Physalopterine nematodes in Australian reptiles: interactions and patterns of infection

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Abstract. Spirurid nematodes (family Physalopteridae) are widespread as adults or as encysted larvae in many species of Australian reptiles. Fifteen species of physalopterine nematodes (subfamily Physalopterinae) in the genera *Kreisiella*, *Abbreviata* and *Skrjabinoptera* infect more than 40 species of reptile in the five families Agamidae, Varanidae, Gekkonidae, Scincidae and Elapidae. Four species of nematode are host-species specific, six are host-family specific to varanid lizards, and three to agamid lizards. Larger species of reptile support a higher prevalence and abundance of nematodes, and often support multiple infections with more than one species, with the potential for interspecific competition. Geographic distribution of nematodes is partially limited by host distribution, and by climatic factors, mainly precipitation and temperature. There are strong positive and negative associations between several pairs of nematodes. Two species of nematode with the most pronounced muscular development at the anterior end, *Abbreviata tumidocapitis* and *Abbreviata glebopalmae*, only occur concurrently, and in low numbers, with species of nematode without these morphological features, suggesting differences in feeding in the hosts' stomachs. A combination of host specificity, geographic distribution and habitat, climatic factors and feeding organ morphology are factors that probably reduce the potential for interspecific competition. There is no evidence that concurrent infections affect either prevalence or abundance of nematodes, or cause discernible pathological changes to their hosts.

Introduction

Spirurid nematodes in the subfamily Physalopterinae are the predominant gastric nematodes in the Australian reptile families Varanidae (monitor lizards), Agamidae (dragon lizards), Scincidae (skinks), Gekkonidae (geckos) and Elapidae (venomous snakes). Adult nematodes in the genera *Abbreviata* and *Skrjabinoptera* occur primarily in larger reptiles, in particular in drier and hotter areas of Australia, and nematodes in the genus *Kreisiella* occur in smaller skinks and agamids (Jones 1983*a*, 1983*b*, 1985*b*, 1986, 1988, 2005, 2007*b*). The anterior ends of physalopterine nematodes possess two lateral lips that border the dorso-ventrally elongate mouth, each lip bearing two sessile papillae and an amphid on the external surface, and denticles on the medial surface of each lip, whose number, size and disposal are important features in identification (Fig. 1). In four species, the anterior end of the muscular oesophagus is enlarged, with the development of accessory musculature. Physalopterine nematodes require an arthropod intermediate host (Anderson 2000), and in Australia one species of *Abbreviata* (*A. antarctica*) has been shown to develop in the tropical cricket, *Teleogryllus oceanicus* (King *et al.* 2013). Many smaller species of reptile, especially of skinks and geckos, act as paratenic hosts to physalopterine larvae (Jones 1995*c*, 2010). At least 15 species of adult nematode (12 species of *Abbreviata*, two of *Kreisiella* and

one *Skrjabinoptera*) occur commonly within these reptile families. Infection prevalence in the larger species of lizards may be close to 100% (e.g. in *Varanus giganteus*, *V. tristis* and *V. rosenbergi*: Jones 1985*b*, 1995*b*, 2005), with intensity of several hundred worms (including larvae), and there may be significant concurrent infection with more than one species. These nematodes vary in their geographical range across the continent, as well as in their prevalence and abundance in different host species and in different habitats and parts of their ranges. Varanid lizards are active predatory species, feeding principally on a range of arthropods, especially orthopterans (James *et al.* 1992); larger species may consume many species of smaller lizards (Pianka 1994). Agamid lizards, on the other hand, primarily use 'sit and wait' tactics, and their diet also comprises arthropods, and small lizards (Pianka 1986). Little is known of life expectancy in the wild; *V. rosenbergi* may live to more than six years, and in captivity *V. gouldii* may live for at least seven years (King and Green 1999). *Physignathus lesueurii* has been recorded to live for 14 years (Hay 1972), and for *Tiliqua rugosa* an age of 20 years has been estimated (Holmes and Light 1983).

Interactions between nematodes in the gastrointestinal organs of their vertebrate hosts have been extensively studied (Quinnell *et al.* 1990; Hatcher and Dunn 2011), revealing a wide range of
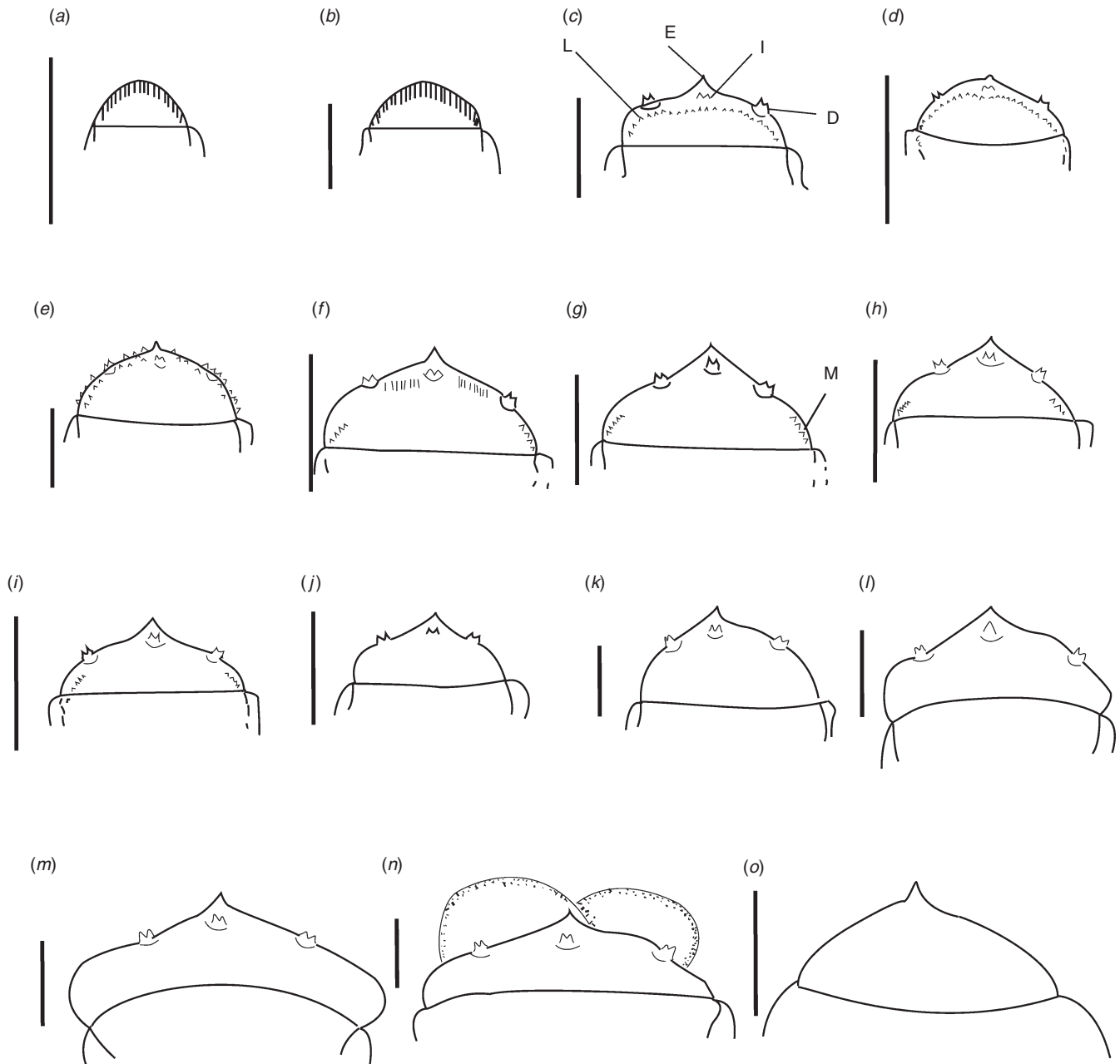
Fig. 1. Anterior end, lateral view of 15 species of physalopterine nematode. (*a*) *Kreisiella chrysocampa*; (*b*) *K. lesueurii*; (*c*) *Abbreviata pilbarensis*; (*d*) *A. anomala*; (*e*) *A. physignathi*; (*f*) *A. kimberleyensis*; (*g*) *A. antarctica*; (*h*) *A. bancrofti*; (*i*) *A. hastaspicula*; (*j*) *A. perenticola*; (*k*) *A. levicauda*; (*l*) *A. barrowi*; (*m*) *A. gleboplama*; (*n*) *A. tumidocapitis* (anterior end of oesophagus partly extruded); (*o*) *Skrjabinoptera goldmanae* (oesophagus withdrawn). E, externolateral apical tooth; I, internolateral tooth; D, doubled submedial lateral teeth; L, internal lip margin; M, mouth corner denticles. Scale bars = 100 μm.

host–parasite relationships, and there is unlikely to be a single explanation for all forms of parasite interactions within a host. Broader patterns of infection are not evident from studies focussed on a single genus or species of reptile host. In the present study, therefore, I bring together data from many studies, cited above and subsequently, to search for patterns in the populations of gastric nematodes. As physalopterine nematodes are abundant in these reptile hosts, and concurrent infections, and infections with multiple species in different habitats or regions, are widespread, a key question is whether competition has a role in shaping these communities. I address this question by examining various parameters, in particular host specificity, geographical distribution, host habitat and methods of feeding deduced from their mouthparts, which may mitigate interspecific competition. From this, I deduce the relevance of competition in the dynamics of these nematode populations.

Materials and methods

Material examined

I dissected a total of 2390 preserved lizards and snakes of 65 species held in The Australian Museum, Northern Territory Museum, Queensland Museum, Tasmanian Museum in Hobart, the Queen Victoria Museum in Launceston, Museum Victoria, the Western Australian Museum, and in collections held by CSIRO in Canberra. All reptiles had been collected in the field in their natural habitats, over a period of many years. In addition, I identified nematodes collected by other workers, in particular the late Dennis King, in the course of their own research, and examined more than 3000 stomachs from 45 species of lizard from the Great Victoria Desert collected E. R. Pianka. These have been published in a series of papers. Data collected and not published have been used (e.g. concurrent infections, host size), and I include previously unpublished data from another 40 *Varanus gouldii* and 10 *V. panoptes*, mostly from Victoria and Queensland, and 76 *V. acanthurus*. I also examined specimens of *Abbreviata* in the Australian Helminth Collection held in the South Australian Museum, Adelaide. The published papers and these previously unpublished data form the basis for the present study. In total, reptiles from the following host families were examined: Acrochordidae, Agamidae, Colubridae, Elapidae, Gekkonidae, Pythonidae, Scincidae, Typhlopidae, and Varanidae.

Methods

Helminths were removed, cleaned and identified. The number of hosts examined was compared with the number of species of nematode recovered from each host species. Host specimens were measured in millimetres, and their food residues noted. All snout–vent lengths (SVL) are those of the reptiles examined. Histological sections of nematodes attached to host stomach wall and cut at 5 or 6 μm, were prepared and stained with haematoxylin and eosin in order to determine host reactions.

Statistical methods

Regression analyses were run on StatPlus for Macintosh (AnalystSoft) and were used to investigate relationships between prevalence, abundance and host size across species. Chi-square tests (2×2) were run on GraphPad QuickCalcs online calculator, and were used to analyse pair-wise associations between nematodes across hosts.

Ecological terms

These follow the definitions of Bush *et al*. (1997). Prevalence refers to the number of hosts infected with one or more individuals of a particular parasite, expressed as a percentage. Intensity refers to the number of individuals of a particular parasite species in a single infected host. Abundance refers to the number of individuals of a particular parasite present in a single infected host, expressed as a mean across all specimens of that host species. For those host species with more than one nematode species present, the combined prevalence was calculated as the percentage of specimens of that species that were infected with one or more species of physalopterine nematode. Likewise, the combined abundance mean was calculated by the total number of physalopterine worms in specimens of that species, divided by the number of host specimens surveyed.

Examples of all nematode species in this study have been re-examined to confirm previous descriptions. Not infrequently, reptiles infected by a dominant species also harboured one or two adult or immature nematodes of related species. Spurious infections can also occur from nematodes ingested in their prey, and for these reasons data from hosts with few worms and low prevalence (generally <3%) have not been considered.

Results

Physalopterine nematodes recovered

Fifteen species of nematode belonging to three genera in the subfamily Physalopterinae were recovered: *Kreisiella chrysocampa*, *K. lesueurii*, *Abbreviata anomala*, *A. antarctica*, *A. bancrofti* (of which *A. confusa* is a junior synonym: Jones 2013*b*), *A. barrowi*, *A. glebopalmae*, *A. hastaspicula*, *A. kimberleyensis*, *A. levicauda*, *A. perenticola*, *A. physignathi*, *A. pilbarensis*, *A. tumidocapitis*, and *Skrjabinoptera goldmanae*. These infected 45 species of lizard in the families Scincidae, Gekkonidae, Agamidae and Varanidae (subgenera *Varanus* and *Odatria*), and 10 species of snakes in the family Elapidae.

Host-specificity (Table 1, Fig. 2)

Specificity varied from one to 21 host species. Ten species of nematode were host-family specific, of which four (*A. physignathi*, *A. glebopalmae*, *A. perenticola* and *A. barrowi*) were host-species-specific. The two species of *Kreisiella* were recovered only from smaller skinks and agamids, and *S. goldmanae* predominantly from agamid lizards.

Infection patterns: single-species infections (Table 2)

Thirty species of reptile, principally smaller species, supported infections with a single species of gastric nematode. Within Scincidae, the four smallest lizard species with adult nematode infection supported only *Kreisiella* spp., and in the four larger skink species, only *A. antarctica* was recorded. Within Gekkonidae four species of leaf-tailed geckos (*Saltuarius cornutus*, *S. swaini*, *S.moritzi* and *Phyllurus platurus*) supported infection with *Abbreviata bancrofti* only. Six species of Agamidae also supported a single nematode species: *Kreisiella* species occurred in the three smallest agamid lizards, *A. antarctica* in two species of *Pogona*, and the host-species-specific *A. physignathi* in the water dragon *Physignathus lesueurii*. Five species of smaller Varanidae (subgenus *Odatria*) supported single-species infections of *A. hastaspicula* (three host species), and *A. levicauda* (two host species). The larger *V.* (*O.*) *scalaris* supported *A. bancrofti* only. *Abbreviata antarctica* occurred in all host families except Gekkonidae, *A. hastaspicula* occurred in several species of Varanidae, and *A. bancrofti* in Varanidae, Gekkonidae and Elapidae. With the exception of *V. giganteus*, which supported only the host-specific *A. perenticola*, single-species infections occurred predominantly in smaller lizards, usually at low mean abundance and prevalence and, except in the largest hosts, at low prevalence. Nematodes in the two largest hosts to support a single species infection, *A. perenticola* in *V. giganteus* and *A. physignathi* in *P. lesueurii*,

Table 1. **Host specificity of 15 nematodes of the genera *Abbreviata*, *Kreisiella* and *Skrjabinoptera* in 45 species of reptile belonging to the families Scincidae, Agamidae, Gekkonidae, Varanidae and Elapidae**

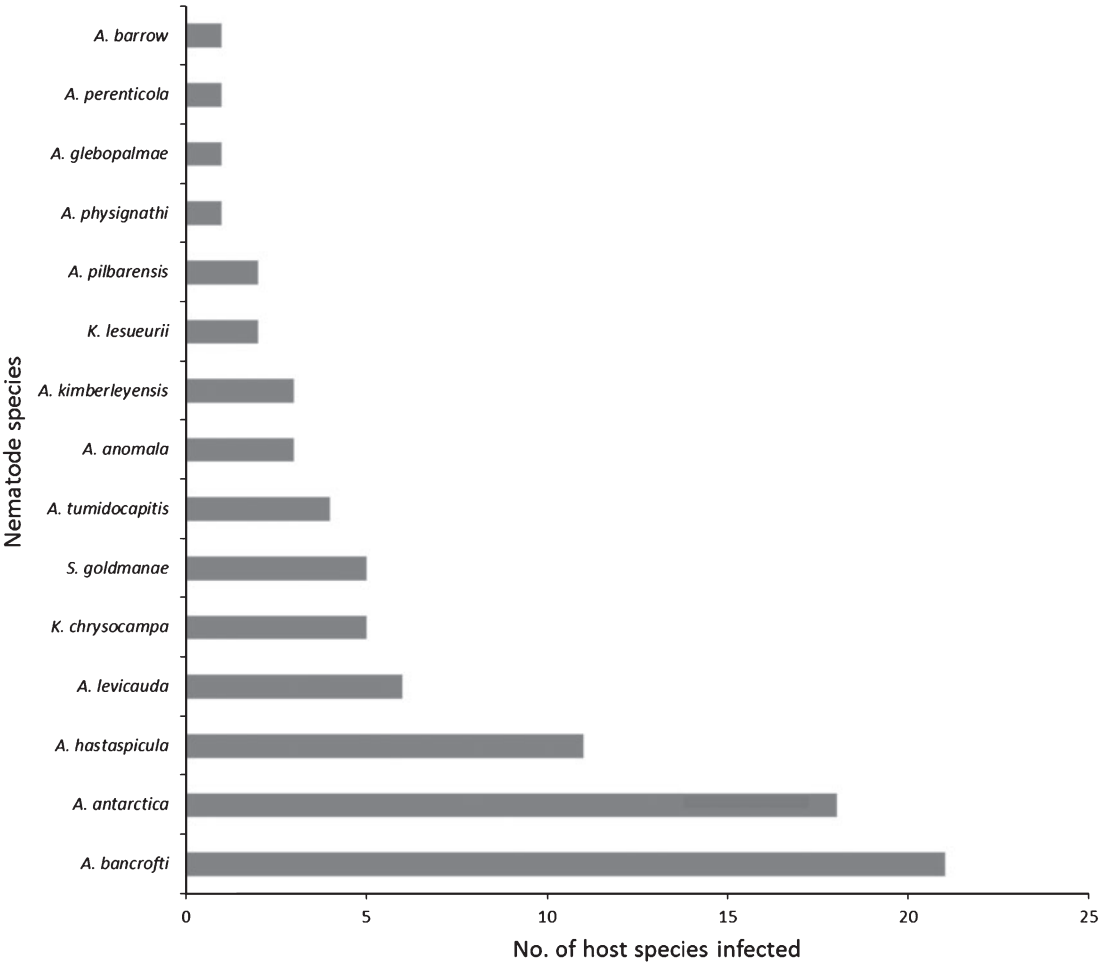| Nematode species	Scincidae	Agamidae	Gekkonidae	Varanidae	Elapidae
K. chrysocampa	3	2	0	0	0
K. lesueurii	1	1	0	0	0
A. physignathi	0	1	0	0	0
A. pilbarensis	0	2	0	0	0
A. anomala	0	3	0	0	0
A. antarctica	4	3	0	5	6
A. glebopalmae	0	0	0	1	0
A. perenticola	0	0	0	1	0
A. kimberleyensis	0	0	0	3	0
A. tumidocapitis	0	0	0	4	0
A. levicauda	0	0	0	6	0
A. bancrofti	0	0	4	7	10
A. hastaspicula	0	0	0	11	0
A. barrowi	0	0	0	0	1
S. goldmanae	0	4	0	1	0
Total nematode species per host family	3	7	1	9	3

Fig. 2. Host-specificity of 15 species of physalopterine nematodes in the genera *Abbreviata* (*A*), *Kreisiella* (*K*), *Skrjabinoptera* (*S*).

Table 2.   Reptile species ($N = 30$) in the families Scincidae, Agamidae, Gekkonidae, Varanidae and Elapidae infected by a single species of nematode in the genera *Abbreviata*, *Kreisiella* and *Skrjabinoptera*, ranked by host family

SVL, snout–vent length (in millimetres)

Host	Number	Mean SVL	Nematode spp.	Prevalence (%)
Scincidae[A]				
Ctenotus brooksi	6	42	*K. chrysocampa*	17
C. dux	124	50	*K. chrysocampa*	11
Egernia inornata	54	76	*K. chrysocampa*	49
Cyclodomorphus branchialis	41	95	*K. lesueurii*	7
Lissolepis luctuosus	39	119	*A. antarctica*	51
Tiliqua multifasciata	30	220	*A. antarctica*	7
T. occipitalis	29	256	*A. antarctica*	79
T. rugosa	23	258	*A. antarctica*	35
Agamidae				
Tympanocryptis diemensis	9	75	*Kreisiella* sp.	11
Lophognathus longirostris	27	76	*K. chrysocampa*	7
Amphibolurus norrisi	20	110	*K. lesueurii*	8
Pogona microlepidotra	9	154	*A. antarctica*	23
P. vitticeps	20	200	*A. antarctica*	30
Physignathus lesueurii	58	207	*A. physignathi*	48
Gekkonidae				
Phyllurus platurus	37	83	*A. bancrofti*	13
Saltuarius moritzi	4	99	*A. bancrofti*	25
S. cornutus	8	129	*A. bancrofti*	62
S. swaini	16	120	*A. bancrofti*	12.5
Varanidae				
Varanus brevicauda	50	93	*A. hastaspicula*	50
V. kingorum	9	93	*A. hastaspicula*	22
V. caudolineatus	40	102	*A. levicauda*	2.5
V. storri	22	108	*A. hastaspicula*	32
V. pilbarensis	24	140	*A. levicauda*	46
V. scalaris	33	183	*A. bancrofti*	23
V. giganteus	13	379	*A. perenticola*	85
Elapidae[A,B]				
Denisonia fasciata	16		*A. antarctica*	12
Drysdalia coronata	22		*A. antarctica*	18
Echiopsis curta	12		*A. antarctica*	8
Notechis ater	23		*A. antarctica*	9
Austrelaps superbus	17		*A. antarctica*	6

[A]The skinks *C. orientalis* and *Morethia obscura* and the snake *Drysdalia coronata* also contained a single *Kreisiella* sp. (Watharow and Jones 2009).

[B]See Discussion for *A. bancrofti* in elapid snakes.

were both host-species specific. Five species of snake in the family Elapidae were host to *A. antarctica* only.

Multiple-species infections

Three species of agamid lizard, eleven species of varanid lizard, and one elapid snake supported infections with 2–6 species of physalopterine nematode. Within Varanidae, species supporting more than a single nematode species were larger (mean SVL 125–474 mm) than those with single-species infections (mean SVL 93–140), apart from *V. (O.) scalaris* (mean SVL 183 mm) and *V. giganteus* (mean SVL 379 mm). Larger lizards supported a higher prevalence and abundance of nematodes; prevalence of *A. kimberleyensis* in *V. glebopalma* and *A. antarctica* in *V. rosenbergi* were higher than 90% (Table 3). Abundance of adult *Abbeviata* spp. in *V. rosenbergi* was 59 per host, and 109 in *V. gouldii*. There was no obvious relationship between number of nematode species infecting one host species, and host specificity

or habitat, nor were there discernible relationships between prevalence, intensity, and concurrent infections (Jones 1983*b*, 2005).

Infection and host size, single and multiple infections

Prevalence ($r = 0.5945$, $P < 0.001$) and abundance ($r = 0.7606$, $P < 0.0005$) (Fig. 3) were both positively associated with increasing host size across species. Within species, there were positive associations between increasing host size and prevalence of infection with *A. hastaspicula* in *V. gouldii* ($r = 0.35$; $P < 0.05$) and in *V. panoptes* ($r = 0.76$; $P < 0.01$).

There was a positive relationship between host size, and multiple infections ($r = 0.0399$; $P < 0.05$). The sample size for each host species, and the number of species of nematode recovered from each host species were also related ($r = 0.505$; $P < 0.001$).

Table 3.   Principal host species for each species of nematode, with host habitat and range
Host data are from Cogger (2014)

| Nematode species	Principal host species	SVL (mm)	Prevalence (%)	Host habitat and range
Kreisiella chrysocampa	*Egernia inornata*	76	51	Arid hot habitats; wide distribution
K. lesueurii	*Pogona minor*	112	12	Semiarboreal, dunes, arid scrub
Abbreviata anomala	*P. minor*	112	12	Semiarboreal, dunes, arid scrub
A. pilbarensis	*P. mitchelli*	127	26	Dry woodlands and scrub; northern
A. bancrofti	*Varanus glauerti*	198	77	Rock-inhabiting; Kimberley
A. bancrofti	*V. varius*	474	43	Arboreal; eastern Australia
A. physignathi	*Physignathus lesueurii*	207	48	Semiaquatic, arboreal; eastern Australia
A. levicauda	*V. tristis*	240	73	Mainly arboreal; most of Australia except south
A. levicauda	*V. pilbarensis*	140	46	Rock-dwelling; Pilbara
A. glebopalmae	*V. glebopalma*	306	43	Rocky outcrops: tropical northern Australia
A. kimberleyensis	*V. glebopalma*	306	92	Rocky outcrops; tropical northern Australia
A. kimberleyensis	*V. glauerti*	198	43	Rock-inhabiting; Kimberley
A. hastaspicula	*V. gouldii*	308	71	Ground-dwelling; all Australia except SE and NE
A. hastaspicula	*V. spenceri*	360	82	Ground-dwelling; black soil country, NT and W Queensland
A. antarctica	*V. rosenbergi*	352	93	Terrestrial; coastal heaths and forests, S Australia
A. perenticola	*V. giganteus*	379	85	Arid interior of Australia
A. tumidocapitis	*V. rosenbergi*	352	25	Terrestrial; coastal heaths and forests, S Australia
A. barrowi	*Pseudechis australis*	–	58	Wide range of habitats; most of Australia
Skrjabinoptera goldmanae	*P. mitchelli*	127	66	Dry woodland and arid scrub, tropical north to SE Queensland
S. goldmanae	*Chlamydosaurus kingii*	202	50	Arboreal, dry woodland, tropical north to SE Queensland
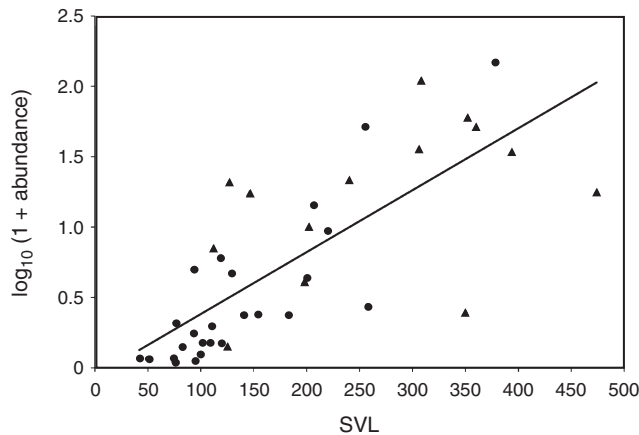
Fig. 3.   Abundance of infection with physalopterine nematodes and host size in millimetres (SVL) in 40 species of lizard. ●, single-species infections; ▲, multiple-species infections.

Fig. 4.   Distribution of *Abbreviata levicauda.* Dotted line represents the 400-mm average annual precipitation. Scale bar = 800 km.

Geographical distribution and environment (Figs 4–14)

The geographical distribution of nematodes is limited to the geographical range of their hosts, and falls into several patterns. *Abbreviata levicauda*, *A. tumidocapitis*, *A. pilbarensis* (Figs 4–6) *and A. perenticola* (Fig. 12) occur almost exclusively in drier central regions where the annual average rainfall is less than 400 mm. *Abbreviata anomala*, *A. hastaspicula*, and *S. goldmanae* (Figs 6–8) also occur in central drier areas and extend into the northern tropics with a mean annual temperature of >18°C. *Abbreviata bancrofti* (Fig. 10) is found predominantly in coastal, south and east, and northern tropical areas with higher rainfall. *Abbreviata antarctica* (Fig. 9) occurs across a wider temperature range than any other species, and is the only species of *Abbreviata* found south of the continent, on Flinders Island, and, at generally
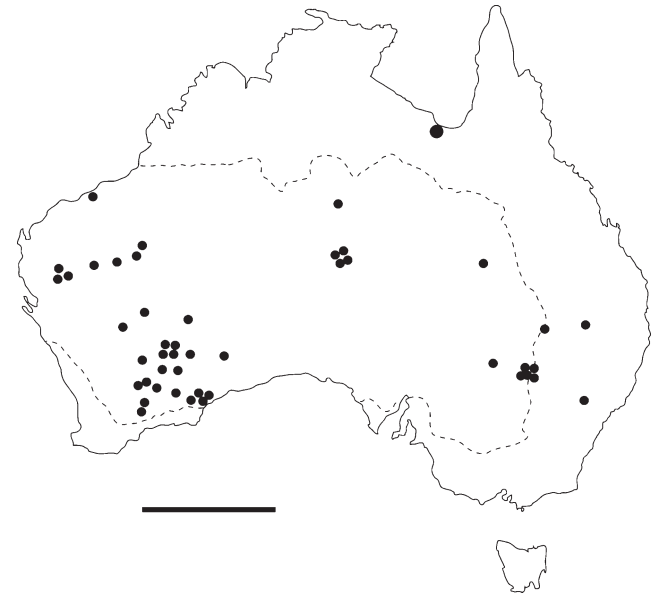
lower prevalence and intensity, in the tropical north in the lizards *V. acanthurus* and *V. glebopalma* (Jones 1988). *Abbreviata kimberleyensis* and *A. glebopalmae* are confined to the localised distribution of their hosts *V. glebopalma* and *V. glauerti* in the Kimberley and tropical Northern Territory with a mean precipitation >600 mm and mean annual temperatures of 21–33°C (Figs 11, 12). *Abbreviata physignathi* in *Physignathus lesueurii* occurs near the east coast (Fig. 12), and *A. barrowi* occurs in western areas of Western Australia (Fig. 13). *Kreisiella chrysocampa* and *K. lesueurii* appear to have a wide distribution,
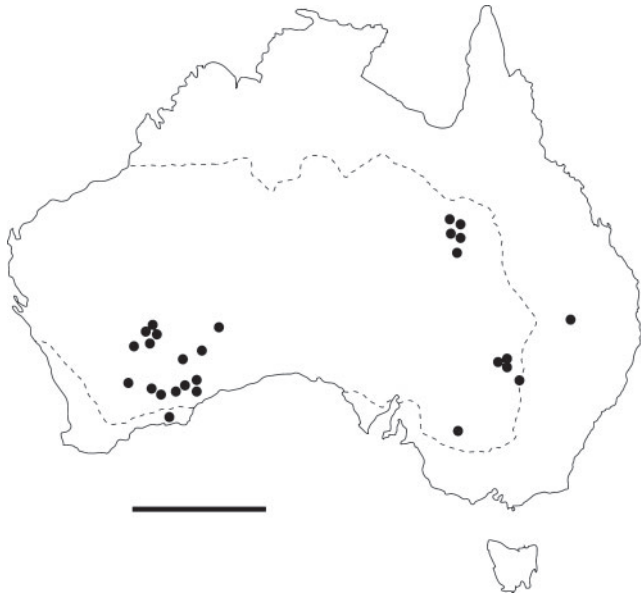
Fig. 5. Distribution of *Abbreviata tumidocapitis.* Dotted line represents the 400-mm average annual precipitation. Scale bar = 800 km.
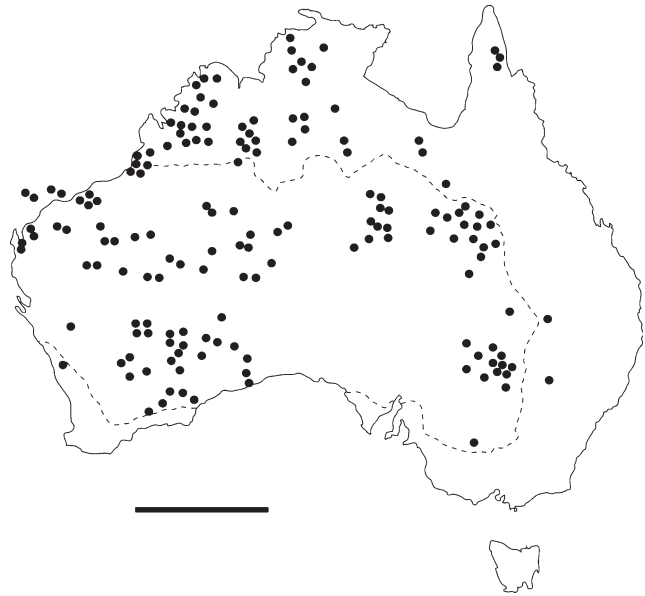

Fig. 7. Distribution of *Abbreviata hastaspicula.* Dotted line represents the 400-mm average annual precipitation. Scale bar = 800 km.
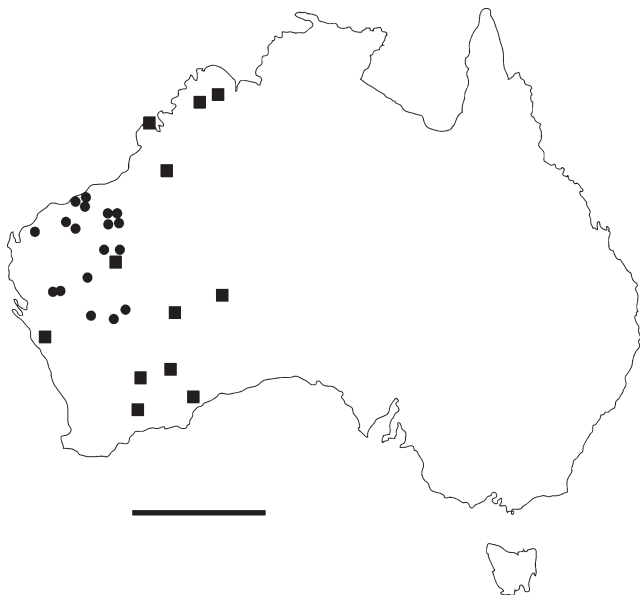

Fig. 6. Distributions of *Abbreviata pilbarensis* (●) and *Abbreviata anomala* (■). Scale bar = 800 km.

Fig. 8. Distribution of *Skrjabinoptera goldmanae.* Dotted line represents the 400-mm average annual precipitation. Scale bar = 800 km.

from Tasmania to the Great Victoria Desert and the tropical north (Fig. 14); owing to their presence as immature worms, or their poor condition, the two species could not always be differentiated from one another.

However, several species of lizards in the families Varanidae and Agamidae, and the snake *Pseudechis australis*, have wide ranges across the continent; and thus there are potentially wide areas of sympatry of their nematodes: *V. gouldii*, *V. rosenbergi*, *V. tristis* and *P. minor* are host to five or six species of nematode.

By contrast, hosts with a more restricted range (*V. pilbarensis* in the Pilbara and *V. glauerti* in the Kimberley) are host to one and two nematode species respectively.

Concurrent infections

There were both strong positive and negative associations between pairs of nematode species. The presence of *Abbreviata levicauda* and *A. hastaspicula* were positively associated
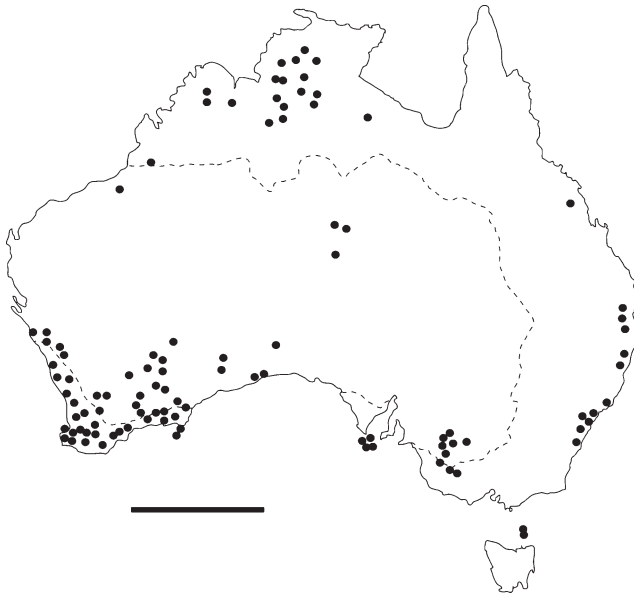
Fig. 9. Distribution of *Abbreviata antarctica*. Dotted line represents the 400-mm average annual precipitation. Scale bar = 800 km.

Fig. 10. Distribution of *Abbreviata bancrofti*. Dotted line represents the 400-mm average annual precipitation. Scale bar = 800 km.

Fig. 11. Distribution of *Abbreviata kimberleyensis* in *Varanus glauerti*, *V. glebopalma*, and *V. tristis*. Dotted line represents the 600-mm average annual rainfall. Scale bar = 800 km.
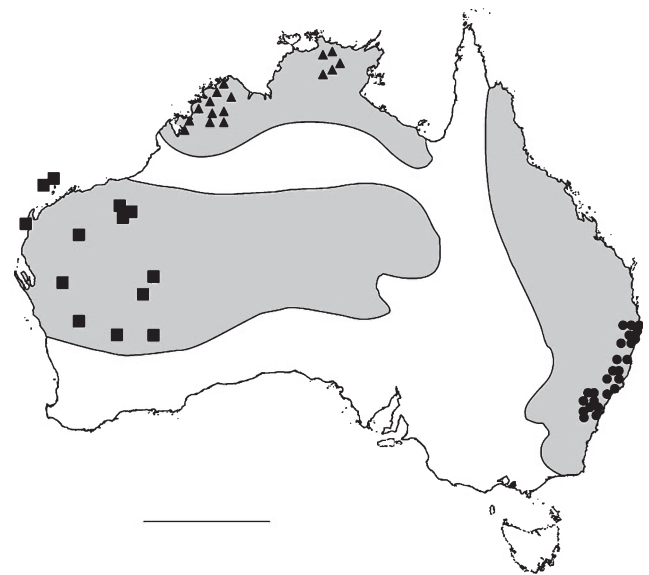

Fig. 12. Distribution of three host-species-specific species of nematode: ●, *Abbreviata physignathi* in *Physignathus lesueurii*; ▲, *Abbreviata glebopalmae* in *Varanus glebopalma*; ■, *Abbreviata perenticola* in *Varanus giganteus*. Shaded area indicates approximate distribution of the host species (from Cogger 2014). Scale bar = 800 km.

($P < 0.0001$) and both these species were strongly positively associated with *A. tumidocapitis* ($P < 0.0001$). *Skrjabinoptera goldmanae* and *A. pilbarensis* were also positively associated ($P = 0.0238$), and all infections with *A. glebopalmae* occurred with *A. kimberleyensis*. There were strong negative associations between *A. antarctica* and *A. bancrofti* ($P = 0.0129$), *A. antarctica* and *A. levicauda* ($P < 0.0001$) and *A. antarctica* and *A. hastaspicula* ($P < 0.0001$), and between *A. bancrofti* and *A. levicauda* ($P < 0.0001$), and *A. bancrofti* and *A. hastaspicula* ($P = 0.0101$), and between *A. hastaspicula* and *A. kimberleyensis*

($P < 0.0001$). There were no significant associations between *S. goldmanae* and *A. anomala*, *A. antarctica* and *A. kimberleyensis*, *A. bancrofti* and *A. kimberleyensis* or *A. antarctica* and *A. tumidocapitis*.

Principal host species (Table 3)

Each species of nematode predominated in one or two host species, at prevalences between 12.5% and 98% (mean 55%). Principal host species occupied a wide range of habitats across
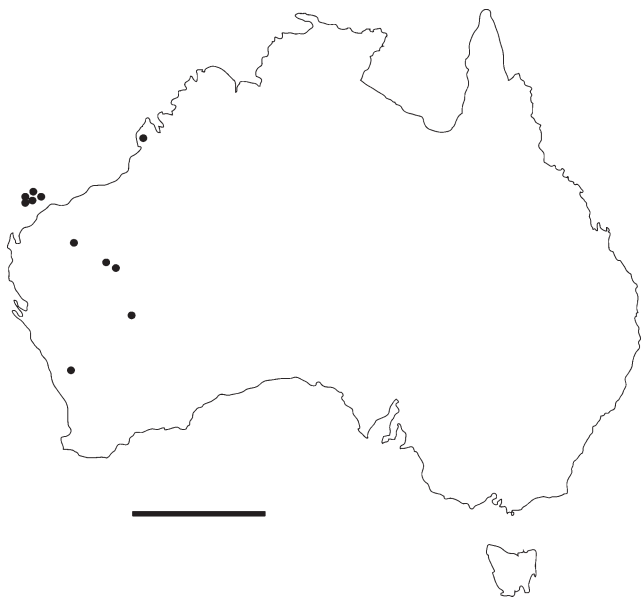
Fig. 13.   Distribution of *Abbreviata barrowi.* Scale bar = 800 km.
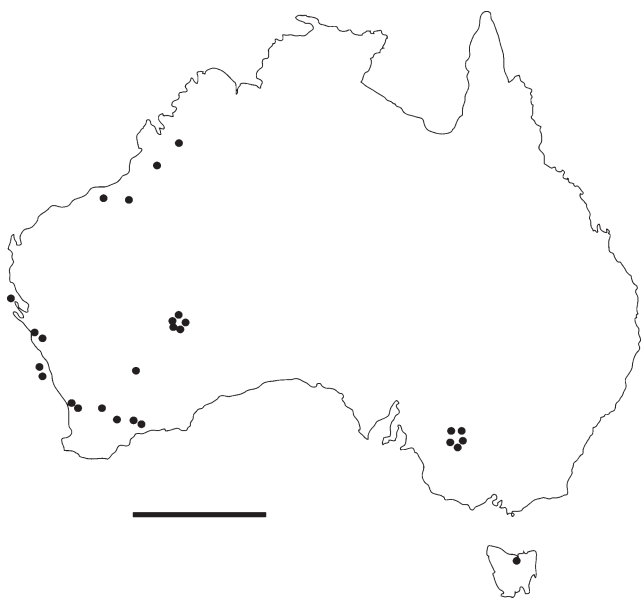

Fig. 14.   Distribution of *Kreisiella* spp. (*K. chrysocampa* and *K. lesueurii*). Immature specimens, which cannot be identified to species, are included. Scale bar = 800 km.

the continent. *Abbreviata levicauda* occurred predominantly in *V. tristis* and *V. pilbarensis*, which occupy different habitats (*V. tristis* being largely arboreal and *V. pilbarensis* being rock-dwelling in the Pilbara). *Abbreviata bancrofti* occurred predominantly in *V. glauerti* and *V. varius*, which also occupy different habitats, and which are allopatric. *Abbreviata hastaspicula*, *A. levicauda*, *A. kimberleyensis*, *A. perenticola*, *A. glebopalmae* and *A. tumidocapitis* were recovered only from varanid lizards; the latter two species always occurred at considerably lower prevalence and intensity than co-occurring

species of parasite. Both *A. bancrofti* and *A. antarctica* have been recovered from many species of reptile in the three and four families respectively of the five families under consideration. *Abbreviata anomala*, *A. pilbarensis* and *A. physignathi* occurred exclusively in agamid lizards, and *Kreisiella* species occurred in skinks and the smaller agamids. *Abbreviata barrowi* was found in elapid snakes, and *S. goldmanae* occurred principally, but not exclusively, in agamid lizards.

Morphology of the anterior end of nematodes (Fig. 1)

The morphology of the anterior end of *A. antarctica*, *A. bancrofti*, *A. levicauda*, *A. hastaspicula* and *A. perenticola* conforms to the basic pattern for this genus, with a large single externolateral and a smaller (usually bifid) internolateral apical tooth, and doubled submedian teeth at the dorsal and ventral lip margin. Mouth corner denticles are present in *A. antarctica*, *A. bancrofti*, and *A. kimberleyensis*, are inconsistent in *A. hastaspicula*, and absent in *A. levicauda*. *Abbreviata kimberleyensis* bears in addition a row of very fine denticles along the lip margin. *Abbreviata anomala*, *A. pilbarensis* and *A. physignathi* bear a row of denticles along the lip margin; the doubled denticles at the dorsal and ventral lip margins are distinguishable from this row, which are small in the first two, and large in *A. physignathi*. In *K. chrysocampa* and *K. lesueurii* the relatively narrow mouth dorso-ventrally is surrounded by a row of small even teeth from which apical denticles cannot be distinguished. The four remaining species are characterised by various degrees of anterior end enlargement. This is least pronounced in *A. barrowi*, is more pronounced in *A. glebopalmae* and *A. tumidocapitis*, and is most extreme in *S. goldmanae*. None of the four species with cephalic muscular enlargement possess mouth corner denticles.

Discussion

Arid-zone Australia has a richer reptile fauna than any other comparable region of the world (Pianka 1986), and this study reveals patterns in the specificity, morphology, and distribution of their gastric nematodes.

Reptile families infected

Adult physalopterine nematodes in the three genera *Kreisiella*, *Abbreviata* and *Skrjabinoptera* are the predominant or exclusive gastric nematodes of reptiles in the families Scincidae (Jones 1985a, 1992a; Jones and Watharow 2010), Varanidae (Johnston and Mawson 1947; Jones 1983a, 1983b, 1985b, 1988, 1992b, 1995b, 2005, 2007b, 2010, 2013c), Agamidae (Baylis 1924; Jones 1986, 1994; 1995a, 2007a), Gekkonidae (Jones 2013a, 2013b), and Elapidae (Johnston and Mawson 1942a, 1942b, 1951; Jones 1978a) (Tables 2, 3). All large species in the four families of lizards that have been studied are host to adult nematodes in one or more of these genera. Adult physalopterine nematodes are infrequent or absent in Typhlopidae (10 *Rhamphotyphlops pinguis* examined) Acrochordidae (12 *Acrocordus* spp. examined), and Colubridae (eight species, 62 individuals examined) (Jones 1978b and unpublished). However, *A. bancrofti* has recently been identified from the colubrid snakes *Stegonotus cucullatus* and *Tropidonophis mairii* in the Northern Territory (D. Barton, unpublished). *Python spilotes* was recorded as host to species of *Abbreviata* from various sites, mainly in

southern and eastern Australia, but I cannot ascertain whether reports of *Abbreviata* spp. from seven species of pythons (Johnston and Mawson 1948; Thomas 1959; Jones 1979, 1980) were genuine infections or spurious infections from ingested prey.

Three other species of gastric nematodes may occur in significant numbers in some of these five families of Australian reptiles. *Tanqua anomala* (Spirurida : Gnathostomatoidea) is found in aquatic snakes and in species of *Varanus* occupying aquatic or coastal habitats in northern Australia (Johnston and Mawson 1948; Jones 1988, 2004; Dewi *et al.* 2008). *Physalopteroides filicauda* (Spirurida : Thubunaeinae) occurs almost exclusively in smaller lizards, principally skinks (often concurrently with *Kreisiella* spp.) and geckos (Jones 1985*a*, 1995*b*; Goldberg and Bursey 2012), in which species of *Abbreviata* occur as encysted third-stage larvae (Jones 1995*b*). *Ophidascaris pyrrhus* (Ascaridida) occurs in many species of elapid snakes (Johnston and Mawson 1942*a*, 1948; Jones 1980; Sprent 1988).

Host-specificity

There is a wide range in the host-specificity of physalopterine nematodes. The two species of *Kreisiella* – *K. chrysocampa* and *K. lesueurii* – occur only in skinks and agamids, and they are found infrequently in the same hosts as adult *Abbreviata.* Nematodes in the genus *Abbreviata* in the subfamily Physalopterinae are closely related (Chabaud 1975), and more than one nematode species may occur in more than one host species. Six species of *Abbreviata* are specific to Varanidae, and have not been recorded outside Australia. Two of these species (*A. glebopalmae* and *A. perenticola*) are host-specific. (I reviewed the nematodes from *V. giganteus* identified as *A. confusa* by Johnston and Mawson (1947) and identified them as *A. perenticola* (Jones, unpublished)). Three nematode species (*A. anomala*, *A. pilbarensis* and *A. physignathi*) are found only in the family Agamidae. *Abbreviata antarctica* occurs in at least 18 species in four host families, and *A. bancrofti* in 21 species in three host families, including several species of elapid snakes (Johnston and Mawson 1942*a*, 1942*b*, 1948, 1951), Varanidae and Gekkonidae (Johnston and Mawson 1947; Jones 2013*a*, 2013*b*). Finally, *A. barrowi* has been found only in the elapid snake *Pseudechis australis* (Jones 1978*a* and unpublished).

Goldberg and Bursey (2012), in a wide-ranging study of helminth parasites of Australian reptiles in the families Agamidae, Gekkonidae and Scincidae, and a review of Australian lizard helminths, concluded that their parasites are generalist, with negligible host-specificity. However, the present study indicates that several species of physalopterine nematodes exhibit strong host-species or host-family specificity. The significance of this specificity in reducing competition between species of nematode cannot yet be conclusively demonstrated.

Infections and host size

Larger lizards support a higher prevalence and abundance of nematodes, and more multiple species infections. Many large lizards (*Varanus*, *Tiliqua*, *Physignathus*) are relatively long lived (Hay 1972; Holmes and Light 1983; King and Green 1999), and often range widely (Pianka 1994), and thus have more opportunities to ingest larval stages in their prey. The association between host size, and prevalence and abundance of infection across species may therefore be a function both of longevity and of behaviour. The number of nematode species infecting a host species was related to sample size for each host. However, multiple infections are also positively related to host size. Though mean sample sizes were smaller for single-species infections (mean = 28 hosts) than for multiple-species infection (mean = 74 hosts), most infections in smaller reptiles were at lower intensity than in larger lizards. This suggests that smaller lizards acquire infections less frequently than larger lizards, the latter therefore having the potential to become infected with more than one species of nematode. The findings presented here are therefore unlikely to be invalidated by the sample sizes.

Species of *Kreisiella* are found only in smaller skinks and agamids with a mean SVL of 42–110 mm. Apart from the small varanids *V. brevicauda*, *V. kingii* and *V. storri* (subgenus *Odatria*), which have evolved dwarfism (Pianka and King 2004), the smallest lizards found infected with species of adult *Abbreviata* had an SVL of >90 mm; it is striking that the host size threshold below which species of *Abbreviata* do not mature is similar in all four lizard families that support infection with these nematodes. The smaller species of lizard in all four lizard families above this size support a single nematode species, usually at low intensity. Adult *Abbreviata* species that occur as single-species infections are (with the exception of the host-specific *A. physignathi* and *A. perenticola*) also the most widespread species, with lowest host-specificity – *A. antarctica*, *A. bancrofti* and *A. hastaspicula*, the latter being confined to several species of *Varanus*.

Many species of skink and gecko below ~90 mm SVL act as paratenic hosts to physalopterid nematodes, with third-stage larvae usually encysted in the abdominal viscera (Jones 1995*b*, 1995*c*, 2010). These lizards ingest third-stage larvae in their arthropod prey. Density-dependent effects may regulate and stabilise nematode populations (Paterson and Viney 2002), their numbers being constrained by the host immune response (Viney *et al.* 2006), but whether this mechanism limits the development and size of parasitic nematodes and prevents the encysted larvae developing into adults has not been investigated in these species. The gecko *Phyllurus platurus* and the aquatic *V. mitchelli* are the only species so far examined that may support both encysted larvae and adult *Abbreviata* species (Jones 1988, 2013*b*).

Geographical distribution of nematodes and host habitat

The number of nematode species to which a reptile is susceptible has been shown to increase with host geographical range in several species (Aho 1990), thus potentially encompassing the distribution of more than one nematode species. Species of *Kreisiella* have a wider geographical range than any species of *Abbreviata* so far studied in Australia, having been recorded in Tasmania (Jones 2003), and in New Britain, Papua New Guinea (as *Physaloptera heterocephala*: Kreis 1940). Of the various environmental parameters examined, annual precipitation and mean annual temperature most closely define distributions of nematodes. These climatic factors determine both vegetation, and, in many species, host distribution. *Abbreviata antarctica* and *A. bancrofti* occur principally in areas with an annual precipitation

above 400 mm (Jones 2005, 2007*b*); two species of snake (*Austrelaps superbus* and *Notechis ater*) were infected with *A. antarctica* on Flinders Island; neither *Abbreviata* spp. nor *Skrjabinoptera* sp. have been recorded from Tasmania itself (Jones 2003). On the other hand, *A. levicauda* and *A. tumidocapitis* occur predominantly in drier areas with an annual precipitation below 400 mm (Jones 1983*b*). *Abbreviata hastaspicula* and *S. goldmanae* occur in both hot drier areas and in the humid tropics (Mawson 1970; Jones 1983*b*, 1988, 1995*b*). Apart from the widespread *A. antarctica* and the species-specific *A. physignathi*, the two other species of *Abbreviata* that inhabit agamid lizards (*A. anomala* and *A. pilbarensis*) occur predominantly in hotter and often drier parts of the continent; neither of these two species have been recorded in areas with annual precipitation >400 mm (Jones 1986). *Skrjabinoptera goldmanae* is mainly specific to the Agamidae, though I have recorded this species in two species of *Varanus* in the Great Victoria Desert (Jones 1995*b*). The distribution of these species of nematode is probably a function of either the distribution of suitable arthropod intermediate hosts, or the ability of the eggs to survive and remain viable in the external environment. The range of intermediate host species is not known; one effective arthropod intermediate host for *A. antarctica* is the native tropical cricket *Teleogryllus oceanicus* (King *et al.* 2013); other species of arthropod hosts remain to be determined. Seasonal changes in food type and availability may expose lizards to different potential intermediate hosts, and these factors may, in part, account for the infrequency with which similar species occur together. Thus the geographical range of nematodes, partly resulting from climatic factors, acting either directly on their eggs in the external environment, or indirectly by affecting the range of suitable arthropod intermediate hosts, may be a factor in reducing competition between species.

There are, however, wide areas of sympatry between many nematode species, which share distributions but not necessarily specific habitats. Host habitat may further limit exposure of potentially suitable hosts to infection. Shine (1986) has shown that four sympatric species of *Varanus* may have major interspecific differences in habitat use and diet. *Varanus tristis* occurs sympatrically with *V. gouldii* over large areas of Australia (Pianka 1994); both species represent species complexes (Pianka and King 2004). The complexity of host–parasite associations is underscored by the fact that the two principal hosts of *A. levicauda*, *V. tristis* and *V. pilbarensis*, occupy different habitats, the former being arboreal (Pianka 1994) and the latter rock-inhabiting (King 2004), and the principal hosts of *A. bancrofti*, *V. glauerti* and *V. varius*, are allopatric. These differences in habitat and range of two principal host species, and variations in nematode morphology, particularly in *A. antarctica* (Irwin-Smith 1922; Johnston and Mawson 1941; Jones 1978*a*) and in *A. hastaspicula* (Jones, unpublished) suggest that molecular studies may reveal these morphospecies to be species complexes.

Cephalic morphology and feeding

The morphology of the cephalic ends of nematodes reflects their methods of feeding. Cephalic dentition with a conspicuous external apical tooth, a small bifid internal apical tooth, and a small bifid tooth on the dorsal and ventral margin of each lip (Chabaud 1956) prevails in the three species that have lowest host specificity and widest geographical range: *A. antarctica*, *A. bancrofti*, and *A. hastaspicula*. The high number of host species in which these three nematodes occur, particularly the first two (Fig. 2), their high prevalence (up to 100%), intensity (to >400 adult worms per host), and large size of worms (females to 38 mm); (Irwin-Smith 1922; Johnston and Mawson 1942*b*; Jones 1983*b*, 1988, 1995*b*, 2005), as well as their ability to feed both from the host tissues, and from ingested prey, suggests that this is an efficient feeding structure. Four species (*A. hastaspicula*, *A. levicauda*, *A. kimberleyensis*, *A. perenticola*) have similar mouthparts, mainly differing in the presence or absence of mouth-corner denticles. From the data available, I cannot ascertain whether this is due to convergence, or to a common line of descent. Both *A. hastaspicula* and *A. levicauda* may attach loosely to the host stomach wall and ingest blood (Jones 1983*b*). However, when there is ample prey in the host stomach, nematodes are deeply embedded in the prey items, especially in tissues such as hind limbs and head capsules of Orthoptera (Jones 1983*b*), indicating that they are feeding. *Abbreviata tumidocapitis*, with strongly hypertrophied musculature at the anterior end, attaches firmly to the stomach wall of the hosts, though its food has not been investigated (whether *A. glebopalmae* also attaches to the host stomach wall was not noted: Jones 1988). The anterior ends of *S. goldmanae* are buried in the host stomach wall for a distance of up to 5 mm, but no blood was seen in the oesophagus or intestine, and possibly these worms feed on inflammatory exudate from the host (Jones 1994). In becoming embedded in host tissues, both the adult female *S. goldmanae* themselves, and the eggs in the uteri, become destroyed by host immune responses (Jones 1994). In the three species of nematode occurring only in Agamidae, *A. anomala*, *A. pilbarensis* and *A. physignathi*, morphological similarities include well defined lines of denticles around the mouth (Jones 1986), particularly well developed in *A. physignathi* (Baylis 1924), and reduced bifid dorsal and ventral denticles bordering the mouth.

Cephalic morphology and concurrent infections

Both *A. levicauda* and *A. hastaspicula* occur in hotter areas of the country, the former being principally a parasite of *V. tristis*, in which *A. hastaspicula* is uncommon. There is little difference in the mouthparts of these two species, mouth corner denticles being absent in *A. levicauda* and inconsistent in *A. hastaspicula*. On the basis of their morphology there is thus the potential for competition between these two species, though I could find no evidence for this, as there was a strong positive correlation between the presence of these two species of nematode. The negative associations between the sympatric *A. antarctica* and *A. bancrofti*, whose mouthparts are similar, may be due to host specificity (the former being the dominant nematode in *V. rosenbergi* and the latter in *V. varius*), or to as-yet unidentified aspects of their biology. Though they may occur in the same host species, it is uncommon to find both species in the same host individual (Jones 2005, 2007*b*). The negative associations between *A. bancrofti* and *A. levicauda* probably result from their environmental preferences, *A. bancrofti* occurring in more humid

regions and *A. levicauda* in drier areas. *Abbreviata hastaspicula*, however, occurs in the tropical north where *A. bancrofti* is also present, but few lizards harboured both species. The musculature development at the anterior end of *A. tumidocapitis* and *A. glebopalmae* suggests different feeding strategies from those of concurrent species, thus reducing the potential for competition.

More studies are needed to ascertain whether these observed associations between geographical distributions of nematodes, host specificities, and differences in their mouthparts, are significant factors in reducing interspecific competition.

Despite this, larger host species may harbour significant numbers of more than one nematode species concurrently. In these instances, to what extent is there competition for food? Several observations show that direct competition for resources among these nematodes is limited; where one lizard species is infected with large numbers of nematodes of more than one species, e.g. *V. gouldii* with *A. antarctica* and with *A. hastaspicula* in the Goldfields area of Western Australia (Jones 1983*b*), and with *V. rosenbergi* in southern Australia (Jones 2005), there is no detectable diminution in numbers, size or fecundity of parasites compared with single-species infections from the same area. Indeed, in *V. rosenbergi* the mean intensity of the predominant nematode, *A. antarctica*, is higher when occurring concurrently with up to four other species (Jones 2005). In *V. gouldii*, intensity of *A. hastaspicula* is similar in single-species infection to that when there were concurrent infections with *A. levicauda*. Possibly the differences in their mouthparts, though slight, effectively reduce the potential for competition in feeding (Jones 1983*b*). Similarly, the prevalence of *A. kimberleyensis* in *V. glauerti* was higher when *A. glebopalmae* was also present (Jones 1988). These examples evidently reflect optimal conditions for transmission of these species of nematodes, and illustrate the complexity of the host–prey–parasite–environment dynamics, and are further evidence that, at least in some biotopes, interspecific competition is not significant. Exceptions are *A. tumidocapitis* and *A. glebopalmae*, which only occur concurrently with more numerous species (*A. hastaspicula* and *A. levicauda*, and *A. kimberleyensis* respectively), and have developed accessory muscles at the anterior end (Jones 1983*b*, 1988) that enable them to exploit different sources of food. The association between *S. goldmanae* and *A. pilbarensis* in agamid lizards is less marked than in the two examples above, as *A. pilbarensis* rarely occurs in the core host of *S. goldmanae*, *C. kingii* (Jones 1994).

Cephalic morphology and host phylogeny

The feeding structures of the nematodes discussed in this paper display a spectrum of development, from *Kreisiella* with numerous undifferentiated labial teeth, through to *Skrjabinoptera* in which there is only a single apical tooth (Fig. 1). Host-family specificity, in particular to the Varanidae and Agamidae, occurs in many nematodes in the genus *Abbreviata*. Varanoid lizards occupy a range of habitats in Australia and despite great differences in size between species, are monophyletic (Baverstock *et al*. 1993; Ast 2001; Fitch *et al*. 2006) and morphologically similar (Pianka and King 2004). A phylogeny of Australian agamid lizards, which have radiated widely in Australian deserts, has been established by Hugall *et al*. (2008)

using nuclear and mitochondrial genes. However, the morphological forms displayed by their physalopterine nematodes may be adaptive, and do not necessarily reflect evolutionary relationships, and I was not able to relate these forms to host phylogenies. Molecular studies of this group of nematodes would be fruitful in this regard.

Intraspecific competition

Evidence for intraspecific competition comes from the large number of larval physalopterids (assumed to be species of *Abbreviata*: Jones 2010) associated with adult *A. hastaspicula* in *V. gouldii*, from >700 to >1500 larvae (Jones 1983*b*, 1988, 1995*b*). These numbers are far in excess of recorded numbers of adults, and the presence of large numbers of adult nematodes may suppress the development of larvae. The presence of species of *Abbreviata* in the intestine may have been due to wandering after the death of the host, but in *V. gouldii*, specimens of *A. antarctica* were found only in the intestine in lizards harbouring more than 55 adult worms (Jones 1983*b*), suggesting the effects of crowding in the stomach.

Effects of host activity

The seasonal activity of the hosts may also affect the population of infecting nematodes. Activity in *C. kingii* is highly seasonal (Shine and Lambeck 1989), and the field metabolic rate in the dry season is about one-quarter of that in the wet season, affecting its food intake (Christian and Green 1994). As there is little concurrent infection with other species of nematode in *C. kingii*, the muscular development of *S. goldmanae* in this host suggests that the feeding regime of the host, rather than competition, may be a crucial factor in determining their feeding strategy, and hence anatomy. Similarly *A. barrowi* from the snake *Pseudechis australis* was recorded concurrently with *A. antarctica* in only one individual snake, and it thus has little competition from congeners in its only recorded host. Snakes, especially larger species, may only feed at long intervals of several months, and may undergo long periods of dormancy. However, other large reptile species are also inactive for several months during the year (Pianka 1970, 1971, 1994; Christian *et al*. 1995), and this diminution or lack of food intake for a prolonged period is likely to have an impact on the feeding regime, and hence potential for competition, among infecting nematodes. At such times the metabolism of their nematodes may adapt to conserve energy, as is known to occur in some free-living nematodes (Lant and Storey 2010). Life expectancy in nematodes is very variable (Gems 2000); that of species of spirurid nematode dwelling in the gastrointestinal tract of poikilotherms is not known.

Effect of parasite load on host

I could find no evidence that high prevalence and intensity of nematodes affects the health of their hosts. Despite often having heavy worm burdens, infected lizards appeared to be in good health, which in turn is conducive to the health and survival of the parasites, and is further evidence of a long evolutionary association. However, whether high numbers affect other aspects of their biology, such as breeding success or longevity, could not be determined, and deserves study.

In conclusion, interspecific competition when two or more species are present is not evident from intensity, maturity or size of worms, and a range of biological, evolutionary and nematode anatomical factors enable host reptiles to support large populations of nematodes. Host specificity, host and nematode distribution, host habitat, host size, and nematode feeding organ morphology are the principal factors I have identified that may limit the potential for interspecific competition. Further, an evident abundance of available food (at least during seasons when the reptiles are active) probably contributes to the success of physalopterine nematodes in these families of Australian reptiles. Thus a long evolutionary association in an environment conducive to the maintenance of infection (high reptile population and diversity, apparent absence of adverse effects on the host, an abundance of actual and potential arthropod hosts, and a climate favourable to ectotherms) has provided a stimulus for the maintenance of a rich spirurid fauna. These factors allow large populations of nematodes to coexist. Studies on further identification of arthropod intermediate hosts, stresses put on nematodes during prolonged periods when the hosts do not feed, molecular studies to investigate the robustness of identifications based on morphology alone, and whether reptiles derive any benefit from supporting an abundance of nematodes, would add considerably to understanding the ecology and evolution of this successful group of nematodes.

Acknowledgements

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