

Domestic mammals facilitate tick-borne pathogen transmission networks in South African wildlife

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Highlights

- The high connectivity of South African mammals by ticks facilitates pathogen transmission.
- Domestic animals enhance the spread of pathogens among South African mammal species.
- Conservation practices that mingle domestic and wild mammals increase the risk of disease.

Abstract

As changes in the environment have brought wild and domestic animals into closer proximity, cross-species disease transmission has become a major concern in wildlife conservation. In Africa, livestock are often kept on the edges of protected areas and frequently share habitat with wild animals. Many tick (Acari: Ixodidae) species can feed successfully on both domestic and wild mammals; and by

feeding on different hosts at different life stages, can transmit pathogens between them. The influence of the composition of the host community on pathogen transmission by ticks remains poorly understood, however, making it difficult to determine whether sharing habitats with domestic livestock increases tick-borne disease in populations of wild animals. We used network analysis to analyse 35,349 collections of 54 tick species in South Africa, treating hosts as nodes and shared tick species as links. Across all life stages, 93 mammalian host species were connected by a total of 3,105 edges. Sheep, goats, and dogs emerged as particularly important domestic species for network connectivity; and for wild animals, soft-skinned, smaller mammals such as the scrub hare. Although some South African ticks show some degree of specialization on wild animals, network analysis showed that opportunistic feeding on domestic hosts can lead to shortened transmission pathways and facilitate pathogen spread between mammal species. Mammal species are highly interconnected through the tick species that they share, and domestic mammals significantly increase the risk of disease transmission. These findings support conservation management measures that limit contact between domestic and wild mammals to reduce tick-borne disease transmission. Proposals to allow local communities grazing access to protected areas must be carefully evaluated in light of the increased disease risks to both domestic and wild animals, and potentially also to people.

Keywords:

Wild mammal species; Domestic animals; Host-parasite dynamics; Cross-species transmission; Disease control; Ixodid ticks

1. Introduction

Infectious diseases are an important and growing concern for conservation, with changes in disease prevalence, diversity, and severity occurring rapidly as the earth's environment is changed by people. Cross-species disease transmission and the (re)emergence of pathogens from wild reservoirs are often facilitated by anthropogenic activities (Antia et al. 2003; Lubroth 2012). Climate change, for example, can alter the geographic distribution of arthropod vectors, augmenting the risk of infectious disease transmission in wild species and the incidence of zoonoses in humans (Cumming & Van Vuuren 2006; Garamszegi 2011). Human activities and associated landscape changes are bringing domestic animals, wild animals and humans into increasingly closer proximity in many places, resulting in reciprocal exchanges of pathogens (Pastoret et al. 1988; Daszak et al. 2001; Patz et al. 2004; Prager et al. 2012a; Hegglin et al. 2015; Han et al. 2016; Hassell et al. 2017). In southern Africa, the wildlife trade and wildlife translocations into conservation and hunting areas near livestock ranches and rural subsistence communities further increase such contacts, in addition to causing stress and undermining the immune systems of wild animals (Karesh et al. 2005; Penzhorn 2006; Chomel et al. 2007). As a result, the increasing anthropogenic alteration of natural environments offers numerous opportunities for generalist pathogens and cross-species pathogen transmission, with negative implications for wildlife, protected areas, and human health (Dobson & Foufopoulos 2001; Altizer et al. 2003; De Vos et al. 2016).

Although wild animals were historically considered natural reservoirs of many infectious diseases of domestic animals (Taylor & Martin 1987), transmission from domesticated species to sympatric wildlife has become a major problem for conservation (Daszak et al. 2000; Daszak et al. 2001; Prager et al. 2012a). Over a quarter of domestic mammal pathogens are infectious to wildlife species (Cleaveland et al. 2001). For example, canine distemper outbreaks recorded in lion populations in the Serengeti National Park were initiated by domestic dogs, but also affected silver-backed jackals, bat-

eared foxes, and African wild dogs (Roelke-Parker et al. 1996; Prager et al. 2012b). Livestock parasites that are shared with African wildlife include rinderpest between cattle and African buffalo, eland and greater kudu; brucellosis between cattle and African buffalo and hippopotamus; foot and mouth disease between cattle and African buffalo; African swine fever between domesticated swine and the common warthog; and bovine tuberculosis between cattle and African buffalo, greater kudu, common duiker and lechwe (Pastoret et al. 1988).

The complexity of the problem of understanding the relative influences of wild and domestic hosts on parasite and pathogen dynamics is increased by host generalism. Many parasites and pathogens can infect multiple host species (Woolhouse et al. 2001; Keesing et al. 2006). The generalist capacity of such pathogens has been linked to pathogen genetic variability and abundant opportunities for cross-species transmission (Woolhouse et al. 2001). However, multi-host pathogen dynamics in host communities remain poorly understood. Previous studies have shown that host species diversity can affect the prevalence of some pathogens, whilst infectious diseases can in turn influence host community structure (Power & Mitchell 2004; Keesing et al. 2006). Multi-host-multi-parasite systems are complex, but it is clear that within these systems, all species are not equal. Some hosts may be particularly susceptible to infection, and some vectors may be particularly good at transmitting particular pathogens. Epidemic disease outbreaks, for example, often arise via a reservoir species which maintains a relatively high pathogen population and from which pathogens spill over to other hosts (Daszak et al. 2000; Power & Mitchell 2004).

In this paper, we explore the roles of wild and domestic mammalian hosts in transmission networks for tick-borne pathogens in South Africa. In particular, we were interested in how alternative conservation approaches, and particularly those that mix wildlife and domestic stock versus those that keep them separate, may affect the potential for exchanges of ticks and tick-borne pathogens. The feeding behaviour of ticks on different host species creates a system of multiple interconnections that

can be viewed as a network, in which hosts are linked by the ticks they share (Caron et al. 2012). Previous studies that have used network analysis to examine the dynamics of parasite infections between individuals of the same host species (Godfrey et al. 2009; Godfrey et al. 2010; MacIntosh et al. 2012) have shown that higher levels of network connectivity tend to increase individual risk of infection and that some parasites may enhance transmission opportunities through their influence on host behaviour (Godfrey et al. 2009). Networks of contacts between different host species and their consequences for pathogen dynamics in multi-species systems have been less investigated, but have the potential to make important contributions to our understanding of multi-host parasite and pathogen transmission pathways (Jeger et al. 2007; Olesen et al. 2008; Salathé & Jones 2010; Piloosof et al. 2015).

We undertook network analysis of an extensive new dataset of 35 349 tick-host interactions to assess the connectivity between 93 South African mammal hosts (85 wild mammals and eight domestic mammals) based on the tick species that they share. We used the analysis to identify the most highly connected hosts that facilitate potential tick-borne disease transmission, and explore the likely effects of domestic species on these associations. We hypothesised (H1) that since many South African ticks show some degree of specialization on wild animals but feed freely on domestic hosts (Cumming 1998; Cumming 1999; Espinaze et al. 2016), adding domestic species to the network should shorten transmission pathways (i.e., by providing shorter routes between different species) and facilitate the spread of pathogens. Alternatively (H2), if ticks were wildlife specialists or pure generalists, adding domestic hosts should have little impact on the spread of pathogens because doing so would either not add new connections to the network or because the network would be highly interconnected independently of the presence of domestic species.

2. Material and methods

2.1. Data

The dataset used in this study results from 36 years of tick collection by [co-author's name] in South Africa. Each tick sampled was either collected from a dead (natural death, roadkill, hunted) or a living or slaughtered host (domestic species). A total of 35 349 collections (a collection is defined as occurring whenever one or more ticks of a given species were obtained from a single host) of 54 tick species (from eight genera, family Ixodidae) (Supporting Information), obtained from 93 mammal host species (85 wild mammals and eight domestic mammals) (Supporting Information) were included in the analyses. For each collection, the tick species, life stage (larva, nymph or adult), number of individual ticks collected, mammalian host species, host health condition, geographic location of the sample, and date of collection were recorded. Occasionally the host species was not known, but its genus or family was indicated (e.g. *Genetta* sp. for genets). Hosts that have been included belonged to 11 orders of mammals: Carnivora (29 spp.), Cetartiodactyla (30 spp.), Rodentia (14 spp), Primates (3 spp.), Perissodactyla (6 spp.), Macroscelidea (4 spp.), Lagomorpha (3 spp.), Proboscidea (1 sp.), Hyracoidea (1 spp.), Eulipotyphla (1 spp.), and Soricomorpha (1 family, Soricidae).

2.2. Network construction

Mammal host species were represented as nodes (vertices) in the network, and tick species shared by pairs of hosts were represented as edges (links). Edges were weighted by the numbers of different tick species shared by each pair of hosts. Since all mammals could work as both donors and recipients of pathogens, the network system was considered “undirected” (Proulx et al. 2005; Poulin 2010). Tick host specificity varies with life-stage (Espinaze et al. 2016), and so three networks were built: a network of hosts sharing all ticks (regardless of life stage), a network of hosts sharing juvenile (i.e., larva and nymph) ticks, and a network of hosts sharing adult ticks. The matrices matching all possible

pairs of hosts and the tick species they shared were generated using SQL-queries in a relational database.

2.3. Measurement of network structure

Quantification of the network structure was achieved by exploring i) network and ii) node properties, in order to investigate i) system-wide relationships (e.g., connectivity); and ii) the most highly connected host species involved in the cross-infestation with ticks and the transmission of tick-borne pathogens, respectively.

2.3.1. Network properties: system-wide relationships

The network property metrics (Table 1) provide information about host connectivity and frequency of interactions within the network (Salathé & Jones 2010; MacIntosh et al. 2012). We measured the network's i) average degree, ii) density, iii) diameter, and iv) average path length (Proulx et al. 2005; Kiss et al. 2006; Jeger et al. 2007; Moore et al. 2014). The presence of sub-groups of hosts was depicted using v) the number of communities, vi) the network transitivity, and vii) the number of components (Newman & Park 2003; Boccaletti et al. 2006; Moore et al. 2014). The properties of the observed networks were compared to 1 000 random graphs generated using the Erdős-Rényi model (Erdős & Rényi 1959). In every randomization, identical network metrics were calculated from randomly assembled graphs with the same number of vertices and edges as those in the observed networks. Each edge was considered to occur independently with the same probability of existing in the random graphs as the other edges.

2.3.2. Node properties: most connected host species

In order to identify host species having a key role in tick cross-infestation and potentially tick-borne disease transmission, we measured the node degree (May 2006) and betweenness score (Boccaletti et

Table 1. Metrics used to measure network and node properties, their definition in terms of network structure and their interpretation in terms of tick-host interactions.

	Network definition	Meaning for tick-host interactions and pathogen circulation
NETWORK PROPERTIES		
Average Degree	Mean number of connections (edges) per node	Quantify the connectivity of hosts by ticks; a high connectivity (indicated by a high average degree, density or diameter or a low average path length) should favour pathogen circulation
Density	Ratio of edges to nodes	
Average path length	Mean shortest path among all nodes on the network	
Diameter	Maximum shortest path between two nodes	
Number of communities	Number of mammal species grouped by dense attachment (connections) internally	Quantify the existence of sub-groups of hosts. Within such groups disease circulation is favoured; between groups, disease circulation is expected to be lower
Transitivity	Tendency of two nodes to be connected when they share a common neighbour	
Number of components	Presence of isolated groups of nodes where the connection of nodes could be interrupted	
NODE PROPERTIES		
Degree	Number of connections (edges) to other nodes	Measures the connectivity of each host to other hosts in the network; a high connectivity favours pathogen transmission to a large number of adjacent hosts
Betweenness	Number of shortest path going through the node	Measures the importance of a node as an intermediary between different parts of the network (i.e., defines the flow pathways); a high betweenness favours pathogen circulation in the network

al. 2006) (Table 1). We considered a highly connected species to be any mammal species whose degree and/or betweenness value was one standard deviation away from the mean.

Since the underlying mechanisms of the transmission of tick-borne disease at an individual level are primarily based on transmission between tick stadia (Jongejan & Uilenberg 2004; Socolovschi et al. 2009), inferences were made at the host community level. The likelihood of pathogen transmission was assumed to be positively correlated with increased network and node connectivity, represented in increased values of all network or node metrics and decreased values of average path length (Proulx et al. 2005; Kiss 2006; Moore et al. 2014).

2.4. Influence of domestic hosts

The influence of domestic mammals on network structure and the potential transmission of tick-borne pathogens was assessed by removing all domestic species from the three networks and comparing the resulting network metrics to those of networks in which the same number of species were randomly removed (hereafter ‘simulated networks’). We removed eight domestic species from the network of mammals sharing all ticks, and seven from both the network of mammals sharing juvenile ticks and the network of mammals sharing adult ticks. The resulting networks were compared to 1 000 simulated networks that were obtained by randomly removing eight or seven mammal species (wild or domestic), respectively. All network graphs were created using Gephi version 0.9.1 (Bastian et al. 2009) and network parameter calculations were carried out using the R package ‘*igraph 0.7.0.*’ (Csárd & Nepusz 2006).

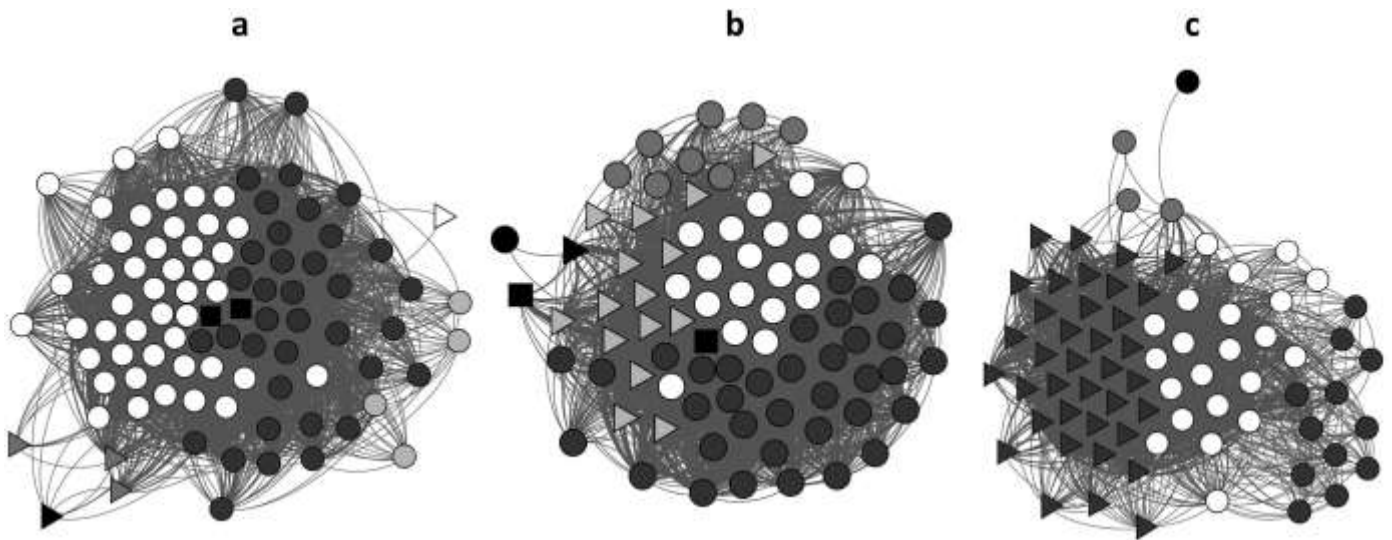


Figure 1. Networks of all mammal hosts connected by shared tick species when all tick life stages (a), juvenile ticks (b) and adult ticks (c) are considered. The different colours represent the different communities identified in each network.

Communities size (number of host species): (a) white circles: 45, dark grey circles: 37, grey triangles: 3, light grey circles: 4, black squares: 2, white triangle: 1, black triangle: 1; (b) grey circles: 8, black squares: 2, light grey triangles: 15, dark grey circles: 37, white circles: 21, black triangle: 1, black circle: 1; (c) grey circles: 3, white circles: 22, dark grey circles: 12, dark grey triangles: 37, black circle: 1.

3. Results

3.1. Networks with all recorded mammal host species

3.1.1. Network of all hosts sharing all ticks

When all tick life stages were considered, 93 host species were connected by a total of 3 105 edges defined by 54 shared tick species. The network displayed seven communities in a single giant component with dense connections internally (Fig. 1a). Domestic species were present in two of the seven communities, which also had the largest number of species, i.e., 45 and 37 mammal species. The observed transitivity was higher and the average path length shorter?? lower than the simulated values. However, the observed network average degree, density, diameter and number of components were similar to that of the random graphs (Table 2). Node degree values ranged from 2 for the African bush elephant to 90 for the scrub hare and sheep. Node betweenness ranged from 0 (yellow mongoose,

donkey, common genet, striped polecat, African bush elephant, round-eared elephant shrew, brown greater galago, western vlei rat, hamadryas baboon and bushveld gerbil) to 93.83 (scrub hare) (Supporting Information). Together with some wild hosts (e.g., scrub hare, lion, leopard, civet, black-backed jackal, caracal, common eland), three domestic mammals (sheep, dog and goat) were identified as the most connected species based on their degree and betweenness values.

Table 2. Values of network properties exhibited by the Erdős-Renyi Graphs (mean value, CI: confidence interval), contrasted with parameter values for the observed mammal network for hosts that share all ticks, juvenile ticks and adult ticks.

NETWORK PROPERTIES	ERDÖS-RENYI GRAPHS			OBSERVED NETWORKS		
	All ticks	Juvenile ticks	Adult ticks	All ticks	Juvenile ticks	Adult ticks
Average degree*	66.77	59.69	41.54	66.77	59.69	41.54
Density*	0.72	0.71	0.56	0.72	0.71	0.56
Diameter*	2	2	2	2	3	3
Number of components*	1	1	1	1	1	1
Average path length	1.28	1.3	1.45	1.27	1.29	1.459
(CI)	(1.2896-1.2897)	(1.3058-1.3059)	(1.4533-1.4535)			
Transitivity	0.71	0.69	0.54	0.84	0.85	0.76
(CI)	(0.7100-0.7102)	(0.693-0.694)	(0.5460-0.5464)			

*Standard deviation = 0

3.1.2. Network of all hosts sharing juvenile ticks

When only juvenile ticks were considered, the network included 85 host mammal species (nodes) connected with a total of 2 537 edges and 48 tick species. The network displayed seven communities in a single giant component with dense connections internally (Fig. 1b). Domestic species were present in three of the seven communities, some of which had the largest number of species, i.e., 8, 37 and 21

mammal species. The observed network diameter and transitivity were higher, and the average path length shorter ??? lower than the simulated values, while the observed values of network average degree, density and number of components were similar to that of the random graphs (Table 2). Node degree values ranged from 2 (round-eared elephant shrew) to 83 (scrub hare). Node betweenness ranged from 0 (southern African hedgehog, Cape porcupine, striped polecat, serval, round-eared elephant shrew, brown greater galago, western vlei rat and bushveld gerbil) to 121.19 (scrub hare) (Supporting Information). Together with some wild hosts (e.g., scrub hare, caracal, civet, lion, cheetah, impala, leopard, African wild dog, black-backed jackal), three domestic mammals were identified as the most connected nodes based on their high degree (dog and sheep) and betweenness (cat) values.

3.1.3. Network of all mammal hosts sharing adult ticks

When only adult ticks were considered, the network connected 75 host species (nodes) with a total of 1 558 edges and 51 tick species. The network displayed five communities in a single giant component with dense connections internally (Fig. 1c). Domestic species were present in two of the five communities, which also had the largest number of species, i.e., 22 and 37 mammal species. The observed network diameter, average path length and transitivity were higher than the simulated values, but the observed network average degree, density and number of components were similar to that of the random graphs (Table 2). Node degree values ranged from 1 for mice to 71 for dog. Node betweenness ranged from 0 (southern African hedgehog, yellow mongoose, donkey, slender mongoose, common genet, Cape genet, white-tailed mongoose, striped polecat, banded mongoose, klipspringer, bat-eared fox, mice, hamadryas baboon, South African springhare and four-striped grass mouse) to 116.10 (scrub hare) (Supporting Information). Together with some wild hosts (e.g., lion, leopard, cheetah, scrub hare, caracal, black-backed jackal, honey badger, eastern rock elephant shrew), four domestic mammals were

identified as the most connected nodes based on their high degree (dog, sheep and goat) and betweenness (sheep, dog and cat) values.

3.2. Networks excluding domestic mammal hosts

3.2.1. Network of wild hosts sharing all tick life stages

From the initial dataset of mammalian hosts that shared ticks of all life stages, eight domestic species (cattle, dog, goat, donkey, horse, cat, sheep and black rat) were identified and removed. A network with 85 nodes (only wild hosts) sharing 52 tick species in 2 526 edges was created. The network displayed eight communities in a single giant component (Fig. 2a). The observed average degree, density and transitivity values were lower, the observed average path length and diameter were higher, and the number of components was similar to those in the simulated networks (Table 3). Node degree values ranged from 2 (African bush elephant) to 82 (scrub hare). Node betweenness ranged from 0 (brown greater galago, western vlei rat, bushveld gerbil, striped polecat, round-eared elephant shrew, yellow mongoose, common genet, African bush elephant and hamadryas baboon) to 95.41 (scrub hare) (Supporting Information). The most connected wild hosts included the same species as in the network of mammals sharing all ticks, adding in five more based on their degree values (caracal, cheetah, common eland, spotted hyena and African wild dog), and two more (greater kudu and leopard) based on their betweenness values.

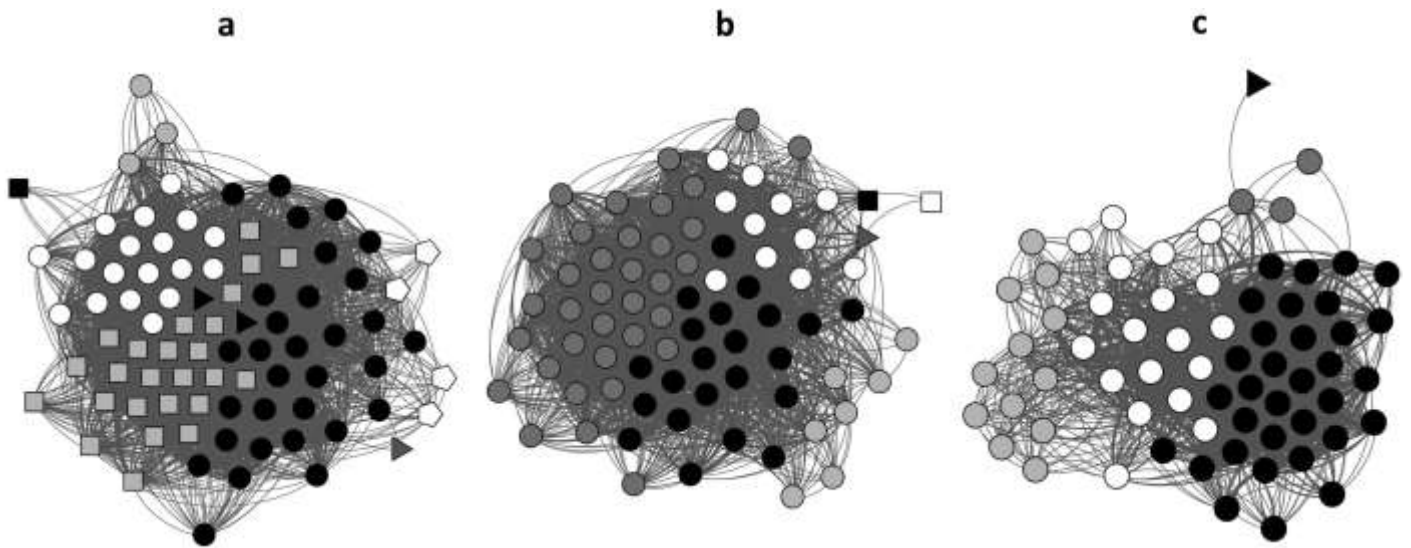


Figure 2. Networks of wild mammal hosts connected by shared tick species when all tick life stages (a), juvenile ticks (b) and adult ticks (c) are considered after domestic host species were removed. The different colours represent the different communities identified in each network. Communities size (number of host species): (a) light grey circles: 3, black circles: 31, white pentagons: 4, white circles: 18, light grey squares: 25, black triangle: 2, grey triangle: 1, black square: 1; (b) light grey circles: 7, grey circles: 35, white circles: 11, black circles: 22, dark grey triangles: 1, black square: 1, white square: 1; (c) white circles: 19, grey circles: 3, light grey circles: 12, black circles: 33, black triangle: 1.

Table 3. Network properties of the observed networks excluding domestic species (mean value, CI: confidence interval), compared to 1 000 simulated graphs obtained after having randomly removed the same number of host species.

NETWORK PROPERTIES	SIMULATED GRAPHS			WILD MAMMAL HOST NETWORKS		
	All ticks	Juvenile ticks	Adult ticks	All ticks	Juvenile ticks	Adult ticks
Average degree	60.97	54.83	37.66	59.43	53.33	34.76
(CI)	(60.90-61.04)	(54.76-54.90)	(37.59-37.73)			
Density	0.72	0.71	0.56	0.70	0.69	0.51
(CI)	(0.725-0.726)	(0.710-0.712)	(0.561-0.564)			
Diameter	2.26	3	2.98	3	3	3
(CI)	(2.23-2.28)	(2.97-3.02)	(2.97-2.99)			
Number of components	1	1	1	1	1	1
Average path length	1.27	1.29	1.45	1.29	1.30	1.51
(CI)	(1.273-1.275)	(1.290-1.292)	(1.456-1.459)			
Transitivity	0.84	0.85	0.76	0.842	0.84	0.75
(CI)	(0.848-0.849)	(0.851-0.852)	(0.767-0.769)			

3.2.2 Networks of wild hosts sharing juvenile ticks

From the initial dataset of mammalian hosts that shared juvenile ticks, seven domestic species (cattle, dog, goat, horse, cat, sheep and black rat) were identified and removed. A network of 78 nodes (only wild hosts) sharing 45 juvenile tick species in 2 080 edges was created. The network displayed seven communities in a single giant component (Fig. 2b). The observed values of average degree, density and transitivity were lower, the observed average path length was higher, and diameter and the number of components were similar to those of the simulated networks (Table 3). The degree values of node properties ranged from 2 (round-eared elephant shrew) to 76 (scrub hare). Betweenness ranged from 0 (serval, brown greater galago, southern African hedgehog, Cape porcupine, western vlei rat, bushveld

gerbil, striped polecat and round-eared elephant shrew) to 114.66 (scrub hare) (Supporting Information). The most connected wild hosts sharing juvenile ticks based on degree and betweenness values included the same species as in the network of all mammals, adding in one more for degree value (black-backed jackal).

3.2.3. Network of wild hosts only sharing adult ticks

From the initial dataset of mammalian hosts that shared adult ticks, seven domestic mammal species (cattle, dog, goat, donkey, horse, cat and sheep) were removed. A network of 68 nodes (only wild hosts) sharing adult ticks from 48 species in 1 182 edges was created. The network displayed five communities in a single giant component (Fig. 2c). The observed values of average degree, density and transitivity were lower, the observed average path length and diameter were higher, and the number of components was similar to those of the simulated networks (Table 3). Node degree values ranged from 1 for mice to 62 for lion and leopard. Node betweenness ranged from 0 (klipspringer, southern African hedgehog, yellow mongoose, slender mongoose, common genet, Cape genet, banded mongoose, white-tailed mongoose, striped polecat, bat-eared fox, South African springhare, four-striped grass mouse, hamadryas baboon and mice) to 136.47 (scrub hare) (Supporting Information). Globally, except for network diameter, the differences between the observed (only wild hosts) and simulated (wild and domestic hosts) networks were more marked when considering adult ticks than when considering juvenile ticks. The most connected wild hosts sharing adult ticks included the same species as in the network of all mammals, adding in five more based on their degree values (African wild dog, spotted hyena, African civet, common eland and greater kudu), and three more (honey badger, African wild dog and spotted hyena) based on their betweenness values.

4. Discussion

Our results showed that South African large and medium-sized mammal host species were highly connected by the tick species that they share, facilitating cross-infestation with ticks and the transmission of tick-borne pathogens. We also found that excluding domestic species from the networks significantly reduced overall network connectivity, indicating that domestic mammals may play a key role in facilitating the spread of ticks and tick-borne diseases in southern African mammal communities. These results indicate that conservation practices that mingle domestic livestock and wild mammals will lead to increased transmission of tick-borne pathogens in **both** domestic and wild populations.

The mean shortest pathway between any two mammal species and the tendency of some groups of mammals to be connected by the presence of others (transitivity) showed that there is a high probability for a potential pathogen to find a path to infect any other mammal species. The structure of the network thus facilitates pathogen spread (Godfrey 2013). This implies that after acquiring a pathogen during a blood meal, and off-host moulting, a tick would be able to choose between many mammal species to which it could spread a potential infection, particularly in the case of two- and three- host ticks.

Some highly connected mammal species appeared to contribute disproportionately to pathogen circulation among hosts. The scrub hare was the most connected (highest degree) and the most central (highest betweenness) in the network of mammals sharing ticks of any life stage and juvenile ticks, while the domestic dog was the most connected and the scrub hare the most central in the network of mammals sharing adult ticks. The eastern rock elephant shrew also appeared highly connected in some networks, but its high connectedness may be artefactual because large numbers (>800) of individuals were examined, but with only a low level of infestation. In contrast, the high connectedness of scrub hare is supported by the large number of individuals infested. Central hosts such as the scrub hare (i.e.,

hosts infested by many ticks that infest many other hosts in the network; Canright & Engoe-Monsen 2006; Opsahl et al. 2010) may receive and transmit tick-borne diseases more frequently than noncentral species and therefore behave as ‘super-spreaders’ (Canright & Engoe-Monsen 2006; Griffin & Nunn 2012). Several tick species shared by the central highly connected mammal hosts, carry important pathogens that represent an animal and human health threat (Table 4). The identification of such host species is therefore crucial for developing surveillance protocols and interventions aimed at preventing future disease emergence.

Table 4. Some of the tick species shared by the most highly connected mammals identified in the networks (i.e., whose degree and/or betweenness value is at least one standard deviation away from the mean), pathogens they potentially transmit and diseases they produce.

Tick species	Highly connected host species (in sequence of connectivity) ????	Tick-borne pathogen potentially transmitted by that tick species	Disease
<i>Amblyomma hebraeum</i> Koch, 1844	cheetah, impala, cat, dog, jackal, goat, caracal, civet, sheep, lion, leopard, scrub hare, wild dog, eland, honey badger, spotted hyena.	<i>Ehrlichia ruminantium</i>	Heartwater or Cowdriosis in ruminants
		<i>Rickettsia africae</i>	African tick-bite fever
<i>Hyalomma rufipes</i> Koch, 1844	goat, eastern rock elephant shrew, scrub hare, sheep, eland.	Crimean–Congo haemorrhagic fever virus (Bunyaviridae: Nairovirus).	Crimean-Congo haemorrhagic fever (CCHF)
<i>Hyalomma truncatum</i> Koch, 1844	cheetah, impala, dog, goat, eastern rock elephant shrew, scrub hare, honey badger, sheep, lion, leopard, eland.	Crimean–Congo haemorrhagic fever virus (Bunyaviridae: Nairovirus).	Crimean-Congo haemorrhagic fever (CCHF)

<i>Rhipicephalus appendiculatus</i> Neumann, 1901	cheetah, impala, dog, jackal, goat, civet, scrub hare, wild dog, honey badger, sheep, lion, leopard, eland, spotted hyena.	<i>Theileria parva</i>	East coast fever and Corridor disease
<i>Rhipicephalus decoloratus</i> Koch, 1844 Boophilus	cheetah, impala, dog, goat, caracal, civet, scrub hare, wild dog, honey badger, sheep, lion, leopard, eland, spotted hyena.	<i>Anaplasma marginale</i>	Bovine anaplasmosis
<i>Rhipicephalus evertsi evertsi</i> Neumann, 1897	cheetah, impala, dog, jackal, goat, caracal, civet, eastern rock elephant shrew, scrub hare, honey badger, sheep, lion, eland.	<i>Babesia bigemina</i> <i>Borrelia theileri</i> <i>Anaplasma marginale</i>	Bovine babesiosis Borreliosis Bovine anaplasmosis
<i>Rhipicephalus microplus</i> Canestrini, 1888 Boophilus	dog, goat, eland.	<i>Anaplasma marginale</i> <i>Babesia bovis, Babesia bigemina</i> <i>Borrelia theileri</i>	Bovine anaplasmosis Bovine babesiosis Borreliosis
<i>Rhipicephalus zambeziensis</i> Walker, Norval and Corwin, 1981	cheetah, impala, jackal, civet, cat, scrub hare, wild dog, lion, leopard, spotted hyena, eland.	<i>Theileria parva</i>	East coast fever and Corridor disease

Our results indicate an important role played by domestic mammals in tick dynamics. Several domestic species (sheep, goat, dog and cat) were key nodes in the networks including all host species. (see Fig. 3 for a simplified network). Also, the exclusion of domestic species reduced the connectivity of the networks. The decrease in connectivity was more marked when considering adult ticks than juvenile ticks. This might indicate some preferences among adult ticks for domestic mammals, in

accordance with a higher specificity of adult ticks previously observed in the same communities (Espinaze et al. 2016). Meanwhile, the high frequency of interactions induced by domestic mammals (in the simulated graphs) offered a greater number of potential routes for a disease to spread, thereby facilitating an interspecific transmission of pathogens. Our results thus support the hypothesis that although some South African ticks show some degree of specialization on wild animals, opportunistic feeding on domestic hosts can lead to shortened transmission pathways and the facilitation of pathogen spread between mammal species.

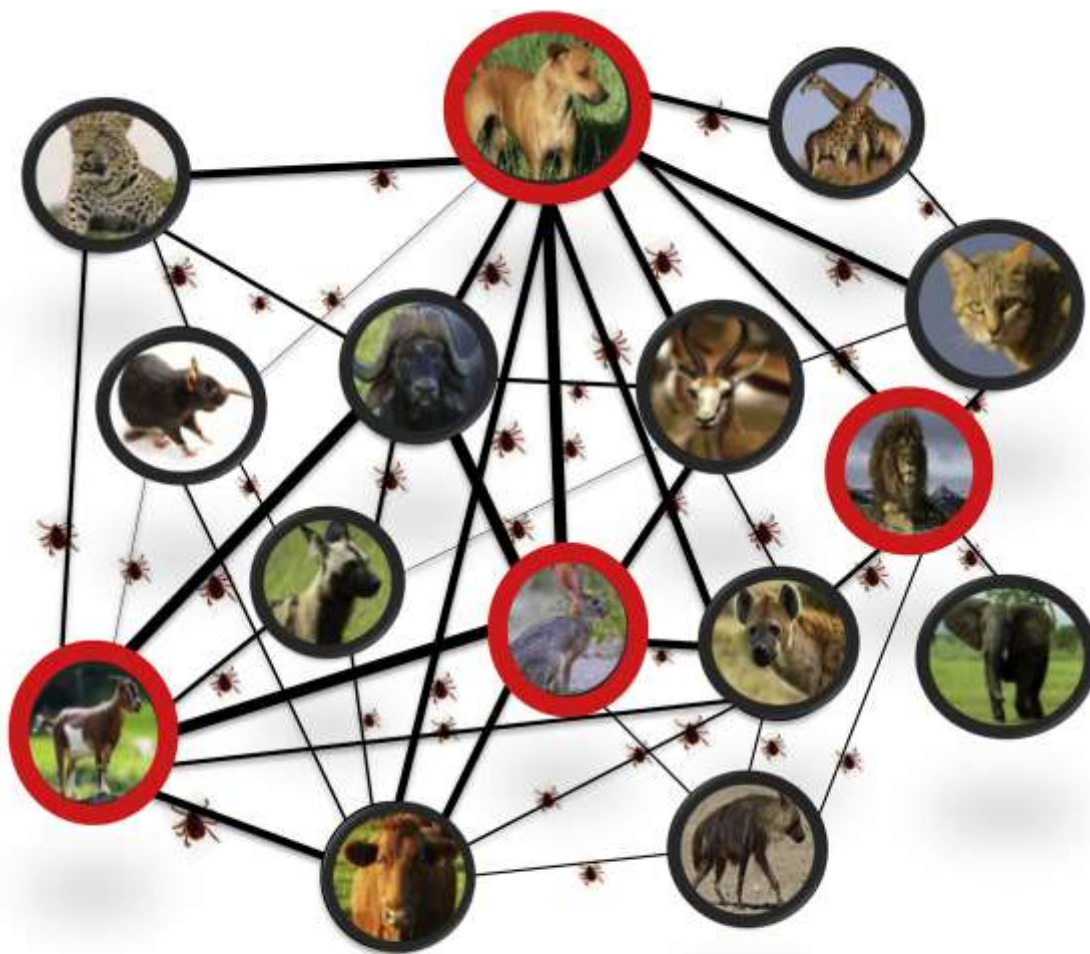


Fig. 3. Subset of a real-life network as a result of this study. Mammal species (wild or domestic) sharing tick species at all life stages are depicted. The thicker the line, the larger the number of tick species shared by the mammal species is. Some of the most-connected mammal species are highlighted with a red circle.

Previous studies using ecological networks have also shown that a system with a large number of vertebrate species induces a cohesive network, and that domestic hosts modify the network structure increasing pathogen circulation and infection dynamics in the western Palearctic (Estrada-Peña et al. 2015). Mathematical analyses such as regression analysis and host community models have revealed that a high host species richness poses a high risk of cross-species parasite infestation. For instance, a higher richness of African bovid species facilitates gastrointestinal parasitism in an impala (*Aepyceros melampus*) population (Ezenwa 2004), and the diversity and identity of several vertebrate species are important factors influencing tick cross-infestation and tick-borne pathogen transmission (LoGiudice et al. 2008; Wells et al. 2013). Similarly, our results, do not support the hypothesis of a dilution effect (Schmidt & Ostfeld 2001) due to an increased host diversity in mixed livestock-game systems .

Limiting contacts between wild and domestic mammals will decrease the risk of ticks and tick-borne disease transmission. Adequate management measures to prevent disease spread in the wildlife-domestic animal interface are crucial, as pathogen spill-over from protected areas may have socio-political implications that represents a risk to wildlife conservation (Daszak et al. 2001; De Vos et al 2016). Small and isolated wild animal populations may be particularly vulnerable to disease, especially if they live in proximity to domestic animals (Daszak et al. 2001). Therefore, management actions should limit wildlife-domestic animal interactions. The use of fences around protected areas is one of the most common procedures to prevent the transmission of infectious diseases in South Africa (Jori et al. 2011; Hayward & Somers 2012). Likewise, the identification and spatial separation of wildlife sub-groups carrying pathogens (zoning) prevents disease spread into areas containing uninfected animals (Artois et al. 2011). The identification of the most connected wild host species and superspreaders allows surveillance systems to target them and more efficiently detect the emergence of possible diseases (Caron et al. 2012; Gortazar et al. 2015). Other management measures include the use of veterinary or medical control. However, it is acknowledged that the relationship between pathogens and

their hosts is a natural element of functional ecosystems (Hudson et al. 2006; Tompkins et al. 2011; De Vos et al 2016), and so management using drugs such as acaricides is not suitable for wild populations. Alternatively, short-term vaccinations aimed at a specific wildlife population may reduce infection prevalence without the risk of drug resistance or harmful residues in the environment (Artois et al. 2011; Gortazar et al. 2015). Our results thus provide a clear indication that mixed systems of livestock and game are likely to prove more rather than less susceptible to tick-borne disease, with important implications for conservation management, particularly in the case of small wild populations and threatened and endangered species.

5. Conclusions

The transmission of ticks and tick-borne pathogens can potentially be facilitated among mammal species in South Africa. This is evidenced in the high connectivity exhibited by domestic and wild mammal species assessed through network analysis. Moreover, this study has uncovered the role played by domestic species in strengthening connectivity, and therefore their important contribution in the transmission of tick-borne pathogens among South African mammal species. This highlights the potential consequences of allowing contact between wild and domestic mammals, such as by sharing the same geographical area.

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Supporting Information

Appendix A. The 54 tick species considered in the network analysis, their scientific names, number of collections and number of mammal host species on which ticks were found. Collections refer to whenever a tick species is sampled from a host (i.e., there can be many ticks of a given species collected in a sample from a host).

Tick species scientific name	Number of collections	Number of host species
<i>Amblyomma nuttalli</i> Dönitz, 1909	2	2
<i>Rhipicephalus lunulatus</i> Neumann, 1907	2	2
<i>Rhipicephalus theileri</i> Bedford and Hewitt, 1925	2	2
<i>Ixodes rhabdomysae</i> Arthur, 1959	3	2
<i>Rhipicephalus evertsi mimeticus</i> Dönitz, 1910	3	2
<i>Rhipicephalus simpsoni</i> Nuttall, 1910	3	3
<i>Rhipicephalus sulcatus</i> Neumann, 1908	3	2
<i>Amblyomma tholloni</i> Neumann, 1899	4	3
<i>Ixodes alluaudi</i> Neumann, 1913	4	2
<i>Rhipicephalus tricuspis</i> Dönitz, 1906	5	2
<i>Ixodes bakeri</i> Arthur and Clifford, 1961	8	4
<i>Ixodes cavipalpus</i> Nuttall and Warburton, 1908	8	2
<i>Rhipicephalus neumanni</i> Walker, 1990	11	5
<i>Ixodes corwini</i> Keirans, Clifford and Walker, 1982	12	2
<i>Dermacentor rhinocerinus</i> Denny, 1843	15	5
<i>Rhipicephalus zumpti</i> Santos Dias, 1950	15	2
<i>Haemaphysalis colesbergensis</i> Apanaskevich and Horak, 2008	27	2
<i>Haemaphysalis aciculifer</i> Warburton, 1913	34	8
<i>Rhipicephalus lounsburyi</i> Walker, 1990	45	10
<i>Rhipicephalus capensis</i> Koch, 1844	47	12
<i>Haemaphysalis parmata</i> Neumann, 1905	91	4
<i>Haemaphysalis hyracophila</i> Hoogstraal, Walker and Neitz, 1971	100	3
<i>Hyalomma glabrum</i> Delpy, 1949	104	10
<i>Haemaphysalis zumpti</i> Hoogstraal and El Kammah, 1974	114	23
<i>Rhipicephalus kochi</i> Dönitz, 1905	118	7
<i>Rhipicephalus turanicus</i> Pomerantzev, 1940	124	12
<i>Rhipicentor nuttalli</i> Cooper and Robinson, 1908	145	5
<i>Rhipicephalus exophthalmos</i> Keirans and Walker, 1993	152	11
<i>Margaropus winthemi</i> Karsch, 1879	160	14
<i>Haemaphysalis spinulosa</i> Neumann, 1906	165	21
<i>Rhipicephalus maculatus</i> Neumann, 1901	203	9
<i>Rhipicephalus oculatus</i> Neumann, 1901	300	7
<i>Rhipicephalus arnoldi</i> Theiler and Zumpt, 1949	392	8
<i>Rhipicephalus muehlensi</i> Zumpt, 1943	398	10
<i>Rhipicephalus nitens</i> Neumann, 1904	514	6
<i>Rhipicephalus gertrudae</i> Feldman-Muhsam, 1960	526	30

<i>Rhipicephalus follis</i> Dönitz, 1910	529	20
<i>Rhipicephalus distinctus</i> Bedford, 1932	549	11
<i>Ixodes pilosus</i> Koch, 1844	562	18
<i>Hyalomma rufipes</i> Koch, 1844	616	17
<i>Rhipicephalus microplus</i> Canestrini, 1888 Boophilus	799	4
<i>Amblyomma marmoreum</i> Koch, 1844	894	46
<i>Haemaphysalis silacea</i> Robinson, 1912	936	17
<i>Rhipicephalus warburtoni</i> Walker and Horak, 2000	950	15
<i>Rhipicephalus zambeziensis</i> Walker, Norval and Corwin, 1981	1052	27
<i>Ixodes rubicundus</i> Neumann, 1904	1104	17
<i>Rhipicephalus simus</i> Koch, 1844	1242	42
<i>Rhipicephalus glabroscutatus</i> Du Toit, 1941	1509	20
<i>Hyalomma truncatum</i> Koch, 1844	1608	39
<i>Haemaphysalis elliptica</i> Koch, 1844	1954	36
<i>Rhipicephalus decoloratus</i> Koch, 1844 _Boophilus	3177	42
<i>Rhipicephalus appendiculatus</i> Neumann, 1901	3380	44
<i>Amblyomma hebraeum</i> Koch, 1844	4236	48
<i>Rhipicephalus evertsi evertsi</i> Neumann, 1897	6393	45

Appendix B. Mammal host species, their scientific names, common names and type of animal (wild or domestic).

Mammal species scientific name	Mammal species common name	Type
<i>Otolemur crassicaudatus</i>	Brown greater galago	wild
<i>Papio hamadryas</i>	Hamadryas baboon	wild
<i>Loxodonta africana</i>	African bush elephant	wild
<i>Macroscelides proboscideus</i>	Round-eared elephant shrew	wild
<i>Otomys occidentalis</i>	Western Vlei Rat	wild
<i>Genetta genetta</i>	Common genet	wild
<i>Ictonyx striatus</i>	Striped polecat	wild
<i>Soricidae</i>	Shrew	wild
<i>Rhynchogale melleri</i>	Meller's mongoose	wild
<i>Oreotragus oreotragus</i>	Klipspringer	wild
<i>Parahyaena brunnea</i>	Brown hyena	wild
<i>Cynictis penicillata</i>	Yellow mongoose	wild
<i>Tatera leucogaster</i>	Bushveld gerbil	wild
<i>Mastomys natalensis</i>	Natal multimammate mouse	wild
<i>Saccostomus campestris</i>	South African pouched mouse	wild
<i>Hystrix africaeaustralis</i>	Cape porcupine	wild
<i>Praomys</i> sp.	Rodent	wild
<i>Hippotragus niger</i>	Sable antelope	wild
<i>Elephantulus brachyrhynchus</i>	Short-snouted elephant shrew	wild
<i>Otocyon megalotis</i>	Bat-eared fox	wild

<i>Suricata suricatta</i>	Meerkat	wild
<i>Leptailurus serval</i>	Serval	wild
<i>Chlorocebus aethiops</i>	Grivet	wild
<i>Mastomys coucha</i>	Southern multimammate mouse	wild
<i>Galerella sanguinea</i>	Slender mongoose	wild
<i>Vulpes chama</i>	Cape fox	wild
<i>Ichneumia albicauda</i>	White-tailed mongoose	wild
<i>Mungos mungo</i>	Banded mongoose	wild
<i>Aethomys namaquensis</i>	Namaqua rock rat	wild
<i>Felis nigripes</i>	Black-footed cat	wild
<i>Galerella pulverulenta</i>	Cape gray mongoose	wild
<i>Proteles cristatus</i>	Aardwolf	wild
<i>Felis silvestris</i>	Wildcat	wild
<i>Genetta sp.</i>	Genets	wild
<i>Lemniscomys rosalia</i>	Single-striped grass mouse	wild
<i>Atelerix frontalis</i>	Southern African hedgehog	wild
<i>Hippotragus equinus</i>	Roan antelope	wild
<i>Raphicerus campestris</i>	Steenbok	wild
<i>Neotragus moschatus</i>	Suni	wild
<i>Alcelaphus buselaphus</i>	Hartebeest	wild
<i>Genetta tigrina</i>	Cape genet	wild
<i>Mellivora capensis</i>	Honey badger	wild
<i>Pedetes capensis</i>	South African springhare	wild
<i>Damaliscus lunatus</i>	Common tsessebe	wild
<i>Crocuta crocuta</i>	Spotted hyena	wild
<i>Aethomys chrysophilus</i>	Red rock rat	wild
<i>Potamochoerus larvatus</i>	Bushpig	wild
<i>Otomys sp.</i>	Mice	wild
<i>Acinonyx jubatus</i>	Cheetah	wild
<i>Raphicerus melanotis</i>	Cape grysbok	wild
<i>Ceratotherium simum</i>	White rhinoceros	wild
<i>Antidorcas marsupialis</i>	Springbok	wild
<i>Canis mesomelas</i>	Black-backed jackal	wild
<i>Elephantulus edwardii</i>	Cape elephant shrew	wild
<i>Rhabdomys pumilio</i>	Four-striped grass mouse	wild
<i>Panthera pardus</i>	Leopard	wild
<i>Lycaon pictus</i>	African wild dog	wild
<i>Diceros bicornis</i>	Black rhinoceros	wild
<i>Civettictis civetta</i>	African civet	wild
<i>Oryx gazella</i>	Gemsbok	wild
<i>Sylvicapra grimmia</i>	Common duiker	wild
<i>Connochaetes gnou</i>	Black wildebeest	wild
<i>Giraffa camelopardalis</i>	Giraffe	wild

<i>Redunca fulvorufula</i>	Mountain reedbuck	wild
<i>Cephalophus natalensis</i>	Red forest duiker	wild
<i>Redunca arundinum</i>	Southern reedbuck	wild
<i>Pronolagus rupestris</i>	Smith's red rock hare	wild
<i>Tragelaphus scriptus</i>	Bushbuck	wild
<i>Equus zebra</i>	Mountain zebra	wild
<i>Lepus capensis</i>	Cape hare	wild
<i>Panthera leo</i>	Lion	wild
<i>Caracal caracal</i>	Caracal	wild
<i>Damaliscus pygargus</i>	Bontebok	wild
<i>Pelea capreolus</i>	Grey rhebok	wild
<i>Taurotragus oryx</i>	Common eland	wild
<i>Connochaetes taurinus</i>	Blue wildebeest	wild
<i>Syncerus caffer</i>	African buffalo	wild
<i>Equus burchelli</i>	Plains zebra	wild
<i>Phacochoerus africanus</i>	Warthog	wild
<i>Elephantulus myurus</i>	Eastern rock elephant shrew	wild
<i>Procavia capensis</i>	Rock hyrax	wild
<i>Tragelaphus angasii</i>	Nyala	wild
<i>Tragelaphus strepsiceros</i>	Greater kudu	wild
<i>Aepyceros melampus</i>	Impala	wild
<i>Lepus saxatilis</i>	Scrub hare	wild
<i>Ovis aries</i>	Sheep	domestic
<i>Equus asinus</i>	Donkey	domestic
<i>Capra hircus</i>	Goat	domestic
<i>Canis lupus familiaris</i>	Dog	domestic
<i>Equus caballus</i>	Horse	domestic
<i>Felis catus</i>	Cat	domestic
<i>Bos</i> sp. (<i>Bos taurus/indicus</i>)	Cattle	domestic
<i>Rattus rattus</i>	Black rat	domestic

Appendix C. Node property values (degree and betweenness) of mammal hosts sharing all ticks. The most connected species in bold.

Mammal species sharing all ticks	Degree	Betweenness
<i>Lepus saxatilis</i>	90	93.83
<i>Ovis aries</i>	90	44.50
<i>Canis lupus familiaris</i>	89	32.66
<i>Panthera leo</i>	88	70.74
<i>Capra hircus</i>	87	29.46
<i>Canis mesomelas</i>	87	29.11
<i>Civettictis civetta</i>	87	28.52
<i>Panthera pardus</i>	87	26.74
<i>Taurotragus oryx</i>	86	27.95
<i>Bos</i> sp.	86	25.98

<i>Crocota crocuta</i>	86	24.78
<i>Lycaon pictus</i>	86	24.78
<i>Acinonyx jubatus</i>	86	22.66
<i>Caracal caracal</i>	85	31.69
<i>Felis catus</i>	84	23.30
<i>Tragelaphus strepsiceros</i>	84	23.24
<i>Mellivora capensis</i>	84	20.44
<i>Aepyceros melampus</i>	84	15.06
<i>Genetta sp.</i>	83	19.16
<i>Damaliscus pygargus</i>	83	16.13
<i>Syncerus caffer</i>	83	14.68
<i>Phacochoerus africanus</i>	83	14.47
<i>Felis silvestris</i>	82	23.02
<i>Giraffa camelopardalis</i>	82	13.56
<i>Mungos mungo</i>	81	17.26
<i>Proteles cristatus</i>	81	14.30
<i>Tragelaphus scriptus</i>	80	12.83
<i>Rhabdomys pumilio</i>	79	23.36
<i>Equus caballus</i>	79	13.31
<i>Ceratotherium simum</i>	79	11.46
<i>Equus burchelli</i>	78	10.29
<i>Cephalophus natalensis</i>	78	8.79
<i>Elephantulus myurus</i>	77	20.24
<i>Hippotragus equinus</i>	77	9.48
<i>Aethomys chrysophilus</i>	76	10.25
<i>Ichneumia albicauda</i>	75	10.64
<i>Connochaetes gnou</i>	74	9.18
<i>Otomys sp.</i>	74	8.51
<i>Redunca arundinum</i>	74	6.66
<i>Tragelaphus angasii</i>	74	6.39
<i>Chlorocebus aethiops</i>	73	7.72
<i>Neotragus moschatus</i>	73	6.06
<i>Genetta tigrina</i>	72	10.70
<i>Diceros bicornis</i>	72	7.04
<i>Connochaetes taurinus</i>	72	5.91
<i>Raphicerus campestris</i>	72	5.91
<i>Lepus capensis</i>	71	7.67
<i>Hystrix africaeaustralis</i>	71	6.94
<i>Equus zebra</i>	71	5.84
<i>Potamochoerus larvatus</i>	70	6.67
<i>Damaliscus lunatus</i>	70	4.91
<i>Sylvicapra grimmia</i>	70	4.91
<i>Pedetes capensis</i>	69	16.31
<i>Procavia capensis</i>	69	13.61
<i>Pronolagus rupestris</i>	69	13.61
<i>Antidorcas marsupialis</i>	69	12.66
<i>Pelea capreolus</i>	69	10.88
<i>Leptailurus serval</i>	69	9.11

<i>Oryx gazella</i>	69	6.65
<i>Redunca fulvorufula</i>	66	10.84
<i>Otocyon megalotis</i>	64	6.40
<i>Praomys</i> sp.	64	4.52
<i>Oreotragus oreotragus</i>	64	2.04
<i>Galerella pulverulenta</i>	63	21.39
<i>Vulpes chama</i>	63	11.35
<i>Mastomys natalensis</i>	63	3.92
<i>Alcelaphus buselaphus</i>	62	2.56
<i>Suricata suricatta</i>	61	9.26
<i>Aethomys namaquensis</i>	61	4.39
<i>Lemniscomys rosalia</i>	61	4.39
<i>Mastomys coucha</i>	61	4.39
<i>Hippotragus niger</i>	60	2.55
<i>Raphicerus melanotis</i>	60	1.91
<i>Parahyaena brunnea</i>	54	1.96
<i>Galerella sanguinea</i>	53	5.28
<i>Atelerix frontalis</i>	52	4.32
<i>Rhynchogale melleri</i>	50	1.86
<i>Felis nigripes</i>	48	5.92
<i>Otolemur crassicaudatus</i>	47	0
<i>Rattus rattus</i>	46	1.33
<i>Soricidae</i>	44	0.18
<i>Equus asinus</i>	43	0
<i>Otomys occidentalis</i>	41	0
<i>Tatera leucogaster</i>	41	0
<i>Elephantulus edwardii</i>	40	8.08
<i>Elephantulus brachyrhynchus</i>	39	0.03
<i>Saccostomus campestris</i>	25	1.61
<i>Cynictis penicillata</i>	22	0
<i>Genetta genetta</i>	22	0
<i>Ictonyx striatus</i>	20	0
<i>Macroscelides proboscideus</i>	10	0
<i>Papio hamadryas</i>	10	0
<i>Loxodonta africana</i>	2	0

Appendix D. Node property values (degree and betweenness) of mammal hosts sharing juvenile ticks. The most connected species in bold.

Mammal species sharing juvenile ticks	Degree	Betweenness
<i>Lepus saxatilis</i>	83	121.19
<i>Caracal caracal</i>	81	50.97
<i>Civettictis civetta</i>	81	43.83
<i>Acinonyx jubatus</i>	80	30.49
<i>Aepyceros melampus</i>	80	30.49
<i>Panthera leo</i>	80	30.49
<i>Canis lupus familiaris</i>	79	24.39
<i>Lycaon pictus</i>	79	24.39

<i>Ovis aries</i>	79	24.39
<i>Panthera pardus</i>	79	24.39
<i>Felis catus</i>	78	33.18
<i>Canis mesomelas</i>	78	31.86
<i>Capra hircus</i>	78	24.92
<i>Genetta sp.</i>	76	19.74
<i>Mungos mungo</i>	75	18.50
<i>Felis silvestris</i>	74	14.95
<i>Tragelaphus scriptus</i>	74	14.86
<i>Crocuta crocuta</i>	73	20.35
<i>Cephalophus natalensis</i>	73	14.19
<i>Proteles cristatus</i>	72	22.23
<i>Giraffa camelopardalis</i>	72	12.89
<i>Phacochoerus africanus</i>	72	8.77
<i>Taurotragus oryx</i>	72	8.77
<i>Tragelaphus angasii</i>	72	8.77
<i>Tragelaphus strepsiceros</i>	72	8.77
<i>Ichneumia albicauda</i>	71	12.51
<i>Bos sp.</i>	71	7.81
<i>Redunca arundinum</i>	71	7.81
<i>Syncerus caffer</i>	71	7.81
<i>Elephantulus myurus</i>	70	23.31
<i>Rhodomys pumilio</i>	69	28.03
<i>Neotragus moschatus</i>	68	6.66
<i>Connochaetes taurinus</i>	68	6.07
<i>Equus burchelli</i>	68	6.07
<i>Raphicerus campestris</i>	68	6.07
<i>Damaliscus pygargus</i>	67	9.66
<i>Genetta tigrina</i>	67	5.73
<i>Damaliscus lunatus</i>	67	5.21
<i>Hippotragus equinus</i>	67	5.21
<i>Mellivora capensis</i>	67	5.21
<i>Sylvicapra grimmia</i>	67	5.21
<i>Otomys sp.</i>	66	14.89
<i>Chlorocebus aethiops</i>	66	10.64
<i>Lepus capensis</i>	65	14.18
<i>Procavia capensis</i>	64	15.16
<i>Pronolagus rupestris</i>	64	15.16
<i>Pedetes capensis</i>	63	19.62
<i>Oreotragus oreotragus</i>	63	3.22
<i>Aethomys chrysophilus</i>	61	18.03
<i>Praomys sp.</i>	61	8.35
<i>Pelea capreolus</i>	61	2.61

<i>Antidorcas marsupialis</i>	60	8.70
<i>Connochaetes gnou</i>	60	8.70
<i>Redunca fulvorufula</i>	60	8.70
<i>Otocyon megalotis</i>	59	14.11
<i>Alcelaphus buselaphus</i>	59	2.93
<i>Raphicerus melanotis</i>	59	2.57
<i>Mastomys natalensis</i>	58	8.60
<i>Equus caballus</i>	58	1.38
<i>Equus zebra</i>	58	1.38
<i>Oryx gazella</i>	58	1.38
<i>Ceratotherium simum</i>	52	1.09
<i>Suricata suricatta</i>	52	0.69
<i>Galerella pulverulenta</i>	51	7.29
<i>Potamochoerus larvatus</i>	51	0.56
<i>Diceros bicornis</i>	49	0.17
<i>Leptailurus serval</i>	47	0
<i>Otolemur crassicaudatus</i>	47	0
<i>Atelerix frontalis</i>	45	0
<i>Hystrix africaeaustralis</i>	45	0
<i>Rhynchogale melleri</i>	44	3.02
<i>Galerella sanguinea</i>	43	0.40
<i>Mastomys coucha</i>	39	4.14
<i>Soricidae</i>	39	0.16
<i>Aethomys namaquensis</i>	37	4.14
<i>Lemniscomys rosalia</i>	37	4.14
<i>Vulpes chama</i>	32	3.49
<i>Rattus rattus</i>	32	0.72
<i>Otomys occidentalis</i>	22	0
<i>Tatera leucogaster</i>	22	0
<i>Elephantulus edwardii</i>	18	9.44
<i>Saccostomus campestris</i>	14	0.12
<i>Elephantulus brachyrhynchus</i>	14	0.02
<i>Ictonyx striatus</i>	8	0
<i>Macroscelides proboscideus</i>	2	0

Appendix E. Node property values (degree and betweenness) of mammal hosts sharing adult ticks. The most connected species in bold.

Mammal species sharing adult ticks	Degree	Betweenness
<i>Canis lupus familiaris</i>	71	82.53
<i>Ovis aries</i>	70	97.36
<i>Panthera pardus</i>	69	73.22
<i>Panthera leo</i>	69	65.49
<i>Lepus saxatilis</i>	67	116.10

<i>Acinonyx jubatus</i>	65	49.13
<i>Mellivora capensis</i>	63	41.74
<i>Caracal caracal</i>	61	42.51
<i>Capra hircus</i>	60	29.87
<i>Canis mesomelas</i>	59	47.07
<i>Lycaon pictus</i>	58	40.38
<i>Crocuta crocuta</i>	58	38.09
<i>Bos</i> sp.	58	20.84
<i>Felis catus</i>	57	43.55
<i>Civettictis civetta</i>	57	37.38
<i>Taurotragus oryx</i>	57	20.54
<i>Tragelaphus strepsiceros</i>	57	20.54
<i>Giraffa camelopardalis</i>	55	16.78
<i>Damaliscus pygargus</i>	54	15.87
<i>Phacochoerus africanus</i>	53	8.94
<i>Syncerus caffer</i>	53	8.94
<i>Equus burchelli</i>	52	8.15
<i>Hippotragus equinus</i>	52	8.15
<i>Tragelaphus angasii</i>	50	8.26
<i>Equus caballus</i>	50	7.32
<i>Aepyceros melampus</i>	50	6.72
<i>Ceratotherium simum</i>	50	5.98
<i>Connochaetes taurinus</i>	49	5.94
<i>Vulpes chama</i>	48	24.66
<i>Leptailurus serval</i>	47	14.62
<i>Connochaetes gnou</i>	47	10.96
<i>Tragelaphus scriptus</i>	47	6.30
<i>Damaliscus lunatus</i>	47	5.03
<i>Redunca arundinum</i>	47	5.03
<i>Diceros bicornis</i>	46	4.04
<i>Felis silvestris</i>	45	28.01
<i>Equus zebra</i>	45	17.60
<i>Potamochoerus larvatus</i>	45	4.16
<i>Oryx gazella</i>	44	4.11
<i>Genetta</i> sp.	43	15.75
<i>Antidorcas marsupialis</i>	43	3.34
<i>Raphicerus campestris</i>	43	2.81
<i>Redunca fulvorufula</i>	42	7.54
<i>Pelea capreolus</i>	42	3.83
<i>Hippotragus niger</i>	39	1.55
<i>Proteles cristatus</i>	38	6.81
<i>Hystrix africaeaustralis</i>	38	1.41
<i>Parahyaena brunnea</i>	37	6.70

<i>Procavia capensis</i>	36	19.80
<i>Felis nigripes</i>	35	8.88
<i>Sylvicapra grimmia</i>	35	0.87
<i>Alcelaphus buselaphus</i>	35	0.32
<i>Cephalophus natalensis</i>	32	8.12
<i>Galerella pulverulenta</i>	29	3.59
<i>Suricata suricatta</i>	29	3.59
<i>Equus asinus</i>	29	0
<i>Oreotragus oreotragus</i>	29	0
<i>Neotragus moschatus</i>	28	0.23
<i>Atelerix frontalis</i>	22	0
<i>Cynictis penicillata</i>	22	0
<i>Galerella sanguinea</i>	22	0
<i>Genetta genetta</i>	22	0
<i>Genetta tigrina</i>	22	0
<i>Mungos mungo</i>	22	0
<i>Elephantulus myurus</i>	21	84.31
<i>Lepus capensis</i>	21	4.29
<i>Raphicerus melanotis</i>	20	0.06
<i>Ichneumia albicauda</i>	20	0
<i>Ictonyx striatus</i>	20	0
<i>Otocyon megalotis</i>	20	0
<i>Pedetes capensis</i>	19	0
<i>Rhabdomys pumilio</i>	19	0
<i>Pronolagus rupestris</i>	6	0.30
<i>Papio hamadryas</i>	3	0
<i>Otomys sp.</i>	1	0

Appendix F. Node property values (degree and betweenness) of wild mammals sharing all ticks. The most connected species in bold.

Wild mammal species sharing all ticks	Degree	Betweenness
<i>Lepus saxatilis</i>	82	95.41
<i>Panthera leo</i>	80	68.05
<i>Canis mesomelas</i>	79	31.29
<i>Civettictis civetta</i>	79	30.27
<i>Panthera pardus</i>	79	28.05
<i>Caracal caracal</i>	78	33.22
<i>Taurotragus oryx</i>	78	33.20
<i>Crocuta crocuta</i>	78	25.69
<i>Lycaon pictus</i>	78	25.69
<i>Acinonyx jubatus</i>	78	23.40
<i>Tragelaphus strepsiceros</i>	77	29.10
<i>Mellivora capensis</i>	77	22.31

<i>Genetta</i> sp.	76	20.71
<i>Phacochoerus africanus</i>	76	15.39
<i>Aepyceros melampus</i>	76	14.69
<i>Felis silvestris</i>	75	25.84
<i>Damaliscus pygargus</i>	75	16.08
<i>Giraffa camelopardalis</i>	75	14.40
<i>Syncerus caffer</i>	75	14.40
<i>Mungos mungo</i>	74	18.57
<i>Proteles cristatus</i>	74	15.31
<i>Rhabdomys pumilio</i>	72	23.98
<i>Tragelaphus scriptus</i>	72	12.34
<i>Ceratotherium simum</i>	72	12.05
<i>Equus burchelli</i>	71	10.60
<i>Elephantulus myurus</i>	70	20.30
<i>Hippotragus equinus</i>	70	9.72
<i>Cephalophus natalensis</i>	70	7.85
<i>Aethomys chrysophilus</i>	69	10.91
<i>Ichneumia albicauda</i>	68	11.00
<i>Connochaetes gnou</i>	67	9.62
<i>Otomys</i> sp.	67	8.85
<i>Redunca arundinum</i>	67	6.48
<i>Tragelaphus angasii</i>	67	6.15
<i>Neotragus moschatus</i>	66	5.82
<i>Genetta tigrina</i>	65	11.14
<i>Lepus capensis</i>	65	8.89
<i>Hystrix africaeaustralis</i>	65	8.13
<i>Diceros bicornis</i>	65	7.12
<i>Chlorocebus aethiops</i>	65	6.68
<i>Connochaetes taurinus</i>	65	5.65
<i>Raphicerus campestris</i>	65	5.65
<i>Equus zebra</i>	64	5.80
<i>Pelea capreolus</i>	63	14.58
<i>Oryx gazella</i>	63	7.70
<i>Damaliscus lunatus</i>	63	4.60
<i>Sylvicapra grimmia</i>	63	4.60
<i>Pedetes capensis</i>	62	16.15
<i>Antidorcas marsupialis</i>	62	15.40
<i>Procavia capensis</i>	62	12.86
<i>Pronolagus rupestris</i>	62	12.86
<i>Leptailurus serval</i>	62	9.45
<i>Potamochoerus larvatus</i>	62	5.82
<i>Redunca fulvorufula</i>	60	14.29
<i>Praomys</i> sp.	58	4.39

<i>Oreotragus oreotragus</i>	58	2.21
<i>Otocyon megalotis</i>	57	6.56
<i>Galerella pulverulenta</i>	56	21.82
<i>Vulpes chama</i>	56	12.30
<i>Mastomys natalensis</i>	56	3.79
<i>Alcelaphus buselaphus</i>	56	2.27
<i>Suricata suricatta</i>	55	9.91
<i>Aethomys namaquensis</i>	54	4.53
<i>Lemniscomys rosalia</i>	54	4.53
<i>Mastomys coucha</i>	54	4.53
<i>Hippotragus niger</i>	54	2.92
<i>Raphicerus melanotis</i>	54	2.07
<i>Galerella sanguinea</i>	47	5.58
<i>Parahyaena brunnea</i>	47	1.79
<i>Atelerix frontalis</i>	46	4.77
<i>Rhynchogale melleri</i>	44	1.72
<i>Felis nigripes</i>	42	6.17
<i>Otolemur crassicaudatus</i>	42	0
<i>Soricidae</i>	39	0.18
<i>Otomys occidentalis</i>	35	0
<i>Tatera leucogaster</i>	35	0
<i>Elephantulus edwardii</i>	34	8.64
<i>Elephantulus brachyrhynchus</i>	34	0.04
<i>Saccostomus campestris</i>	21	1.22
<i>Cynictis penicillata</i>	19	0
<i>Genetta genetta</i>	19	0
<i>Ictonyx striatus</i>	17	0
<i>Papio hamadryas</i>	10	0
<i>Macroscelides proboscideus</i>	7	0
<i>Loxodonta africana</i>	2	0

Appendix G. Node property values (degree and betweenness) of wild mammals sharing juvenile ticks. The most connected species in bold.

Wild mammal species sharing juvenile ticks	Degree	Betweenness
<i>Lepus saxatilis</i>	76	114.67
<i>Caracal caracal</i>	74	52.68
<i>Civettictis civetta</i>	74	46.39
<i>Acinonyx jubatus</i>	73	30.72
<i>Aepyceros melampus</i>	73	30.72
<i>Panthera leo</i>	73	30.72
<i>Canis mesomelas</i>	72	35.76
<i>Lycaon pictus</i>	72	25.15
<i>Panthera pardus</i>	72	25.15

<i>Genetta sp.</i>	70	22.12
<i>Mungos mungo</i>	69	20.77
<i>Crocuta crocuta</i>	67	22.39
<i>Felis silvestris</i>	67	14.72
<i>Tragelaphus scriptus</i>	67	14.33
<i>Cephalophus natalensis</i>	66	13.89
<i>Giraffa camelopardalis</i>	66	13.21
<i>Phacochoerus africanus</i>	66	9.59
<i>Taurotragus oryx</i>	66	9.59
<i>Tragelaphus angasii</i>	66	9.59
<i>Tragelaphus strepsiceros</i>	66	9.59
<i>Proteles cristatus</i>	65	22.38
<i>Ichneumia albicauda</i>	65	12.77
<i>Redunca arundinum</i>	65	8.56
<i>Syncerus caffer</i>	65	8.56
<i>Elephantulus myurus</i>	63	21.74
<i>Rhabdomys pumilio</i>	62	26.80
<i>Neotragus moschatus</i>	62	7.27
<i>Connochaetes taurinus</i>	62	6.42
<i>Equus burchelli</i>	62	6.42
<i>Raphicerus campestris</i>	62	6.42
<i>Damaliscus pygargus</i>	61	9.73
<i>Genetta tigrina</i>	61	6.28
<i>Damaliscus lunatus</i>	61	5.51
<i>Hippotragus equinus</i>	61	5.51
<i>Mellivora capensis</i>	61	5.51
<i>Sylvicapra grimmia</i>	61	5.51
<i>Otomys sp.</i>	60	15.40
<i>Chlorocebus aethiops</i>	60	10.33
<i>Lepus capensis</i>	59	13.99
<i>Procavia capensis</i>	57	12.74
<i>Pronolagus rupestris</i>	57	12.74
<i>Oreotragus oreotragus</i>	57	3.36
<i>Pedetes capensis</i>	56	17.95
<i>Aethomys chrysophilus</i>	55	17.09
<i>Praomys sp.</i>	55	7.96
<i>Pelea capreolus</i>	55	2.86
<i>Antidorcas marsupialis</i>	54	8.39
<i>Connochaetes gnou</i>	54	8.39
<i>Redunca fulvorufula</i>	54	8.39
<i>Alcelaphus buselaphus</i>	54	3.10
<i>Mastomys natalensis</i>	53	9.83
<i>Raphicerus melanotis</i>	53	2.65

<i>Otocyon megalotis</i>	52	13.77
<i>Equus zebra</i>	52	1.57
<i>Oryx gazella</i>	52	1.57
<i>Ceratotherium simum</i>	47	1.18
<i>Suricata suricatta</i>	47	0.76
<i>Potamochoerus larvatus</i>	46	0.61
<i>Galerella pulverulenta</i>	44	5.56
<i>Diceros bicornis</i>	44	0.19
<i>Leptailurus serval</i>	42	0
<i>Otolemur crassicaudatus</i>	42	0
<i>Rhynchogale melleri</i>	39	2.85
<i>Atelerix frontalis</i>	39	0
<i>Hystrix africaeaustralis</i>	39	0
<i>Galerella sanguinea</i>	38	0.39
<i>Soricidae</i>	35	0.18
<i>Aethomys namaquensis</i>	32	3.68
<i>Lemniscomys rosalia</i>	32	3.68
<i>Mastomys coucha</i>	32	3.68
<i>Vulpes chama</i>	27	3.30
<i>Otomys occidentalis</i>	19	0
<i>Tatera leucogaster</i>	19	0
<i>Elephantulus edwardii</i>	18	9.67
<i>Elephantulus brachyrhynchus</i>	14	0.02
<i>Saccostomus campestris</i>	13	0.06
<i>Ictonyx striatus</i>	7	0
<i>Macroscelides proboscideus</i>	2	0

Appendix H. Node property values (degree and betweenness) of wild mammals sharing adult ticks. The most connected species in bold.

Wild mammal species sharing adult ticks	Degree	Betweenness
<i>Panthera pardus</i>	62	92.89
<i>Panthera leo</i>	62	81.12
<i>Lepus saxatilis</i>	60	136.48
<i>Acinonyx jubatus</i>	58	60.05
<i>Mellivora capensis</i>	56	50.96
<i>Caracal caracal</i>	55	56.54
<i>Canis mesomelas</i>	53	61.35
<i>Lycaon pictus</i>	51	46.06
<i>Crocuta crocuta</i>	51	43.52
<i>Civettictis civetta</i>	50	42.06
<i>Taurotragus oryx</i>	50	24.46
<i>Tragelaphus strepsiceros</i>	50	24.46
<i>Giraffa camelopardalis</i>	48	18.83

<i>Damaliscus pygargus</i>	47	19.49
<i>Phacochoerus africanus</i>	46	9.13
<i>Syncerus caffer</i>	46	9.13
<i>Equus burchelli</i>	45	8.19
<i>Hippotragus equinus</i>	45	8.19
<i>Ceratotherium simum</i>	44	6.85
<i>Tragelaphus angasii</i>	43	9.21
<i>Aepyceros melampus</i>	43	6.64
<i>Connochaetes taurinus</i>	43	6.08
<i>Vulpes chama</i>	42	29.77
<i>Connochaetes gnou</i>	41	13.65
<i>Tragelaphus scriptus</i>	41	7.42
<i>Damaliscus lunatus</i>	41	5.07
<i>Redunca arundinum</i>	41	5.07
<i>Felis silvestris</i>	40	37.58
<i>Leptailurus serval</i>	40	15.32
<i>Diceros bicornis</i>	40	4.49
<i>Equus zebra</i>	39	22.82
<i>Genetta sp.</i>	38	18.95
<i>Oryx gazella</i>	38	5.13
<i>Potamochoerus larvatus</i>	38	3.82
<i>Raphicerus campestris</i>	38	3.32
<i>Redunca fulvorufula</i>	37	9.62
<i>Antidorcas marsupialis</i>	37	4.09
<i>Pelea capreolus</i>	36	4.72
<i>Hippotragus niger</i>	33	1.59
<i>Proteles cristatus</i>	32	7.29
<i>Hystrix africaeaustralis</i>	32	1.72
<i>Procavia capensis</i>	31	18.83
<i>Parahyaena brunnea</i>	31	8.33
<i>Felis nigripes</i>	30	9.46
<i>Sylvicapra grimmia</i>	30	1.33
<i>Alcelaphus buselaphus</i>	30	0.39
<i>Cephalophus natalensis</i>	27	10.51
<i>Galerella pulverulenta</i>	26	4.75
<i>Suricata suricatta</i>	26	4.75
<i>Oreotragus oreotragus</i>	25	0
<i>Neotragus moschatus</i>	23	0.23
<i>Atelerix frontalis</i>	19	0
<i>Cynictis penicillata</i>	19	0
<i>Galerella sanguinea</i>	19	0
<i>Genetta genetta</i>	19	0
<i>Genetta tigrina</i>	19	0

<i>Mungos mungo</i>	19	0
<i>Elephantulus myurus</i>	17	76.13
<i>Lepus capensis</i>	17	5.71
<i>Ichneumia albicauda</i>	17	0
<i>Ictonyx striatus</i>	17	0
<i>Otocyon megalotis</i>	17	0
<i>Raphicerus melanotis</i>	15	0.07
<i>Pedetes capensis</i>	15	0
<i>Rhabdomys pumilio</i>	15	0
<i>Pronolagus rupestris</i>	5	0.41
<i>Papio hamadryas</i>	3	0
<i>Otomys sp.</i>	1	0
