krecek *et al*., 1983), *P. vivipara* is clearly a most prominent nematode in helminth assemblages of warthogs, having a prevalence of 100% at all studied localities and an abundance either close to or in their millions (Horak *et al*., 1983, 1988; Boomker *et al*., 1991a; van Wyk and Boomker, 2011; this study). Their extraordinary abundance is likely the result of autoinfection, as females are viviparous and larvae develop to maturity in the large intestine; transmission from host to host is thought to occur when faeces containing larvae are ingested (Anderson, 2000). Allogrooming, including anal licking, has been reported in warthogs (Skinner and Chimimba, 2005) and might contribute towards the transmission of *P. vivipara* between hosts.

Of the species with an indirect life cycle, the nematode *P. sexalatus*, which uses a variety of dung beetles as intermediate hosts (Anderson, 2000; Schuster *et al*., 2014), had the highest prevalence in this and other studies conducted in southern Africa (48–92%), with a moderate abundance, except for the warthogs in Namibia and the HNR, where mean abundance was as high as 341.92 and 371.47, respectively (Horak *et al*., 1983, 1988; Boomker *et al*., 1991a; van Wyk and Boomker, 2011). The cestode genus *Moniezia* is transmitted by oribatid mites that serve as intermediate hosts (Xiao and Herd, 1992; Denegri *et al*., 1998; Schuster *et al*., 2000). While its prevalence in this and previous studies was moderate to low, with few individuals collected from infected hosts (Horak *et al*., 1983, 1988; Boomker *et al*., 1991a; van Wyk and Boomker, 2011), the genus nevertheless has a wide geographic range. The occurrence of *P. sexalatus* and representatives of *Moniezia* in a large variety of geographic localities suggests that their intermediate hosts are wide-spread and readily ingested by the warthogs while feeding.

To the contrary, *G. aegyptiacus*, whose life cycle entails a freshwater snail and metacercariae that encyst on vegetation near waterbodies (Malek, 1971; Mukaratirwa *et al*., 2004), was found only in the PGR and one locality within the KNP (Horak *et al*., 1988). We believe that the presence of this digenean in the PGR is attributable to the Pongolapoort Dam, which forms part of the PGR and offers ample suitable habitat for freshwater snail intermediate hosts. The low prevalence of the parasite might be a result of warthogs being relatively independent of permanent sources of water (Skinner and Chimimba, 2005) and suggests that trematode infections play a minor role in this host.

Our finding of a metacestode of *T. hydatigena* in the mesenteries of one of the warthogs is not unexpected, and taeniids, including *Echinococcus* spp. and *Taenia* spp., have repeatedly been reported from warthogs (Horak *et al*., 1983, 1988; Boomker *et al*., 1991a; van Wyk and Boomker, 2011). They are some of the relatively few parasite species shared between warthogs and domesticated or feral pigs (Fabiyi, 1979; Eslami and Farsad-Hamdi, 1992; Rajković-Janje *et al*., 2002). Interestingly though, the *Taenia* spp. found in warthogs, are those using carnivores as definitive hosts, whereas *T. solium* Linnaeus, 1758, one of the main helminths of zoonotic concern in pigs (Sinha and Sharma, 2009), has not been reported from warthogs.

We found few effects of host sex or age on parasite assemblages in warthogs from the PGR. However, while the burdens of *Murshidia* spp. were similar in males and females, adults harboured significantly more worms than yearlings. While no comparative data exist for warthogs, studies on the influence of age on the composition of helminth assemblages in wild boar yielded mixed results. Some studies report a higher intensity of lung and stomach nematodes in younger animals (Humbert and Henry, 1989; Senlik *et al*., 2011), whereas others record an increase of infection with age (Foata *et al*., 2006). Yet others found no difference between intensity of infection and hosts of different ages (Magi *et al*., 2002; Rajković-Janje *et al*., 2002). The increase of intensity in *Murshidia* spp. in adults observed in the present study is likely attributable to the accumulative effect of repeated exposure to infective stages of this genus in older animals over time, as has been demonstrated for direct life cycle nematodes in other mammalian hosts (Behnke *et al*., 1999).

A similarly varied picture emerges when looking at gender-bias in helminth infections in Suidae. Although not statistically significant, Rajković-Janje *et al*. (2002) found that female wild boars carried higher worm burdens than their male counterparts, whereas Senlik *et al*. (2011) found male wild boars infected with higher numbers of the digenean *Dicroceolium dendriticum* (Rudolphi, 1819) when compared to females. In the present study, male warthogs supported larger numbers of *T. thomasi* as well as helminth assemblages that were more species rich than those seen in females, although the latter difference was only marginally significant. A number of factors pre-dispose males to parasite infections, e.g. immune-suppression based on male hormones, especially testosterone, larger body size, territoriality and movement patterns, dietary preferences and sociality, to name but a few (Folstad and Karter, 1992; Poulin, 1996; Arneberg, 2002; Moore and Wilson, 2002; Wirsing *et al*., 2007). According to Somers *et al*. (1994), warthog males disperse more widely than females, following a dispersal pattern typical for mammals that are mostly polygamous. In addition, while Somers *et al*. (1994) found female home ranges to be slightly larger than those of males in a small reserve in South Africa, the opposite was true for warthogs in Kenya (Radke, 1990). An increased vagility in males will likely expose them to a higher number as well as larger diversity of infective stages of parasites in habitats frequented by co-occurring antelope and other possible reservoir species. Furthermore, males in the present study weighed significantly more than females (Rudman *et al*., 2018). Increased food intake to maintain body mass would equally lead to increased exposure rates (Arneberg, 2002; George-Nascimento *et al*., 2004).

We found no host-related differences in the incidence of *Moniezia* sp. in the present warthogs. Contrary to this, Boomker *et al*. (1991a) detected *Moniezia* sp. in young animals only, which is in accordance with *Moniezia* spp. in ruminants, where older animals develop immunity against infection (Reinecke, 1983). A possible explanation for the absence of an age effect in this study might be that yearlings at 12–24 months of age would likely have had previous exposure to the parasite, triggering their immune response to subsequent infections.

Bushpigs, *Po. larvatus*, are the only species of wild suids that are sympatric with warthogs in South Africa. Originally, bushpigs in the southern African subregion were referred to as *Po. porcus*, as reflected in the zoological and parasitological literature; they should, however, be referred to as *Po. larvatus* (Skinner and Chimimba, 2005). Few bushpigs have been examined for their parasites, possibly because of their nocturnal habits and relatively limited distribution in forested areas (van Wyk and Boomker, 2011). Nevertheless, the few data from localities in South Africa and Mozambique suggest that warthogs and bushpigs have fairly distinct helminth assemblages, with only *P. sexalatus* and *G. aegyptiacus* being shared between the two (Ortlepp, 1964; van Wyk and Boomker, 2011). On the other hand, *Morgascaridia sellsi* (Morgan, 1927), *O. aethiopicum* Duthy, 1948 and

Globocephalus versteri Ortlepp, 1964 appear restricted to bushpigs and have also not been detected in *H. meinertzhageni*, the remaining species of wild pigs in sub-Saharan Africa. Although originally described from an East African 'wart-hog' (Duthy, 1948), Ortlepp (1964) believed the bushpig to be the normal host of *O. aethiopicum* and considered the warthog an accidental host. Moreover, it was Ortlepp's (1964) contention that 'as the habitats and the feeding habits of the two hosts are quite different, one would not expect them to harbour the same species of parasites'.

Interestingly, *Ascarops strongylina* (Rudolphi, 1819), a common parasite in *Sus* spp. worldwide, and also present in domesticated pigs in South Africa (Horak, 1978), appears absent in *Ph. africanus* as well as in *H. meinertzhageni*. The parasite was, however, collected from *Po. larvatus* (Ortlepp, 1964). Similarly, *Hyostrongylus rubidus* (Hassall and Stiles, 1892), a common parasite of *S. scrofa* (Rajković-Janje *et al*., 2002; Senlik *et al*. 2007) and widespread in domesticated as well as feral pigs in Africa (Fabiyi, 1979; Permin *et al*., 1999; Nganga *et al*., 2008; Nissen *et al*., 2011), was found in *Po. larvatus* (Boomker *et al*., 1991b), but not in *P. africanus* or *H. meinertzhageni*.

Furthermore, in areas in Central and East Africa, where the distribution ranges of *Phacochoerus* and *Hylochoerus* overlap, these two genera share a number of parasite species, which incidentally, are absent from *Potamochoerus*: *Bourgelatia hylochoeri* (van den Berghe, 1943), *B. pricei* (Schwartz, 1928), *D. farchai* Troncy, Graber and Thal, 1973, *D. goodeyi* (Daubney, 1926), *D. mwanzae* (Daubney, 1924), *D. yorkei* (Thornton, 1924), *M. hamata* and *M. pugnicaudata* (Troncy *et al*., 1973; Iori and Lanfranchi, 1996). Frantz *et al*. (2016) present a phylogeny of extinct and extant Suidae in which *Hylochoerus* and *Phacochoerus* form a sistergroup to *Potamochoerus*. The above findings suggest that the closer relatedness of the former two genera is also reflected in their parasite communities. One should, however, not lose sight of the actual paucity of records (numerically as well as geographically) on the parasite communities of especially *Hylochoerus* and *Potamochoerus* in Africa. Hence, in some cases, the apparent absence of a given parasite, as for example that of the rather ubiquitous *P. sexalatus* in *H. meinertzhageni*, might simply be because of a lack of data.

In fact, *P. sexalatus* has the widest host range of helminths in suids and peccaries worldwide (Ortlepp, 1964; Corn *et al*., 1985; Pence *et al*., 1988; McKenzie and Davidson, 1989; Järvis *et al*., 2007; Sato *et al*., 2008; Senlik *et al*., 2011; Chaisiri *et al*., 2017), and, to date, only seems absent in *Hylochoerus* in Africa and babirusas in Asia. Again, this phenomenon might be because of a lack of data for these species.

Generally speaking, helminth communities of wild suids in Africa have little in common with those of other pigs or pig-like hosts worldwide. A typically African genus that seems to have emerged within its African hosts and undergone successful radiation in especially warthogs is *Daubneyia* Leroux, 1940. To date, *Daubneyia* is represented by 13 species in *Phacochoerus* and *Hylochoerus* (Ortlepp, 1964; Troncy *et al*., 1973). Its counterpart in *S. scrofa* and, to an extent, in babirusas and peccaries is the genus *Oesophagostomum* Molin, 1861, with five species reported from these hosts (Troncy *et al*., 1973; Horak, 1978; Munro *et al*., 1990; Eslami and Farsad-Hamdi, 1992; Rajković-Janje *et al*., 2002; Romero-Castañón *et al*., 2008). A single species described from a warthog, *O. aethiopicum*, is likely a parasite of *Po. larvatus* (see above; Duthy, 1948; Ortlepp, 1964).

Interestingly, the lungworm genus *Metastrongylus* Molin, 1861 is absent from any of the wild African suids, but is species rich in *S. scrofa*, with a wide geographic range (Pence *et al*., 1988; Humbert and Henry, 1989; Järvis *et al*., 2007; Sato *et al*., 2008; Senlik *et al*., 2011). Furthermore, it has also been recorded from domesticated and feral pigs in Africa (Horak, 1978; Fabiyi, 1979; Permin *et al*., 1999). We believe that wild African suids in their natural environment had little exposure to earthworms, which serve as intermediate hosts for *Metastrongylus* spp. (Anderson, 2000), and that this parasite has been introduced into Africa and other parts of the world with the extensive translocation of domesticated pigs by humans.

Other genera, such as *Ascaris* Linnaeus, 1758 and *Bourgelatia* Railliet, Henry and Bauche, 1919 have a wide host range in Suidae and occur in wild suids in Africa as well as in *S. scrofa* and babirusas, but are represented by different species in different hosts (Troncy *et al*., 1973; Foata *et al*., 2006; Sato *et al*., 2008; Widyarsi *et al*., 2011; Chaisiri *et al*., 2017). Similarly, *G. versteri* parasitises *Po. larvatus* (Ortlepp, 1964), whereas its congener in *S. scrofa* and peccaries is *G. urosubulatus* Alessandrini, 1909 (Rajković-Janje *et al*., 2002; Foata *et al*., 2006; Romero-Castañón *et al*., 2008), while a further two species *G. longimucronatus* Molin, 1861 and *G. samoensis* Lane, 1922 occur in *S. s. leucomystax* in Japan (Sato *et al*., 2008).

In conclusion, warthogs have the most diverse helminth assemblages of the three genera of wild suids in sub-Saharan Africa. Their helminth fauna is most similar to that of *H. meinertzhageni* and both hosts have few helminth species in common with *Po. larvatus*, possibly reflecting the closer phylogenetic relatedness of *Phacochoerus* and *Hylochoerus*. Despite some helminth species being shared by wild suids in Africa and other Suidae and/or Tayassuidae, the helminth faunae of these pig and pig-like hosts, are largely divergent. It is quite clear from the literature that there is paucity of data on helminth parasites of wild suids in Africa and a need for further studies, inclusive of all three host genera and covering a wider geographic range.

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Ethical standards. All applicable institutional, national and international guidelines for the care and use of animals were followed.

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References

Ahn KS, Ahn AJ, Kim TH, Suh GH, Joo KW and Shin SS (2015) Identification and prevalence of *Globocephalus samoensis* (Nematoda: Ancylostomatidae) among wild boars (*Sus scrofa coreanus*) from Southwestern regions of Korea. *Korean Journal of Parasitology* **53**, 611–618.

Ajayi JA, Arabs WL and Adeleye GA (1988) Helminths and protozoa of pigs on the Jos Plateau, Nigeria: occurrence, age incidence and seasonal distribution. *Bulletin of Animal Health and Production in Africa* **36**, 47–54.

Altrichter M, Taber A, Noss A, Maffei L and Campos J (2015) *Catagonus wagneri*. *The IUCN Red List of Threatened Species* 2015: e.T4015A72587993. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T4015A72587993.en. Accessed on 27 February 2019.

Anderson RM (1987) The role of mathematical models in helminth population biology. *International Journal of Parasitology* **17**, 519–529.

Anderson RC (2000) Nematode parasites of vertebrates. Their development and transmission, 2nd edn. Wallingford, UK: CABI Publishing.

Arneberg P (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**, 88–94.

Barton K (2018) MuMIn: Multi-Model Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn.

Behnke JM, Lewis JW, Zain SM and Gilbert FS (1999) Helminth infections in *Apodemus sylvaticus* in southern England: interactive effects of host age, sex and year on the prevalence and abundance of infections. *Journal of Helminthology* **73**, 31–44.

Beveridge I (2014) A review of the genus *Paramoniezia* Maplestone et Southwell, 1923 (Cestoda: Anoplocephalidae), with a new genus, *Phascolocestus*, from wombats (Marsupialia) and redescriptions of *Moniezia mettami* Baylis, 1934 and *Moniezia phacochoeri* (Baylis, 1927) comb. n. from African warthogs (Artiodactyla). *Folia Parasitologica* **61**, 21–33.

Boomker JDF (1977) A revision of the genus *Impalaia* Mönnig, 1924. *Onderstepoort Journal of Veterinary Research* **44**, 131–138.

Boomker J (1990) Parasites of South African wildlife. V. A description of the males of *Oesophagostomum mocambiquei* Ortlepp, 1964 from warthogs, *Phacochoerus aethiopicus* (Pallas, 1766). *Onderstepoort Journal of Veterinary Research* **57**, 169–173.

Boomker J, Horak IG, Booyse DG and Meyer S (1991a) Parasites of warthogs, *Phacochoerus aethiopicus,* in the eastern Transvaal. *Onderstepoort Journal of Veterinary Research* **58**, 195–202.

Boomker J, Horak, IG and Flamand JRB (1991b) Parasites of South African wildlife. X. Helminths of red duikers, *Cephalophus natalensis*, in Natal. *Onderstepoort Journal of Veterinary Research* **58**, 205–209.

Chaisiri K, Aueawiboonsri S, Kusolsuk T, Dekumyoy P, Sanguankiat S, Homsuwan N, Peunipoom G, Okamoto M, Yanagida T, Sako Y and Ito A (2017) Short Communication Gastrointestinal helminths and *Taenia* spp. in parenteral tissues of free-roaming pigs (*Sus scrofa indicus*) from hill-tribe village at the western border of Thailand. *Tropical Biomedicine* **34**, 464–470.

Corn JL, Pence DB and Warren RJ (1985) Factors affecting the helminth community structure of adult collared peccaries in southern Texas. *Journal of Wildlife Diseases* **21**, 254–263.

da Silva D and Müller G (2013a) Parasites of the respiratory tract of *Sus scrofa scrofa* (wild boar) from commercial breeder in southern Brazil and its relationship with *Ascaris suum*. *Parasitology Research* **112**, 1353–1356.

da Silva D and Müller G (2013b) Parasitic helminths of the digestive system of wild boars bred in captivity. *Revista Brasileira de Parasitologia Veterinária* **2**, 433–436.

de Jong YA, Butynski TM and d'Huart J-P (2016a) *Phacochoerus aethiopicus* (errata version published in 2016). *The IUCN Red List of Threatened Species* 2016: e.T41767A99376685. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41767A44140316.en. Accessed on 27 February 2019.

de Jong YA, Cumming D, d'Huart J and Butynski T (2016b) *Phacochoerus africanus* (errata version published in 2017). *The IUCN Red List of Threatened Species* 2016: e.T41768A109669842. http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T41768A44140445.en. Accessed on 19 February 2019.

Denegri G, Bernadinaz W, Perez-Serrano J and Rodriguez-Caabeiro F (1998) Anoplocephalid cestodes of veterinary and medical significance: a review. *Folia Parasitologica* **45**, 1–8.

d'Huart J and Reyna R (2016) *Hylochoerus meinertzhageni* (errata version published in 2016). *The IUCN Red List of Threatened Species* 2016: e.T41769A100471546. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41769A44140722.en. Accessed on 26 February 2019.

Duthy BL (1948) XXIV.—Three new nematodes of the genus *Oesophagostomum* from the East African wart-hog, *Phacochoerus aethiopicus*. *Journal of Natural History* **14**, 280–288.

Eslami A and Farsad-Hamdi S (1992) Helminth parasites of wild boar, *Sus scrofa*, in Iran. *Journal of Wildlife Diseases* **28**, 316–318.

Esrony K, Kambarage DM, Mtambo MMA, Muhairwa AP and Kusiluka LJM (1997) Helminthosis in local and cross-bred pigs in the Morogoro region of Tanzania. *Preventive Veterinary Medicine* **32**, 41–46.

Fabiyi JP (1979) Helminths of the pig on the Jos Plateau, Nigeria: relative prevalence, abundance and economic significance. *Journal of Helminthology* **53**, 65–71.

Foata J, Culioli JL and Marchand B (2005) Helminth fauna of wild boar in Corsica. *Acta Parasitologica* **50**, 168–170.

Foata J, Mouillot D, Culioli JL and Marchand B (2006) Influence of season and host age on wild boar parasites in Corsica using indicator species analysis. *Journal of Helminthology* **80**, 41–45.

Folstad I and Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *American Naturalist* **139**, 603–622.

Frantz L, Meijaard E, Gongora J, Haile J, Groenen MA and Larson G (2016) The evolution of Suidae. *Annual Review of Animal Biosciences* **4**, 61–85.

George- Nascimento M, Muñoz G, Marquet PA and Poulin R (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecology Letters* **7**, 527–531.

Gibbons LM, Durette-Desset MC and Daynes P (1977) A review of the genus *Impalaia* Mönnig, 1923 (Nematoda: Trichostrongyloidea). *Annales de Parasitologie Humaine et Comparée* **52**, 435–446.

Gongora J, Biondo C, Cooper JD, Taber A, Keuroghlian A, Altrichter M, do Nascimento FF, Chong AY, Miyaki CY, Bodmer R and Mayor P (2011a) Revisiting the species status of *Pecari maximus* van Roosmalen *et al*., 2007 (Mammalia) from the Brazilian Amazon. *Bonn Zoological Bulletin* **60**, 95–101.

Gongora J, Reyna-Hurtado R, Beck H, Taber A, Altrichter M and Keuroghlian A (2011b) *Pecari tajacu*. *The IUCN Red List of Threatened Species* 2011: e.T41777A10562361. http://dx.doi.org/10.2305/IUCN.UK.2011-2.RLTS.T41777A10562361.en. Accessed on 27 February 2019.

Grubb P and d'Huart J-P (2010) Rediscovery of the Cape warthog *Phacochoerus aethiopicus*: A review. *Journal of East African Natural History* **99**, 77–102.

Horak IG (1978) Parasites of domestic and wild animals in South Africa. VII. Helminths in pigs slaughtered at the Pretoria municipal abattoir. *Onderstepoort Journal of Veterinary Research* **45**, 43–48.

Horak IG, Biggs HC, Hanssen TS and Hanssen RE (1983) The prevalence of helminth and arthropod parasites of warthog, *Phacochoerus aethiopicus*, in South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research* **50**, 145–148.

Horak IG, Boomker J and Potgieter FT (1988) Parasites of domestic and wild animals in South Africa. XXIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus,* in the eastern Transvaal Lowveld. *Onderstepoort Journal of Veterinary Research* **55**, 145–152.

Humbert JF and Henry C (1989) Studies on the prevalence and the transmission of lung and stomach nematodes of the wild boar (*Sus scrofa*) in France. *Journal of Wildlife Diseases* **25**, 335–341.

Hudson P and Greenman J (1998) Competition mediated by parasites: biological and theoretical progress. *Trends in Ecology and Evolution* **13**, 387–390.

Hudson PJ, Rizzoli AP, Grenfell BT, Heesterbeek JAP and Dobson AP (2002) The ecology of wildlife diseases. Oxford Biology, Oxford, UK.

Inglis WG (1958) A redescription of the nematode *Paraspidodera sellsi* Morgan, 1927 and its removal to a new genus, *Morgascaridia*. *Journal of Helminthology* **32**, 65–72.

Iori A and Lanfranchi P (1996) Contribution to the knowledge of helminthofauna of wild mammals of Somalia. *Parassitologia* **38**, 511–515.

Järvis T, Kapel CH, Moks E, Talvik and H Mägi E (2007) Helminths of wild boar in the isolated population close to the northern border of its habitat area. *Veterinary Parasitolology* **150**, 366–369.

Keuroghlian A, Desbiez A, Reyna-Hurtado R, Altrichter M, Beck H, Taber A and Fragoso JMV (2013) *Tayassu pecari*. *The IUCN Red List of Threatened Species* 2013: e.T41778A44051115. http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T41778A44051115.en. Accessed on 27 February 2019.

Leroux PL (1940) On the division of the genus *Oesophagostomum* Molin, 1861, into subgenera and the creation of a new genus for the oesophagostomes of the wart-hog. *Journal of Helminthology* **18**, 1–20.

Leus K, Macdonald A, Burton J and Rejeki I (2016) *Babyrousa celebensis*. *The IUCN Red List of Threatened Species* 2016: e.T136446A44142964. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T136446A44142964.en. Accessed on 27 February 2019.

Macdonald AA, Burton J and Leus K (2008) *Babyrousa babyrussa*. *The IUCN Red List of Threatened Species* 2008: e.T2461A9441445. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T2461A9441445.en. Accessed on 27 February 2019.

Macdonald A, Leus K, Masaaki I and Burton J (2016) *Babyrousa togeanensis*. *The IUCN Red List of Threatened Species* 2016: e.T136472A44143172. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T136472A44143172.en. Accessed on 27 February 2019.

MacIntosh AJ, Hernandez AD and Huffman MA (2010) Host age, sex, and reproductive seasonality affect nematode parasitism in wild Japanese macaques. *Primates* 51, 353–364.

Magi M, Bertani, M, Dell'Omodarme M and Prati MC (2002). Epidemiological study of the intestinal helminths of wild boar (*Sus scrofa*) and mouflon (*Ovis gmelini musimon*) in central Italy. *Parassitologia* **44**, 203–205.

Malek EA (1971) The life cycle of *Gastrodiscus aegyptiacus* (Cobbold, 1876) Looss, 1896 (Trematoda: Paramphistomatidae: Gastrodiscinae*). Journal of Parasitology* **57**, 975–979.

Mansouri M, Sarkari B and Mowlavi GR (2016) Helminth parasites of wild boars, *Sus scrofa*, in Bushehr Province, Southwestern Iran. *Iranian Journal of Parasitology* **11**, 377–382.

McKenzie ME and Davidson WR (1989) Helminth parasites of intermingling axis deer, wild swine and domestic cattle from the island of Molokai, Hawaii. *Journal of Wildlife Diseases* **25**, 252–257.

Moore SL and Wilson K (2002) Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* **297**, 2015–2018.

Mucina L and Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, South Africa.

Mukaratirwa S, Munjere IF, Takawira M and Chingwena G (2004) Susceptibility of 7 freshwater gastropod species in Zimbabwe to infection with *Gastrodiscus aegyptiacus*

(Cobbold, 1876) Looss, 1896. *Journal of the South African Veterinary Association* **75**, 186–188.

Munro SA, Kaspe L, Sasmita R and Macdonald AA (1990) Gastrointestinal helminthosis in the babirusa (*Babyrousa babyrussa*) and response to albendazole. *Veterinary Record* **126**, 16 pp.

Nganga CJ, Karanja DN and Mutune MN (2008) The prevalence of gastrointestinal helminth infections in pigs in Kenya. *Tropical Animal Health and Production* **40**, 331–334.

Narayan G, Deka P and Oliver W (2008) *Porcula salvania*. *The IUCN Red List of Threatened Species* 2008: e.T21172A9254675. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T21172A9254675.en. Accessed on 26 February 2019.

Nissen S, Poulsen IH, Nejsum P, Olsen A, Roepstorff A, Rubaire-Akiiki C and Thamsborg SM (2011) Prevalence of gastrointestinal nematodes in growing pigs in Kabale District in Uganda. *Tropical Animal Health and Production* **43**, 567–572.

O'Connor LJ, Walkden-Brown SW and Kahn LP (2006) Ecology of the free-living stages of major trichostrongylid parasites of sheep. *Veterinary Parasitology* **142**, 1–15.

Oliver W and Leus K (2008) *Sus scrofa*. *The IUCN Red List of Threatened Species* 2008: e.T41775A10559847. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41775A10559847.en. Accessed on 27 February 2019.

Ortlepp RJ (1964) Observations on helminths parasitic in warthogs and bushpigs. *Onderstepoort Journal of Veterinary Research* **31**, 11–38.

Pence DB, Warren RJ and Ford CR (1988) Visceral helminth communities of an insular population of feral swine. *Journal of Wildlife Diseases* **24**, 105–112.

Permin A, Yelifari L, Bloch P, Steenhard N, Hansen NP and Nansen P (1999) Parasites in cross-bred pigs in the Upper East Region of Ghana. *Veterinary Parasitology* **87**, 63–71.

Poulin R (1996) Sexual inequalities in helminth infections: A cost of being a male? *American Naturalist* **147**, 287–295.

Radke R (1990) Die soziale Organisation des Warzenschweins (*Phachochoerus aethiopicus* Pallas). Inaugural-Dissertation zur Erlangung der Doktorwürde, Freie Universität Berlin, Berlin.

Rajković-Janje R, Bosnić S, Rimac D, Dragičević P and Vinković B (2002) Prevalence of helminths in wild boar from hunting grounds in eastern Croatia. *Zeitschrift für Jagdwissenschaft* **48**, 261–270.

Ransom BH (1907) *Probstmayria vivipara* (Probstmayr, 1865) Ransom, 1907, a nematode of horses heretofore unreported from the United States. *Transactions of the American Microscopical Society* **27**, 33–40.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reinecke RK (1983) Veterinary Helminthology. Durban/Pretoria: Butterworths.

Reyna R, Jori F, Querouil S and Leus K (2016) *Potamochoerus porcus* (errata version published in 2016). *The IUCN Red List of Threatened Species* 2016: e.T41771A100469961. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41771A44141118.en. Accessed on 26 February 2019.

Romero-Castañón S, Ferguson BG, Güiris D, González D, López S, Paredes A, Weber M (2008) Comparative parasitology of wild and domestic ungulates in the Selva Lacandona, Chiapas, Mexico. *Comparative Parasitology* **75**, 115–127.

Rossanigo CE and Gruner L (1995) Moisture and temperature requirements in faeces for the development of free-living stages of gastrointestinal nematodes of sheep, cattle and deer. *Journal of Helminthology* **69**, 357–362.

Round MC (1968) Check list of the helminth parasites of African mammals of the orders Carnivora, Tubulidentata, Proboscidea, Hyracoidea, Artiodactyla and Perossidactyla. Technical communication No. 38 of the Common Wealth Bureau of Helminthology, St Albans. Farnham Royal, UK: CAB.

Rudman M, Leslie AJ, van der Rijst M, Hoffman LC (2018). Quality characteristics of Warthog (*Phacochoerus africanus*) meat. *Meat Science* **145**, 266–272.

Samuel WM and Low WA (1970) Parasites of the collared peccary from Texas. *Journal of Wildlife Diseases* **6**, 16–23.

Sato H, Suzuki K and Yokoyama M (2008) Visceral helminths of wild boars (*Sus scrofa leucomystax*) in Japan, with special reference to a new species of the genus *Morgascaridia* Inglis, 1958 (Nematoda: Schneidernematidae). *Journal of Helminthology* **82**, 159–168.

Schuster R, Coetzee L and Putterill JF (2000) Oribatid mites (Acari, Oribatida) as intermediate hosts of tapeworms of the family Anoplocephalidae (Cestoda) and the transmission of *Moniezia expansa* cysticercoids in South Africa. *Onderstepoort Journal of Veterinary Research* **67**, 49–55.

Schuster RK, Wibbelt G and Kinne J (2014) A re-description of *Physocephalus dromedarii* stat. nov. (Nematoda: Spirocercidae), an abomasal nematode of dromedaries (*Camelus dromedarius*). *Journal of Helminthology* **88**, 499–505.

Schwartz B and Alicata JE (1933) Description of two parasitic nematodes from the Texas peccary. *Proceedings of the United States National Museum* **82**, 1–6.

Scialdo-Krecek RC (1983) Studies on the parasites of zebras. I. Nematodes of the Burchell's zebra in the Kruger National Park. *Onderstepoort Journal of Veterinary Research* **50**, 111–114.

Scialdo-Krecek RC, Reinecke RK and Biggs HC (1983) Studies on the parasites of zebras. III. Nematodes of the mountain zebra from the farm "Kelpie" and the Namib-Naukluft Park, South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research* **50**, 283–290.

Senlik B, Cirak VY, Girisgin O and Akyol CV (2011) Helminth infections of wild boars (*Sus scrofa*) in the Bursa province of Turkey. *Journal of Helminthology* **85**, 404–408.

Seydack AHW (2016) *Potamochoerus larvatus*. *The IUCN Red List of Threatened Species* 2016: e.T41770A44140926. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41770A44140926.en. Accessed on 26 February 2019.

Sinha S and Sharma BS (2009) Neurocysticercosis: a review of current status and management. *Journal of Clinical Neuroscience* **16**, 867–876.

Skinner JD and Chimimba CT (2005) The mammals of the southern African subregion, 3rd edn. Cape Town, South Africa: Cambridge University Press.

Solaymani-Mohammadi S, Mobedi I, Rezaian M, Massoud J, Mohebali M, Hooshyar H, Ashrafi K and Rokni MB (2003) Helminth parasites of the wild boar, *Sus scrofa*, in Luristan province, western Iran and their public health significance. *Journal of Helminthology* **7**, 263–267.

Somers MJ, Penzhorn BL and Rasa AE (1994) Home range size, range use and dispersal of warthogs in the eastern Cape, South Africa. *Journal of African Zoology* **108**, 361–374.

Somers MJ, Rasa OAE and Penzhorn BL (1995) Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. *Acta Theriologica* **40**, 257–282.

Stanko M, Fričová J, Miklisová D, Khokhlova IS and Krasnov BR (2015) Environment-related and host-related factors affecting the occurrence of lice on rodents in Central Europe. *Parasitology* **142**, 938–947.

Torchin ME, Lafferty KD and Kuris AM (2001) Release from parasites as natural enemies: Increased performance of a globally introduced marine crab. *Biological Invasions* **3**, 333–345.

Troncy PM, Graber M and Thal J (1973) Oesophagostominae des Suidés sauvages d'Afrique Centrale. *Bulletin du Muséum National d'Histoire Naturelle Zoologie* **184**, 1425–1450.

van den Berghe L (1943) Enquêtes parasitologiques. II. Helminthes parasites. Exploration du Parc national Albert et du Parc national de la Kagera. I. Mission L. van den Berghe (1936), Brussels, 2, pp. 30.

van Wyk IC and Boomker J (2011) Parasites of South African wildlife: XIX. The prevalence of helminths in some common antelopes, warthogs and a bushpig in the Limpopo province, South Africa. *Onderstepoort Journal of Veterinary Research* **78**, 1–11.

Widyarsi S (2011) Prevalence of gastrointestinal nematodes in babirusa (*Babyrousa babyrussa celebensis*) in Surabaya Zoo and Prigen Safari Park by fecal examination. PhD thesis, Universitas Airlangga.

Wilson DE and Reeder DAM (2005) Mammal species of the world. A taxonomic and geographic reference. Available at http://www.press.jhu.edu. Accessed on 20 February 2019.

Wirsing AJ, Azevedo FCC, Larivière S and Murray DL (2007) Patterns of gastrointestinal parasitism among five sympatric prairie carnivores: are males reservoirs? *Journal of Parasitology* **93**, 504–510.

Xiao L and Herd RP (1992) Infectivity of *Moniezia benedeni* and *Monieza expansa* to oribatid mites from Ohio and Georgia. *Veterinary Parasitology* **45**, 101–110.