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Using social networks to deduce whether residents or dispersers spread parasites in a lizard population

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Summary

1. Heterogeneity of host behaviour can play an important role in the spread of parasites and pathogens around wildlife populations. Social networks have previously been suggested to represent transmission pathways within a population, but where the dynamics of host–parasite interactions are difficult to observe, networks may also be used to provide insights into transmission processes.

2. Pygmy bluetongue lizards, *Tiliqua adelaidensis*, occupy individual territories, live exclusively in burrows constructed by spiders in Australian native grasslands and are hosts to a tick, *Bothriocroton hydrosauri*, and a nematode, *Pharyngodon wandillahensis*.

3. On five monthly occasions, the locations of all individual lizards in three study plots were used to construct weighted, undirected networks based on proximity of adjacent burrows.

4. The networks were used to explore alternative hypotheses about the spread of each parasite through the population: that stable population members that remained in the same burrow over the study period played a major role in influencing the pattern of infection or that dispersing individuals played a more significant role.

5. For ticks, host individuals that were infected were more connected in the network than uninfected hosts and this relationship remained significant for connections to residents in the population, but not for connections to dispersers.

6. For nematodes, infected and uninfected hosts did not differ in their overall strength of connection in the network, but infected hosts were more connected to dispersers than were uninfected hosts, suggesting that lizards moving across the population are the major agents for the transmission of nematodes.

7. This study shows how network analyses can provide new insights into alternative pathways of parasite spread in wildlife populations, where it is difficult to make direct observations of transmission-related behaviours.

Key-words: nematode, parasite transmission, Scincidae, social network, tick

Introduction

One of the challenges for wildlife disease ecology is to identify how different parasites and pathogens are spread through and maintained in host populations (Tompkins *et al*. 2011). This study explores alternative hypotheses about the spread of indirectly transmitted parasites in a wildlife species, using social network analysis. Early models of parasite dynamics assumed homogeneously mixed host populations, with all individuals equally likely to become infected (Anderson & May 1979). However, significant roles are now recognised for both individual variation in susceptibility among hosts (Segal & Hill 2003; Lloyd-Smith *et al*. 2005; Jirtle & Skinner 2007) and the behaviour and social structure within the host population (McCallum, Barlow & Hone 2001; Altizer *et al*. 2003; Clay *et al*. 2009) in the patterns of infection in a host population. Part of this awareness has developed as wildlife ecologists focus on the threats of parasites to wildlife populations (Daszak *et al*. 1999; Woodroffe 1999; McCallum *et al*. 2009).

Because both direct and indirect contacts among hosts may allow parasite transmission, the patterns of contact among hosts within a population are likely to play a central role in how parasites spread. Social networks have allowed new insights into the importance of heterogeneous contact patterns for disease transmission, by modelling pathways for transmission as edges among nodes (individuals) in a social network (Keeling 2005; Ferrari *et al*. 2006; Bansal, Grenfell & Meyers 2007). Early epidemiological studies of sexually transmitted diseases in human populations have provided a strong empirical basis for these models, through documenting

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sexual contacts among individuals (Klovdahl 1985; De *et al.* 2004). Social network theory has been extended to model the transmission of other directly transmitted parasites, such as foot and mouth disease (Kiss, Green & Kao 2006) and influenza (Masuda, Konno & Aihara 2004). This provided a methodology for modelling the spread in a host population of either hypothetical or real contagious diseases.

A central concept developed through these models is the importance of connectivity in the network in the transmission of disease. Individuals more highly connected in the network are theoretically at greater risk of becoming infected, because they are likely to contact more potential sources of infection (Shirley & Rushton 2005) (although this is not always the case (Drewe 2010)). Similarly, highly connected individuals may be more efficient at transmitting the infection once they become infected, as they are connected to a greater proportion of the population (Keeling 2005; Shirley & Rushton 2005). These concepts have been used in designing disease management protocols, through targeting disease control at highly connected nodes, particularly in humans and domestic livestock, where public health and economic pressures are highest (Kiss, Green & Kao 2006; Hsu & Shih 2010).

Network theory can also be used to model the spread of parasites and pathogens in wildlife populations. Social networks in wildlife populations have been directly derived either from snapshot observations of group membership (Croft, Krause & James 2004; Sundaresan *et al.* 2007) or from continuously monitoring associations among neighbouring individuals within a population, for instance using GPS recorders or contact loggers (Hamede *et al.* 2009; Leu *et al.* 2010a). Alternatively, associations can be inferred from spatial proximity, either from trap captures, where contact is deduced if individuals are captured in the same or adjacent traps (Perkins *et al.* 2009), or from overlap of home ranges. In the latter case, it has been assumed that the likelihood of individuals interacting, and of parasites being transmitted, is increased where individuals substantially overlap in home range (Formica *et al.* 2010; Godfrey *et al.* 2010). Observed network structures have then been used to model the dynamics of contagious pathogens through wildlife populations (Porphyre *et al.* 2008; Hamede *et al.* 2009). In some cases, empirically derived patterns of infection in populations (Godfrey *et al.* 2009, 2010; Drewe 2010; Leu, Kappeler & Bull 2010b), or empirical observations of the spread of a pathogen through a population (Otterstatter & Thomson 2007; Craft *et al.* 2009), have been matched to patterns predicted by the network structure.

Many parasites are not transmitted directly during contact between one host and another. For instance, ectoparasitic ticks and endoparasitic gut nematodes spend time in the off-host environment between leaving one host and finding the next (Bull & Sharrad 1980; Soulsby 1982). When these indirectly transmitted parasites have low mobility and remain close to where they left the first host, transmission to another host relies on the asynchronous use by host individuals of the same space (Godfrey *et al.* 2009). For example, Leu, Kappeler & Bull (2010b) developed a transmission network for ticks in the sleepy lizard (*Tiliqua rugosa*), based on asynchronous sharing of refuges during an infective time window. Host individuals with overlapping home ranges also provide opportunities for indirect transmission of parasites with infectious stages that persist in the off-host environment (Godfrey *et al.* 2010). Studies that estimate transmission risk from host contacts when individuals of the host population are captured in adjacent traps also use this assumption (Perkins *et al.* 2009).

In these circumstances, social network models can do more than simply describe pathways of parasite transmission. They can allow testable hypotheses of the dynamics of disease or parasite spread and of the relative importance in this spread of different components of the host population. For instance, in a population where individuals occupy separate home ranges, a pathogen may spread either by contacts among adjacent stable home range occupants or by itinerant dispersers moving across the population. Network models can incorporate both elements and explore their relative importance in explaining the observed infection patterns. Using this approach, Craft *et al.* (2009) took empirically derived data on the spread of a pathogen through a lion population, and compared the relative roles of transmission through direct contact between adjacent prides, and of transmission to lions by other coexisting carnivores.

The current study develops social network models for a solitary, territorial scincid, the pygmy bluetongue lizard, *Tiliqua adelaidensis*, based on spatial proximity of adjacent territories. This endangered lizard is now restricted to a few fragments of once more extensive native grasslands near Burra in South Australia. The potential for pathogen spread through a population is of conservation concern. Individual lizards exclusively occupy narrow vertical burrows, constructed by spiders (Fellows, Fenner & Bull 2009), and maintain a central-place territorial defence of the burrow entrance from conspecifics (Fenner & Bull 2011a). Lizards also appear to use scats as social signals to indicate their presence or burrow ownership (Fenner & Bull 2011b). The burrows are used for shelter, and as sites to ambush passing invertebrate prey Milne, Bull & Hutchinson (2003). Lizards prefer the deepest available burrows (Milne & Bull 2000), and optimal refuges are often in short supply within the population (Fellows, Fenner & Bull 2009). Resident lizards move infrequently away from their burrow refuges and usually for periods of < 20 mins (Milne, Bull & Hutchinson 2003). With many lizards remaining in the same burrow for three months or more, direct encounters with resident neighbours are rare outside of the mating season (Milne, Bull & Hutchinson 2003).

Pygmy bluetongue lizards are host to an ixodid tick, *Bothriocroton hydrosauri*, and an oxyurid nematode, *Pharyngodon wandillahensis* (Fenner & Bull 2007; Fenner, Smales & Bull 2008). *Bothriocroton hydrosauri* is a generalist reptile tick from southern Australia (Roberts 1953). The tick life cycle requires three hosts. Larvae, nymphs and adult females each attach to a host, engorge and then detach. Detached larvae and nymphs moult to the next stage in the off-host environment. Detached females lay eggs that hatch into larvae. Tick activity and development occur in the spring and summer

months when the weather is warm and lizard activity is at its peak (Bull & Sharrad 1980). *Bothriocroton hydrosauri* adopts a 'sit and wait' host-seeking strategy, moving < 50 cm to locate and attach to a new host (Petney, Andrews & Bull 1983). This suggests that transmission of ticks among pygmy bluetongue lizards relies upon individual lizards encountering ticks in the environment.

The oxyurid nematode, *Pharyngodon wandillahensis*, has only been found infecting pygmy bluetongue lizards, with a reported prevalence of 37% in the population used in the current study (Fenner, Smales & Bull 2008). In other oxyurids, eggs are passed out of the host in faecal material and new hosts are probably infected when they ingest those eggs (Soulsby 1982). Lizards use their tongues to sense environmental cues (De Fazio *et al*. 1977; Bull *et al*. 2000), and in pygmy bluetongue lizards, transmission might occur during the inspection of territory marking scat deposits or by accidental ingestion of contaminated material during feeding (Fenner, Smales & Bull 2008).

This study describes infection patterns of the tick and the nematode in three lizard subpopulations and uses their social networks to explore two alternative hypotheses about the spread of each parasite, (i) that transmission occurs mainly across adjacent home range boundaries of resident lizard hosts in the population or (ii) that nonterritory holding dispersing lizards play a more significant role. There were no specific predictions, at the start of the study, that one or the other group of individuals would have a greater role, because there is little natural history knowledge of the parasite–host system. Indeed, this is symptomatic of much wildlife disease ecology where it is difficult to make relevant observations to quantify transmission rates. Instead, we suggest that a network approach can be used to derive insights that are normally unavailable to ecologists interested in these interactions.

The study examined the stability of individuals in the network and tested the hypothesis that individuals more connected in the network would be more susceptible to infection and, subsequently, more likely to be infected with parasites. Then, the relative roles of infected resident or dispersing individuals were inferred from the infection patterns of individuals connected to each in the network.

Materials and methods

STUDY SITE

The study site was located near Burra, South Australia (33°42′S; 138°56′E), in a semi-arid, remnant area of native grassland that was lightly grazed by sheep. The area has hot, dry summers and cool moist winters, with an annual rainfall between 400 and 500 mm.

LIZARD SURVEYS

In November 2009, three 0·64-ha plots were chosen (and referred to as plot 1, plot 2 and plot 3), within a continuous population of pygmy bluetongue lizards at the study site. Each plot was separated by at least 400 m and beyond the recorded short-term dispersal range of this species (Milne, Bull & Hutchinson 2003; Fellows, Fenner & Bull 2009; Smith *et al*. 2009). Individuals captured and marked in one plot were never recaptured in another plot, and populations within each plot were considered independent replicates. Each plot was intensely searched for burrows, which were inspected for occupant lizards with an optic fibre scope and portable light source, as described by Milne & Bull (2000). Each occupied burrow was marked with a numbered peg, and its position was recorded using a Garmin 60 global positioning system (GPS). Lizards were lured from their burrows with a mealworm tethered to a piece of string (Milne & Bull 2000), captured by hand and toe clipped for individual identification. Lizard sex was determined by cloacal examination. Each lizard was inspected visually for attached ticks, and when possible, a fresh scat was collected by gently running a thumb along the belly of the lizard to encourage defecation. Scats were placed individually into 10-mL plastic tubes, preserved in sodium acetate formalin (SAF) and later examined for nematode eggs. The lizard was then returned to its original burrow.

This process was repeated monthly between November 2009 and March 2010 in each plot, treating new lizards as described previously, and reassessing parasites of recaptured lizards. If a lizard had moved within the plot, its new location was marked and its new GPS location recorded. The five-month study period represented most of the period when this lizard species is active in the field (Fenner & Bull 2011a).

PARASITE SURVEYS

Attached ticks were detected by visual inspection. Although other tick life history stages attach to pygmy bluetongue lizards (Fenner & Bull 2007), during our study, there were only larval ticks of the species *B. hydrosauri* on lizards and these were only found in plot 1.

For nematodes, the McMaster faecal floatation technique (Seivwright *et al*. 2004; Hallas & Bull 2006) was used to assess the presence or absence of worms or eggs of *P. wandillahensis* in collected scats.

For each parasite, a lizard was scored as infected if parasites were detected in at least one of the five surveys and uninfected if parasites were not detected in any survey. Individual lizards that could not be lured from their burrows in any of the five lizard surveys were assigned an unknown infection status.

TRANSMISSION NETWORKS

To test transmission hypotheses, a hypothetical transmission network was constructed for each plot, based on empirical observations of the spatial arrangements of lizards in the plot. Links in these networks were based on the spatial proximity of host burrows, assumed to represent the likelihood of spatial overlap in home ranges, and the likely exposure of an individual host to infective stages of either parasites that were shed by its neighbours. Hypotheses were tested by determining whether the pattern of infection among individual hosts in each plot conformed with network predictions that infected individual hosts would be more connected in the network than noninfected individual hosts.

Construction of the hypothetical transmission networks, in each plot and for each month, used the distances between GPS locations of burrows of each pair of lizards. Lizards in burrows spaced more than 20 m apart were considered to be unconnected in the network because lizards rarely forage more than 20 m from their burrows (Milne, Bull & Hutchinson 2003). Allowing for a 5·5-m precision error (instrument specifications) on the GPS unit for each burrow location, GPS burrow locations within 31 m of each other were included as connected in the network. Then, edge weights from 1 to 5 were assigned to all connected pairs of lizards, based on their

proximity (Table 1, Fig. 1). Closer lizards were assigned a higher edge weight assuming a higher chance of cross-infection. Edge weights were used to construct weighted, undirected networks.

Previous studies reported that lizards normally remain in the same burrow for many months, (Milne, Bull & Hutchinson 2003; Fellows, Fenner & Bull 2009). However, some lizards can disperse from their burrow to another closely located burrow or completely away from the local area. The stability of the transmission network among months was examined using Mantel tests with 10 000 permutations to test whether the position of each individual relative to each other individual in the network was significantly correlated in sequential pairs of months, for those individuals that remained in each plot in sequential months. Because the monthly networks did not differ significantly (see Results), an integrated network was constructed for each plot, covering the whole study period by summing edge weights for each pair of lizards in each month, and used to calculate node-based measures to describe the overall position and connectivity of individuals in the network.

Table 1. Classification of edge weights based on pairwise distances among lizards

Distance	Edge weight
> 30·5 m	0
25·5–30·5 m	1
20·5–25·5 m	2
15·5–20·5 m	3
10·5–15·5 m	4
< 10·5 m	5

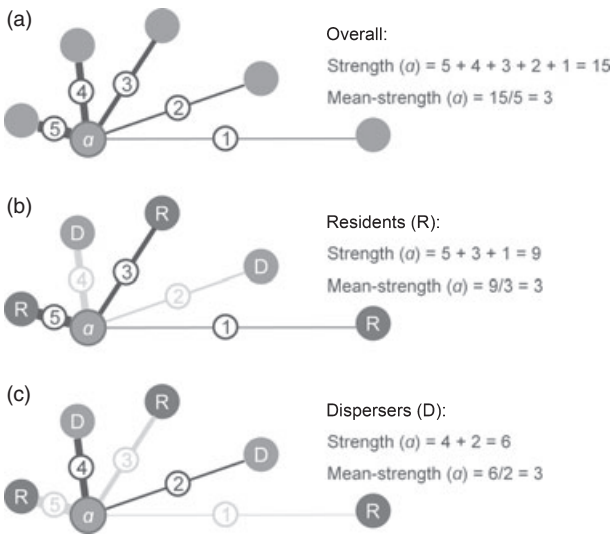

Fig. 1. Diagram demonstrating the calculation of edge weights and node-based measures in pygmy blue tongue (*Tiliqua adelaidensis*) networks. Edges were weighted by ranks (1–5, numbers in circles) based on the spatial proximity between lizard burrows (Table 1); so lizards closer together had higher (stronger) edge weights. The diagram demonstrates the calculation of node-based measures for lizard *a* for (a) strength, the sum of edge weights connected to *a*, and mean strength, the average weight of edges connected to *a*; (b) resident strength, the sum of edge weights connected to *a* from all residents, and mean resident strength, the average weight of edges connected to *a* from all connected residents; (c) disperser strength, the sum of edge weights connected to *a* from all dispersers, and mean disperser strength, the average weight of edges connected to *a* from all connected dispersers.

Node-based 'strength' was the sum of edge weights connected to an individual (Fig. 1). 'Mean strength' was the average weight of all of the edges connected to an individual (Fig. 1). Mean strength was a measure of how strongly an individual was connected in the network, and in this case, how exposed it was to infection risk. An individual could have a high strength if it was connected to many other individuals, but a low mean strength if none of the connections was substantial. Similarly, a high strength could result from a few connections with high edge weights.

Residents were defined as individuals that remained in their study plot for 3 or more months, and dispersers were individuals that were detected in a plot for no more than two months. 'Resident strength' and 'disperser strength' were the sum of edge weights of an individual to residents and to dispersers, respectively, and 'mean resident strength' and 'mean disperser strength' were the mean edge weights of an individual to residents and to dispersers (Fig. 1b,c). If parasite movement was principally by passage across stable neighbouring territories, then infected individuals should be more strongly connected to residents than should uninfected individuals. Alternatively, if dispersers played a more significant role in the transmission of parasites, infected individuals should be more strongly connected to dispersers than should uninfected individuals.

To test the robustness of any observed patterns, the analyses described later were repeated, redefining residents as individuals that remained in their study plot for 2 or more months and for 4 or more months.

NETWORK ANALYSIS

Network parameters derived for individual members of the network are not independent of each other, so data were analysed using a series of randomisation tests (Croft, James & Krause 2008; James, Croft & Krause 2009). In these, it was determined whether a value that quantified the association between two variables was more extreme than values derived from randomised permutations of the data.

The Mann–Whitney *u* statistic, a scaled version of the Mann–Whitney *U* statistic that lies between 0 and 1 (Croft, James & Krause 2008), was used to quantify the difference in measures of strength between infected and uninfected individuals. Values of *u* closer to 1 indicated that infected individuals had a higher measure of strength than uninfected individuals. For each comparison, the original data were re-sampled without replacement in a Monte Carlo randomisation test (Manly 1997) with 10 000 permutations. The *u* statistic was recalculated for each randomised version of the data, and the resultant distribution of values was compared with the observed value of the statistic. *P*-values were derived from the number of randomised values that were greater than the observed value. For each analysis, separate randomisation tests were conducted within each study plot. The randomisation procedures were conducted in PopTools 2.7 for Excel (Hood 2006).

A common problem with network analysis is that individuals at the edge of a study plot will have lower strength because more of their edges are directed to unsurveyed individuals. We assumed this bias applied equally to infected and uninfected individuals and would not influence trends.

Results

NETWORK STABILITY AND STRUCTURE

There were 106 different lizards found across the three plots over the study period (Table 2). Sixty-five were considered

Table 2. Summary of the plot characteristics, lizard population, parasite prevalence and network structure among the three plots. N is the number of lizards captured in each plot, N_R is the number of 'residents' in each plot (remained in the plot for ≥3 months), N_D is the number of 'dispersers' in each plot (remained in the plot for ≤2 months), area (ha) is the area of each plot, lizards per ha is estimated density of lizards, burrows per lizard is the mean number of burrows per lizard, parasite prevalence shows the percentage of lizards infected with ticks and worms, density is the density of the network (total number of edges divided by the total possible number of edges), mean degree is the mean number of individuals an individual is connected to in the network, and mean strength is the mean strength of individuals in each network

							Parasite prevalence				
Plot	N	N_R	N_D	Area (ha)	Lizards per ha	Burrows per lizard	Ticks	Worms	Density	Mean degree	Mean strength
1	48	22	26	0·64	75	1·1 ± 0·04	12·5%	30·0%	0·251	11·83 ± 0·67	62·21 ± 5·52
2	34	28	6	0·64	53	1·1 ± 0·05	–	50·0%	0·217	7·18 ± 0·52	79·59 ± 9·88
3	24	15	9	0·63	38	1·2 ± 0·08	–	57·1%	0·279	6·42 ± 0·76	52·00 ± 9·49

Table 3. Mantel test comparing the similarity of network matrices between sequential pairs of months. r is the observed correlation coefficient, $r_{(rand)}$ is the mean random correlation coefficient with 95% confidence intervals (CI) calculated from 10 000 permutations and P is the one-tailed probability ($r > r_{(rand)}$). P values in bold denote statistical significance ($P < 0·05$)

Plot	Months	N	r	$r_{(rand)}$	95% CI	P
1	November + December	19	0·594	−0·001	−0·129 to 0·173	**< 0·0001**
	December + January	17	0·872	0·000	−0·142 to 0·195	**< 0·0001**
	January + February	23	1·000	0·000	−0·109 to 0·143	**< 0·0001**
	February + March	24	1·000	0·000	−0·101 to 0·138	**< 0·0001**
2	November + December	17	0·813	0·002	−0·140 to 0·203	**< 0·0001**
	December + January	21	0·947	0·000	−0·136 to 0·207	**< 0·0001**
	January + February	28	1·000	0·000	−0·089 to 0·124	**< 0·0001**
	February + March	28	1·000	0·000	−0·089 to 0·123	**< 0·0001**
3	November + December	9	0·731	0·003	−0·284 to 0·460	**0·0009**
	December + January	14	1·000	0·001	−0·190 to 0·268	**< 0·0001**
	January + February	15	0·993	0·000	−0·188 to 0·252	**< 0·0001**
	February + March	15	1·000	−0·001	−0·187 to 0·254	**< 0·0001**

residents, remaining in their plot for three or more months, while 41 were considered dispersers, remaining in their plot for two or less months (Table 2). Plot 1 had more dispersers than residents, while the other two plots had more residents than dispersers (Table 2). Tick and nematode prevalences were 8·9% and 46·4% for residents and 0·0% and 34·6% for dispersers. Over the study period, each individual lizard used between one and two burrows within its plot (mean 1·12 ± 0·03) (Table 2). Among those individuals that remained in the plot in sequential pairs of months, the position of individuals relative to each other in the networks was significantly correlated between successive months for all plots (Table 3).

The social network formed one linked unit in each of plot 1 (Fig. 2) and plot 2 and two components in plot 3. There was one isolate (an unconnected individual) in each of plot 2 and plot 3. The networks had a mean density of 0·25, meaning they contained 25% of all possible edges.

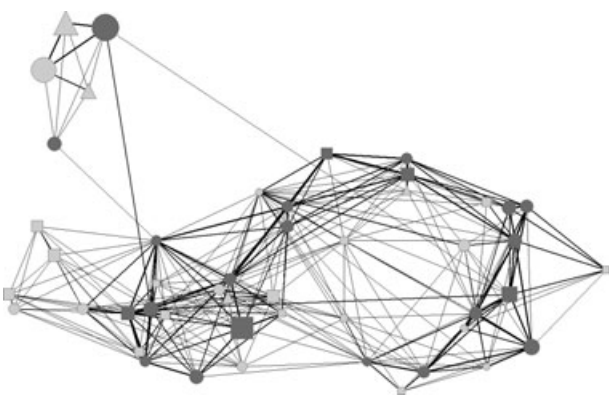

Fig. 2. Network diagram of plot 1. Each node represents a lizard in the study population, and the lines connecting them represent edges. Edge thickness represents the extent of home range overlap between each pair of nodes. Node shape indicates lizard sex (circles = females; squares = males; triangles = unknown sex), node colour represents lizard persistence in the plot (dark grey = resident; light grey = disperser) and node size is scaled by the measured value of strength (sum of edge weights connected to an individual).The two-dimensional placement of nodes corresponds to the geographical location of individuals within the study site.

NETWORK STRUCTURE AND PARASITE INFECTION PATTERNS

Lizards infected with ticks in plot 1 had a significantly higher strength, and a marginally higher mean strength, than

Table 4. Mann–Whitney *u* randomisation test comparing the strength of infected and uninfected individuals in the network. *u* is the observed *u* value, $u_{(rand)}$ is the mean random *u* value with 95% confidence intervals (CI) calculated from 10 000 permutations and *P* is the one-tailed probability ($u > u_{(rand)}$). *P* values in bold denote statistical significance ($P < 0{\cdot}05$)

			Strength				Mean Strength			
Plot	Parasite	*N*	*u*	$u_{(rand)}$	95% CI	*P*	*U*	$u_{(rand)}$	95% CI	*P*
1	Ticks	40	0·828	0·499	0·766–0·226	**0·0071**	0·722	0·501	0·771–0·229	0·0561
1	Worms	40	0·497	0·501	0·696–0·302	0·5198	0·647	0·500	0·690–0·304	0·0726
2	Worms	22	0·628	0·500	0·752–0·252	0·1572	0·504	0·500	0·744–0·256	0·4945
3	Worms	21	0·620	0·499	0·750–0·241	0·185	0·629	0·502	0·750–0·241	0·1742

uninfected lizards (Table 4, Fig. 3). Tick-infected lizards had more close neighbours. No ticks were found on lizards in plot 2 or plot 3. There were no significant differences in strength or mean strength between lizards infected or uninfected with nematodes in any plot (Table 4).

Individuals infected with ticks had a significantly higher resident strength and higher mean resident strength than uninfected lizards in plot 1 (Table 5, Fig. 3). Tick-infected lizards had more close neighbours that were residents. Tick-infected and uninfected lizards did not differ significantly in disperser strength measures (Table 5).

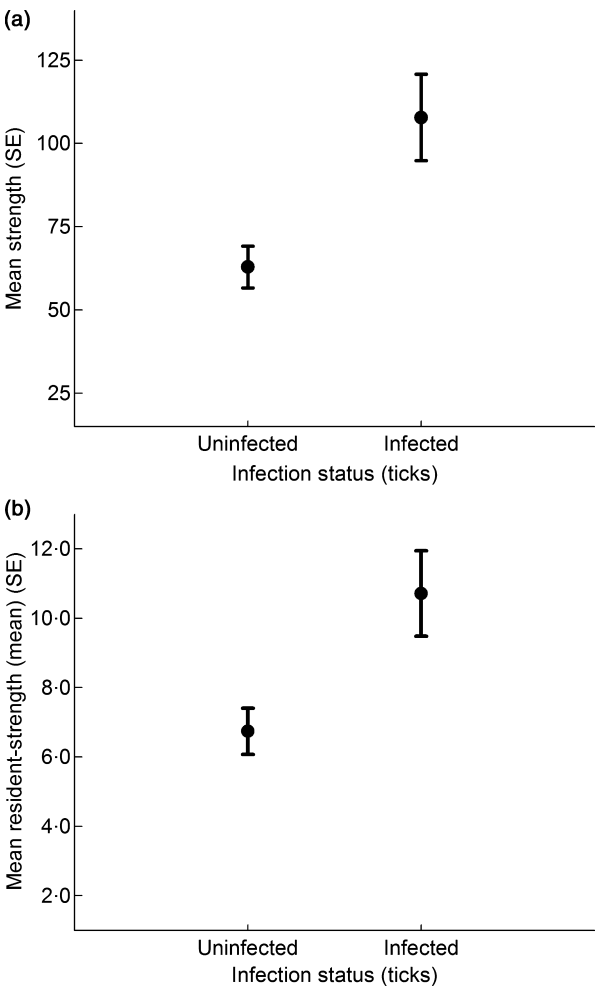

Fig. 3. Mean strength (a) and mean resident strength (b), in the network of individuals uninfected or infected with ticks in plot 1.

Individuals infected with nematodes had a significantly higher mean disperser strength in plots 1 and 2, and a significantly higher disperser strength in plot 2, than uninfected individuals (Table 5, Fig. 4). Infected lizards had more close neighbours that were dispersers. Infected and uninfected lizards did not differ in resident strength or mean resident strength in any plot (Table 5).

The relationships for each parasite remained consistent whether residents were defined as present for at least 2 or at least 3 months, but changed when 4 months were required for residence status (Table 6). In the latter case, individuals that stayed for up to 3 months as dispersers may be less ecologically relevant.

Discussion

The population dynamics of each of the parasites will be partly driven by self-re-infection of hosts. The analyses in this study focussed on the spread of infection from one host to another.

For ticks (in the one plot where ticks were found), host individuals that were infected were more connected in the network than uninfected hosts. This relationship remained significant for connections to the residents in the population, but not for connections to the less permanent dispersers. That is, the average intensity of the associations (in this case, the proximity to other host individuals) was important in predicting infection patterns, and stable resident individuals were more important in influencing tick distribution in the population.

For nematodes, there was no parallel pattern to suggest that infected and uninfected hosts differed in overall strength of connection in the network. However, there was strong support for the role of dispersers, in that infected hosts were more connected to dispersers than were uninfected hosts in plots 1 and 2. This suggests that lizards moving across the population are the major agents for the spread of nematodes. The parameter mean disperser strength was a significant predictor of infection with nematodes in both plots suggesting that the average intensity of associations, which reflected the average proximity to burrows occupied by disperser individuals, was more important than the absolute number of associations with dispersers.

Table 5. Mann–Whitney *u* randomisation test results, comparing infected and uninfected hosts for resident strength and for disperser strength. *u* is the observed *u* value, $u_{(rand)}$ is the mean random *u* value with 95% confidence intervals (CI) calculated from 10 000 permutations and *P* is the one-tailed probability ($u > u_{(rand)}$). *P* values in bold denote statistical significance ($P < 0{\cdot}05$)

				Resident strength measures				Disperser strength measures			
Plot	Parasite	Strength measure	*N*	*u*	$u_{(rand)}$	95% CI	*P*	*u*	$u_{(rand)}$	95% CI	*P*
1	Ticks	Strength	40	0·828	0·501	0·229–0·771	**0·0074**	0·628	0·500	0·229–0·777	0·1869
		Mean strength	40	0·788	0·503	0·234–0·777	**0·0208**	0·520	0·500	0·229–0·774	0·4463
1	Worms	Strength	40	0·520	0·499	0·302–0·696	0·4208	0·425	0·500	0·307–0·693	0·7644
		Mean strength	40	0·546	0·501	0·302–0·702	0·3338	0·757	0·502	0·307–0·693	**0·0042**
2	Worms	Strength	22	0·600	0·500	0·245–0·750	0·2141	0·709	0·502	0·259–0·750	**0·0457**
		Mean strength	22	0·563	0·498	0·245–0·745	0·3194	0·709	0·499	0·268–0·736	**0·0452**
3	Worms	Strength	21	0·625	0·500	0·245–0·750	0·1691	0·444	0·498	0·245–0·750	0·6641
		Mean strength	21	0·634	0·499	0·250–0·750	0·1516	0·384	0·499	0·250–0·755	0·8116

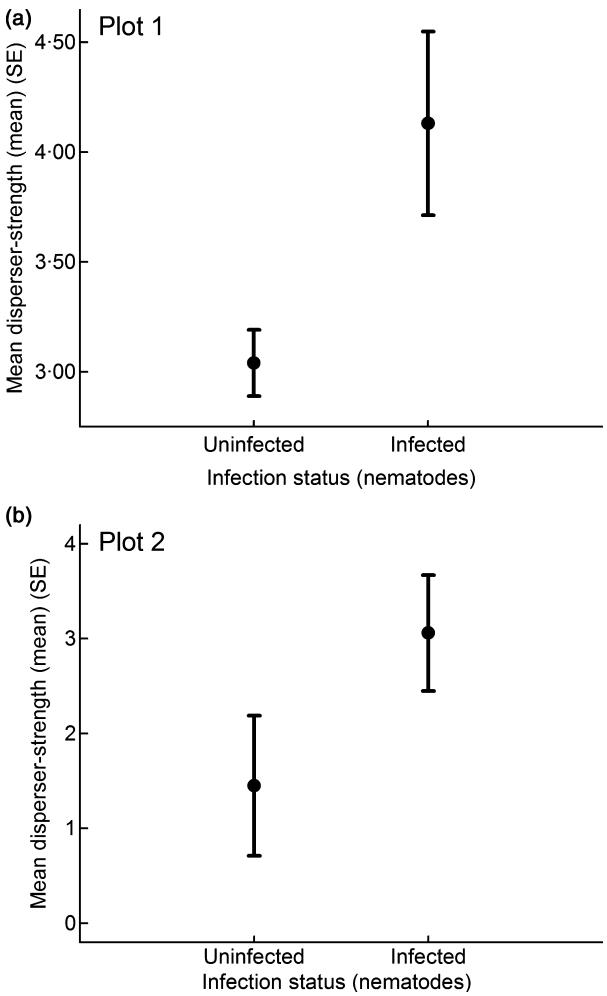

Fig. 4. Mean disperser strength of individuals uninfected and infected with nematodes in (a) plot 1 and (b) plot 2.

In plot 3, there was no significant effect of any network measures on nematode infection patterns. This plot had the lowest host density and the lowest values of mean network degree and strength. This is consistent with a pattern where higher levels of connection lead to greater infection risk, but we lacked sufficient replication to test whether less connected networks have less influence on parasite transmission.

In summary, the network analyses suggested major differences in the transmission pathways through the lizard population for these two indirectly transmitted parasites. One explanation is that the two parasites have different survival times in the off-host environment. Eggs of a related nematode in exposed scats of a related lizard desiccated to become inviable within 10 days (Hallas & Bull 2006). A similarly short survival period for *P. wandillahensis*, combined with infrequent contact between neighbouring lizards (Milne, Bull & Hutchinson 2003), may explain an ineffective transmission of nematodes between lizard hosts across neighbour boundaries. Survival times of unengorged stages of the tick *B. hydrosauri* vary with life stage and with ambient conditions (Chilton & Bull 1993), but in sheltered conditions, they may be expected to remain alive for at least 40 days (Leu, Kappeler & Bull 2010b), four times longer than the nematodes. This increased time would increase the chance that a lizard would become exposed to a live tick that had been shed by its neighbour.

An additional factor might be that nematode transmission relies on lizards inspecting conspecific scats by tongue flick. There were no data on inspection rates in field conditions, but resident lizards may infrequently inspect the scats of their familiar neighbours, but be more likely to inspect new scats deposited near their burrows by unfamiliar dispersers (Bull *et al.* 2000). Similarly, dispersing lizards may behave more cautiously and inspect any scats as they move through occupied habitat. Thus, dispersers may be more effective than residents in transmitting nematodes.

Previous studies have found that the risk of infection may vary depending on the transmission mode of the parasite (Cote & Poulin 1995; Altizer *et al.* 2003) or the mobility of the vector in cases of vector-transmitted parasites (Godfrey, Bull & Gardener 2006). The social network models in our study, based on spatial proximity of home burrows, were differentially effective as explanatory transmission networks for the two parasites we examined. Explanations for the difference are currently speculative. However, more importantly, the network analysis identified differences in the probable

Table 6. Probability values (*P*) for Mann–Whitney *u* randomisation tests as in Table 5, comparing infected and uninfected hosts for resident strength and for disperser strength, when the definition of a resident is set at 2, 3 or 4 months of consecutive occupancy in a study plot. *P* values in bold denote statistical significance ($P < 0{\cdot}05$). Values for 3 months are as in Table 5

			P values for resident strength measures			*P* values for disperser strength measures		
Plot	Parasite	Strength measure	2 months	3 months	4 months	2 months	3 months	4 months
1	Ticks	Strength	**0·0102**	**0·0074**	**0·0179**	0·2852	0·1869	**0·0168**
		Mean strength	**0·0201**	**0·0208**	**0·0095**	0·6769	0·4462	0·0552
1	Worms	Strength	0·4994	0·4208	0·3855	0·6806	0·7644	0·6222
		Mean strength	0·2283	0·3338	0·3672	0·0605	**0·0042**	**0·0167**
2	Worms	Strength	0·2183	0·2141	0·3445	**0·0482**	**0·0457**	0·3255
		Mean strength	0·3226	0·3194	0·2837	**0·0471**	**0·0452**	0·3471
3	Worms	Strength	0·1684	0·1691	0·1980	0·6667	0·6641	0·2749
		Mean strength	0·1594	0·1516	0·1647	0·1892	0·8116	0·4818

transmission pathways of two naturally occurring parasites. Similarly, Godfrey *et al*. (2010) found that social networks predicted infection patterns of ticks more effectively than chigger mites on a territorial reptile, the tuatara. These differences in the response of parasites to social network structure reflect how different aspects of host behaviour may affect the spread of parasites with different transmission modes. To construct effective transmission networks, aspects of both host and parasite behaviour will need to be incorporated.

This study highlights the potential importance of host movement in the dynamics of parasite spread for some parasites. Similarly, Tuyttens *et al*. (2000) found that increased movement of badgers because of the disruption of the social structure (caused by culling) increased transmission rates of bovine tuberculosis. Other studies have also demonstrated that dispersers have a major role in the dynamics of disease outbreaks and spread (Morgan *et al*. 2007; Watts *et al*. 2009). Understanding how parasites are transmitted and their transmission mode is crucial for developing conservation strategies to minimise the risk to wildlife and to correctly target interventions (Li *et al*. 2005; Donnelly *et al*. 2006).

This study has shown how network analyses can provide new insights into parasite spread in wildlife populations, where it is difficult to make direct observations of transmission-related behaviours. Social networks have previously been used to illustrate pathways of parasite spread through populations. They have had a descriptive and predictive role. In this, and related studies, the role of network analysis has been extended to explore alternative hypotheses about the dynamics of infection patterns. This has the potential to become a powerful tool in understanding the ecology of wildlife diseases and parasites.

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