Distribution and prevalence of ticks and tick-borne pathogens of wild animals in South Africa: A systematic review

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ABSTRACT

Ticks are significant ectoparasites of animals and humans. Published data indicate that most vectors that transmit livestock and human pathogens in sub-Saharan Africa, are native to the region and originate from wild animals. Currently, there is a paucity of information on the role of wild animals on the epidemiology of zoonotic tick-borne pathogens in South Africa. This systematic review focuses on the distribution of ticks and prevalence of tick-borne pathogens in different wild animals in South Africa to identify potential reservoir hosts and possible hotspots for emergence of novel tick-borne pathogens. Following several screening processes, 38 peer-reviewed studies published from 1970 to 2021, were deemed eligible. The studies reported on ticks collected from 63 host species of 21 host families, mostly Canidae, Felidae, Bovidae and Muridae. A total of 49 tick species of nine genera, i.e. *Amblyomma, Dermacentor, Haemaphysalis, Hyalomma, Ixodes, Margaropus, Nuttalliella, Rhipicentor* and *Rhipicephalus*, were reported. Nine tick species, i.e. *Amblyomma marmoreum, Am. hebraeum, Haemaphysalis elliptica, Hyalomma truncatum, I. rubicundus, Rh. appendiculatus, Rh. (B.) decoloratus, Rh. evertsi evertsi* and *Rh. simus* were the most commonly reported. Pathogens of the genera *Anaplasma, Babesia, Hepatozoon* and *Theileria* were identified in the wild animals. This review provides more insight on the ecology of ticks and tick-borne pathogens of wild animals in South Africa and gives useful information for predicting their future spread. It also demonstrates that wild animals habour a diverse range of tick species. This level of diversity entails a similarly high potential for emergence of novel tick-borne pathogens. The review further indicates that wild animals in South Africa are sentinels of tick-borne protozoans of veterinary importance and some bacterial pathogens as most ticks they habour are known vectors of pathogens of domestic animals and humans. However, studies on potential tick-borne zoonoses are under-represented and should be included in future epidemiological surveys, especially in the light of climate change and other anthropogenic threats which might result in the emergence of novel tick-borne pathogens.

1. Introduction

Ticks are significant ectoparasitic arthropods responsible for substantial economic losses that result from the direct or indirect effect caused on their hosts (Jongejan & Uilenberg, 1994). They are obligate blood-feeders and vectors of pathogens of domestic and wild animals and rank second to mosquitoes as disease transmitting agents of zoonotic pathogens (de la Fuente et al., 2008; Colwell et al., 2011). Over 900 tick species have been described globally and they transmit a diverse number of viral, bacterial and protozoan pathogens to their hosts (Jongejan & Uilenberg, 2004).

Jongejan & Uilenberg (2004) reported that the abundance of ticks and tick-borne pathogens are determined by both biotic and abiotic factors such as the presence of hosts, rainfall, humidity and temperature. Moreover, the increasing geographical range and incidence of animal reservoir hosts and tick vectors has resulted in emergence of new/novel infections in new habitats globally. According to Ellis & Ramankutty (2008), more than 70% of the earth's dry land has been altered mostly by

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replacement with infrastructure or farming. Similarly, Wikel (2018) indicated that any compromise on the factors that have a direct or indirect effect on ticks will lead to changes in the distribution and prevalence of tick populations. Thus, the continuous identification of novel tick-borne pathogens results in a constant change in the epidemiology and diversity of known vector-borne diseases and pathogens (Paddock et al., 2016).

The role of domestic and companion animals in the transmission of tick-borne diseases has been studied extensively worldwide, including South Africa (Matjila et al., 2008a; Bhoora et al., 2009; Mbizeni et al., 2013; Mtshali et al., 2015, 2017; Stoltsz et al., 2020) but very little is known about the role of wild animals as sentinels of animal and human diseases. Moreover, there is paucity of information on the role of wild and domestic animals in South Africa as reservoirs of zoonotic pathogens such as *Rickettsia* spp., *Borrelia burgdorferi*, *Anaplasma phagocytophilum* and *Coxiella burnetii* (Mtshali et al., 2017). In most cases, domestic animals are regarded as the preferred hosts for ticks; however, a considerable number of ticks that are native to sub-Saharan Africa are natural parasites of wild animals and they affect livestock and humans, particularly at the wildlife-livestock-human interface. South Africa has various nature reserves and private game parks that have a vast number of animals for conservation, wildlife trade, ecotourism and human consumption/bush meat. The huge diversity and distribution of wild animals in these game reserves render these facilities a potential source of ticks of conservation and zoonotic importance as the distribution and abundance of the ticks is significantly associated with host preference and availability which are important for the continuity of the tick life-cycle (Cumming, 1998).

The main indigenous tick species affecting both domestic and wild animals in South Africa belong to the genera *Amblyomma*, *Rhipicephalus*, *Ixodes* and *Hyalomma* with *Amblyomma hebraeum*, *Ixodes rubicundus*, *Rhipicephalus appendiculatus* and *Rh.* (*Boophilus*) *decoloratus* being the most prevalent species (Horak et al., 2015). The notably invasive Asian tick *Rh.* (*Boophilus*) *microplus* was introduced in South Africa with cattle translocated from Madagascar and East Africa (Theiler, 1962) and it appears to be replacing *Rh.* (*B.*) *decoloratus* in most areas with high rainfall (Nyangiwe et al., 2013). Even though cattle are the preferred hosts of this species (Walker et al., 2003), it has been also collected from various wild animals in South Africa (Latif & Walker, 2004; Tonetti et al., 2009). Both *Rh.* (*B.*) *microplus* and *Rh.* (*B.*) *decoloratus* transmit *Babesia bigemina*, the causal agent of African redwater disease (De Vos et al., 2004). *Amblyomma hebraeum* transmits *Erhlichia ruminantium*, which causes heartwater in domestic and wild ruminants (Bezuidenhout et al., 1994) while *I. rubicundus* can cause paralysis to the host, especially sheep (Walker et al., 2003). *Rhipicephalus appendiculatus* is linked with numerous outbreaks of *Theileria parva* subspecies (*T. parva parva*, *T. parva bovis* and *T. parva lawrencei*; Lawrence, 1992; Lawrence et al., 2004a, b) in domestic and wild ruminants (Norval, 1994).

Tick distribution surveys are necessary as they aid in estimating the distribution of tick-borne diseases as well as the ecological conditions to which the ticks are exposed (Sonenshine et al., 2006). Typically, culture-based, serology and microscopy methods have been used to detect and identify tick pathogens (Clay & Fuqua, 2011). However, less than 2% of microorganisms can be isolated in the laboratory because of the low sensitivity of culturing (Wade, 2002). Nevertheless, isolation of the pathogen remains the gold standard since the presence of the isolate allows for further identification and characterization of the pathogen with robust approaches like polymerase chain reaction (PCR), next-generation sequencing (NGS), DNA barcoding and metagenomics. The distribution of ticks for various wild animals in South Africa has previously been reported (Horak et al., 1984; Nijhof et al., 2003; Golezardy & Horak, 2007; Oosthuizen et al., 2009; Tonetti et al., 2009; Horak et al., 2011a, b, 2017; Harris et al., 2018) but, with global climate change and the increasing rate of game farming in South Africa, reporting on the distribution of ticks and tick-borne pathogens affecting wild animals and humans should continue. Thus, the main focus of this review is

to determine (i) the distribution of ticks and prevalence of tick-borne protozoan and bacterial pathogens of veterinary and zoonotic importance of wild animals in South Africa and (ii) the most frequently used diagnostic methods in epidemiological studies of ticks and tick-borne pathogens in South Africa.

2. Materials and methods

2.1. Search and selection criteria

A systematic search of literature from January 1970 to April 2021 was conducted by two of the co-authors (LMB and DT) independently as per the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) (Page et al., 2021) (Supplementary Table S1). The search was conducted in Google Scholar and SpringerLink databases, using the key terms "distribution", "prevalence", "ticks and tick-borne pathogens", "morphology", "molecular", "wild animals" and "South Africa". These key terms were used individually or in combination using Boolean operators "AND", "OR" and "NOT". The search was restricted to articles reporting the work done on ticks, blood or tissue samples collected from wild animals in South Africa. After completion of the searches, both authors met to reconcile conflicts between the outputs. In addition, grey literature search was conducted on the selected articles for inclusion. The search outputs were filtered by removing duplicates and then screening for articles with relevant titles and abstracts. Articles that were selected were downloaded to enable screening of the full text for eligibility.

2.2. Inclusion and exclusion criteria

To screen for the articles that can answer our research questions, the eligibility of every article was assessed based on the pre-set criteria. Briefly, the records were screened based on questions such as (i) Is the study written in English, peer-reviewed and published between January 1970 and April 2021? (ii) Did the study report the distribution of ticks and tick-borne pathogens in wild animals in South Africa? (iii) Did it report on samples collected from wild animals in South African game reserves and national parks? (iv) Is the sample population including controls well-defined in the study? (v) Did the study report the area of study? (vi) Did the study clearly state the diagnostic method employed in the investigation? Moreover, the review excluded: (i) all articles reporting on samples from communal farms/domestic animals in South Africa; (ii) studies not written in English, not peer-reviewed and published before 1970; (iii) studies with unclear sample information (i.e. collection area, size, host and the controls) and unclear diagnostic methods employed; and (iv) studies that report the distribution of ticks and tick-borne pathogens outside South Africa.

2.3. Data extraction

The studies that fulfilled the inclusion criteria were documented and a spreadsheet was created to chart the data extracted from these articles. The following information was recorded on the spreadsheet: author names, geographical area, sample collection year, number and sample type screened, diagnostic techniques used for screening, tick species identified, sex and life-cycle stage of the identified tick as well as the identity and number of the detected pathogen. In the case of studies which used and reported more than one diagnostic test, data were separated based on the tests where possible. Data were compiled and analysed using Excel 2016 and heat maps were generated from the compiled data. The following abbreviations for genus names were used in the text and tables: *A.*, *Anaplasma*; *Am.*, *Amblyomma*; *D.*, *Dermacentor*; *Ha.*, *Haemaphysalis*; *Hy.*, *Hyalomma*; *I.*, *Ixodes*; *M.*, *Margaropus*; *N.*, *Nuttalliella*; *Rh.*, *Rhipicephalus*.

3. Results

3.1. Outcome of the literature search

The systematic search yielded a total of 3298 articles from the two databases, which included peer-reviewed publications, duplicate articles, books, and reports (Fig. 1). Thirty-nine additional articles were obtained from the reference lists of the selected articles. Initial screening resulted with the exclusion of 1966 duplicates leaving a total of 1332 articles. After screening the titles and abstracts, 1258 articles were deemed ineligible and were excluded from the review. Seventy-four articles were selected for full-text evaluation, of which 36 articles were removed as their focus was not on ticks and tick-borne pathogens of wild animals and/or the samples were not collected from South Africa. A total of 38 articles were deemed eligible for inclusion and are discussed in this review (Fig. 1).

3.2. Characteristics of the studies included in the systematic review

Characteristics of all the studies included in this review are summarized in Table 1. Studies included in this review used either morphological or molecular assays for the identification of ticks and the diagnosis of tick-borne pathogens, except for a few studies ($n = 4$) that employed both techniques. Data from four studies (Golezardy & Horak, 2007; Halajian et al., 2016; Penzhorn et al., 2017; Harris et al., 2020) involving multiple provinces were clearly separated into their different respective provinces where samples were collected. Most of the included studies ($n = 26$) described single host species, whereas others involved multiple host species, ranging from 2 to 26. A total of 63 host species including mammals, birds and reptiles of 21 families (Bovidae, Canidae, Equidae, Felidae, Giraffidae, Herpestidae, Hyaenidae, Leporidae, Macroscelididae, Muridae, Mustelidae, Numididae, Phasianidae, Procaviidae, Rhinocerotidae, Sciuridae, Suidae, Testudinidae, Varanidae and Viverridae) were studied. Animals of the families Canidae, Felidae, Bovidae and Muridae were the most studied and the black-backed jackal, lion, leopard and murid rodents were the most studied host species (Table 1).

All samples collected from all sampled animals as reported in the individual study originated from all nine provinces in South Africa (Fig. 2). Most of the eligible studies were from wild animals in different regions of Mpumalanga and Western Cape provinces. Eleven studies were conducted on samples originating from different provinces (Table 1). A total of 49 tick species were identified in samples originating from different regions in all nine provinces. Results show that nine tick species, i.e. *Amblyomma marmoreum*, *Am. hebraeum*, *Haemaphysalis elliptica*, *Hyalomma truncatum*, *I. rubicundus*, *Rh. appendiculatus*, *Rh. (B.) decoloratus*, *Rh. evertsi evertsi* and *Rh. simus* were the most commonly reported. *Nuttalliella namaqua* and *I. neitzi* were only reported in Limpopo while *Ha. colesbergensis* was only reported in the Northern Cape. *Amblyomma sylvaticum*, *I. fynbosensis* and *Rh. neumanni* were also only documented in the Western Cape. *Rhipicephalus maculatus* was reported in Kwa-Zulu Natal while *I. bakeri* and *Rh. capensis* were only identified in the Western Cape and Eastern Cape provinces.

Pathogen genera identified from the animals were species of *Anaplasma*, *Babesia*, *Hepatozoon* and *Theileria*, and their prevalence ranged from 0.7% to 100% (Table 1). *Hepatozoon canis* was the most prevalent species infecting black-backed jackals (46.5%) and African wild dogs (89.0%). The prevalence of *Theileria bicornis* infection was higher in the black rhinoceros (58.3%), followed by the nyala (52.6%) and the white rhinoceros (36.4%). Furthermore, higher prevalence of *Theileria buffeli* (87.6%) and *Theileria* sp. (kudu) (89.7%) were recorded in the nyala (Table 1). *Theileria equi* was the least prevalent pathogen observed in both the black (9.0%) and white rhinoceros (9.2%) while *Babesia bicornis* was recorded in the black rhinoceros with the prevalence ranging from 2.0% to 50.0%. Generally, the prevalence of *Hepatozoon* spp. was higher
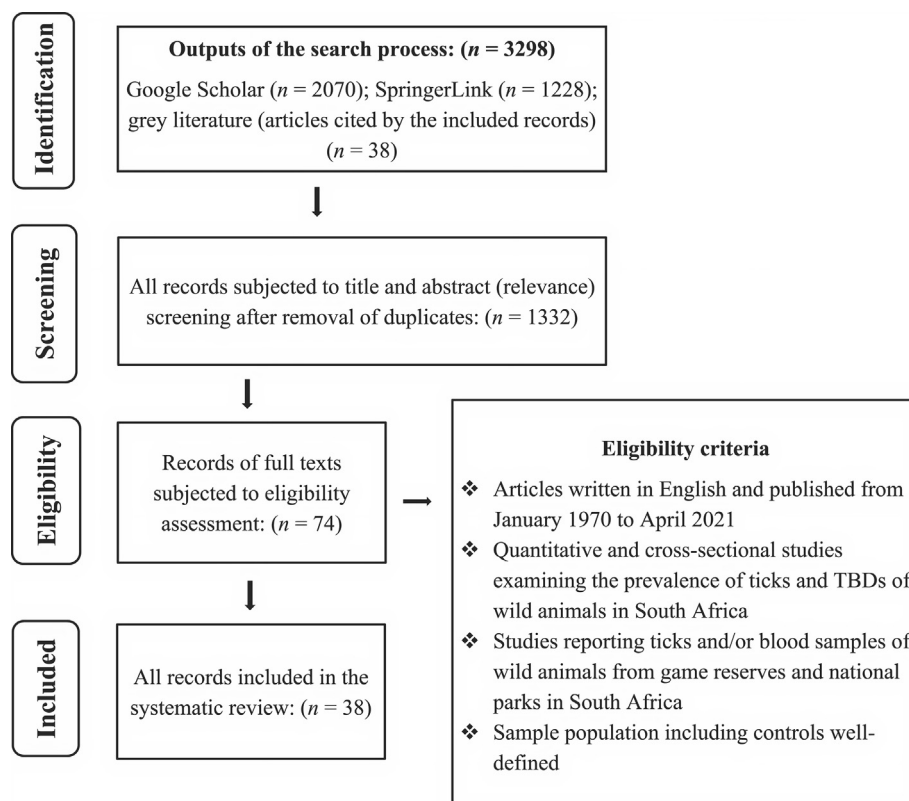

Fig. 1. A flow diagram outlining the search and screening processes following the PRISMA guidelines.

The flow diagram contains:

Identification: Outputs of the search process: ($n = 3298$). Google Scholar ($n = 2070$); SpringerLink ($n = 1228$); grey literature (articles cited by the included records) ($n = 38$)

Screening: All records subjected to title and abstract (relevance) screening after removal of duplicates: ($n = 1332$)

Eligibility: Records of full texts subjected to eligibility assessment: ($n = 74$)

Eligibility criteria
- Articles written in English and published from January 1970 to April 2021
- Quantitative and cross-sectional studies examining the prevalence of ticks and TBDs of wild animals in South Africa
- Studies reporting ticks and/or blood samples of wild animals from game reserves and national parks in South Africa
- Sample population including controls well-defined

Included: All records included in the systematic review: ($n = 38$)

Table 1

Characteristics of all eligible studies reporting on the occurrence of ticks and tick-borne pathogens on different wild animals in South Africa.

Province	Host species	N	Pathogens (n; Prevalence)	Tick species[a]	Diagnostic method	Reference
Western Cape	Black-backed jackal (*Canis mesomelas*)	43	*Hepatozoon canis* (n = 20; 46.5%); *Theileria* sp. (n = 2; 4.7%)	*Am. marmoreum; Ha. elliptica; I. rubicundus*	Morphological and molecular	Viljoen et al. (2021)
Western Cape	Caracal (*Caracal caracal*)	57	*Hepatozoon felis* (n = 38; 66.7%); *Babesia felis* (n = 16; 28.1%); *Babesia leo* (n = 11; 19.3%); *Anaplasma* sp. (n = 14; 24.6%)	*Am. marmoreum; Ha. elliptica; Ha. zumptii; I. rubicundus; I. pilosus; Rh. capensis; Rh. gertrudae*	Morphological and molecular	Viljoen et al. (2020)
Western Cape	Angulate tortoise (*Chersina angulata*)	1	ND	*Am. sylvaticum*	Morphological	Halajian et al. (2016)
Western Cape	Four-striped grass mouse (*Rhabdomys pumilio*)	510	ND	*Am. sylvaticum; Ha. aciculifer; Ha. leachi; Hy. truncatum; I. alluaudi; I. bakeri* group; *I. rubicundus; Ixodes* sp.; *Rh. gertrudae; Rh. lounsburyi*	Morphological	Matthee et al. (2007)
Western Cape	Murid rodents; four-striped grass mouse (*Rhabdomys pumilio*); Southern African vlei rat (*Otomys irroratus*)	41	ND	*Ha. elliptica; Hy. truncatum; I. bakeri; I. fynbosensis; I. pilosus; Ixodes* sp. 1; *Ixodes* sp. 2; *Rh. follis; Rh. gertrudae* group	Morphological	Matthee et al. (2010)
Western Cape	Rock hyrax (*Procavia capensis*); eland (*Taurotragus oryx*); gemsbok (*Oryx gazella*); bontebok (*Damaliscus pygargus dorcas*); springbok (*Antidorcas marsupiali*); grey rhebok (*Pelea capreolus*); black wildebeest (*Connochaetes gnou*); scrub hare (*Pronolagus rupestris*); red rock rabbit (*Pronolagus rupestris*); mountain reedbuck (*Redunca fulvorufula*)	26	ND	*Am. marmoreum; Hy. glabrum; Hy. truncatum; Ixodes pilosus* group; *Rh. arnoldi; Rh. capensis; Rh. distinctus; Rh. evertsi evertsi; Rh. exophthalmos; Rh. gertrudae; Rh. glabroscutatum; Rh. neumanni*	Morphological	Golezardy & Horak (2007)
Northern Cape	Eland (*Taurotragus oryx*); blue wildebeest (*Connochaetes taurinus*); gemsbok (*Oryx gazella*); Cape ground squirrel (*Xerus inauris*); steenbok (*Raphicerus campestris*); gemsbok (*Oryx gazella*); scrub hare (*Lepus saxatilis*)	22	ND	*Hy. marginatum rufipes; Hy. truncatum; Rh. theileri; Rh. exophthalmos*	Morphological	Golezardy & Horak (2007)
Northern Cape	Meerkat (*Suricata suricatta*)	46	*Babesia* and/or *Cytauxzoon* sp. (n = 42; 91.3%)	ND	Molecular	Leclaire et al. (2014)
Northern Cape	Common tsessebe (*Damaliscus lunatus*)	71	*Theileria* spp. (n = 6; 8.5%)	ND	Molecular	Brothers et al. (2011)
Northern Cape	Southern African hedgehog (*Atelerix frontalis*)	12	ND	*Am. marmoreum; Ha. colesbergensis; Haemaphysalis* sp.	Morphological	Horak et al. (2011b)
Limpopo	Murid rodents (*Micaelamys namaquensis; Elephantulus myurus; Aethomys chrysophilus; Acomys spinosissimus*)	78	ND	*N. namaqua*	Morphological	Horak et al. (2012)
Limpopo	Leopard (*Panthera pardus*); hyena (*Hyaena brunnea*)	10	ND	*Am. hebraeum; Ha. elliptica; Hy. rufipes; I. neitzi; Rhipicentor nuttalli; Rh. appendiculatus; Rh. simus; Rh. zambeziensis*	Morphological	Baauw et al. (2019)
Limpopo	Scrub hare (*Lepus saxatilis*)	277	ND	*Am. hebraeum; Am. marmoreum; Ha. leachi; Haemaphysalis* sp.; *Hy. marginatum rufipes; Hy. truncatum; Ixodes* sp.; *Rh. appendiculatus; Rh. (B.) decoloratus; Rh. evertsi evertsi; Rh. kochi; Rh. simus; Rhipicephalus* sp. (near *Rh. parvus*); *Rh. turanicus; Rh. zambeziensis*	Morphological	Horak et al. (1993)
Limpopo	Impala (*Aepyceros melampus*); red hartebeest (*Alcelaphus buselaphus caama*); Southern African hedgehog (*Atelerix frontalis*); white rhinoceros (*Ceratotherium simum*); blue wildebeest (*Connochaetes taurinus*); waterbuck (*Kobus ellipsiprymnus*); bushveld gerbil (*Gerbilliscus leucogaster*); greater kudu (*Tragelaphus strepsiceros*)	15	ND	*Am. hebraeum; Ha. spinulosa; Rh. appendiculatus; Rh. evertsi evertsi; Rh. simus; Rhipicephalus* sp.	Morphological	Halajian et al. (2016)
Limpopo	African wildcat (*Felis silvestris lybica*); caracal (*Caracal caracal*)	22	*Hepatozoon felis* (n = 11; 50.0%)	ND	Molecular	Harris et al. (2020)
Mpumalanga				ND		

Table 1 (*continued*)

Province	Host species	N	Pathogens (*n*; Prevalence)	Tick species[a]	Diagnostic method	Reference
	Leopard (*Panthera pardus*); lion (*Panthera leo*); serval (*Leptailurus serval*)					
Mpumalanga	African wild dog (*Lycaon pictus*)	54	*Hepatozoon canis* sp. (*n* = 48; 89.0%)	ND	Molecular	Netherlands et al. (2021)
Mpumalanga	Lion (*Panthera leo*)	16	*Babesia leo* (*n* = 16; 100%)	ND	Molecular	Penzhorn et al. (2001)
Mpumalanga	White rhinoceros (*Ceratotherium simum*)	195	*Theileria bicornis* (*n* = 71; 36.4%); *Theileria equi* (*n* = 18; 9.2%)	ND	Molecular	Govender et al. (2011)
Mpumalanga	Impala (*Aepyceros melampus*)	229	ND	*Am. hebraeum*; *Am. marmoreum*; *Am. tholloni*; *Ha. aciculifer*; *Hy. truncatum*; *Ixodes* sp.; *Rh. appendiculatus*; *Rh. (B.) decoloratus*; *Rh. evertsi evertsi*; *Rh. kochi*; *Rh. pravus* group; *Rh. simus*; *Rh. zambeziensis*	Morphological	Horak et al. (2003)
North-West	Black-backed jackal (*Canis mesomelas*)	142	*Ehrlichia/Anaplasma* (*n* = 82; 57.8%); Haemogregarines (*n* = 20; 14.1%); *Hepatozoon* genotypes (*n* = 14; 9.9%)	ND	Molecular	Penzhorn et al. (2018)
North-West	Black-backed jackal (*Canis mesomelas*)	16	*Babesia rossi* (*n* = 6; 37.5%)	ND	Molecular	Penzhorn et al. (2017)
Gauteng	Black-backed jackal (*Canis mesomelas*)	91	*Babesia rossi* (*n* = 77; 84.6%)	ND		
Gauteng	Black-backed jackal (*Canis mesomelas*)	9	ND	*Ha. elliptica*; *Rh. evertsi evertsi*; *Rh. gertrudae*; *Rh. simus*; *Rh. turanicus*	Morphological	Penzhorn et al. (2020)
Free State	Gemsbok (*Oryx gazella*); common eland (*Taurotragus oryx*); springbok (*Antidorcas marsupialis*); black wildebeest (*Connochaetes gnou*); red hartebeest (*Alcelaphus buselaphus caama*); blesbok (*Damaliscus pygargus phillipsi*); greater kudu (*Tragelaphus strepsiceros*); roan antelope (*Hippotragus equinus*); plain zebra (*Equus burchellii*); lion (*Panthera leo*)	59	*Ehrlichia/Anaplasma* (*n* = 2; 3.4%); *Babesia/Theileria* (*n* = 9; 15.3%); *A. marginale* (*n* = 1; 1.7%)	*Ha. leachi*; *Hy. marginatum rufipes*; *I. rubicundus*; *M. winthemi*; *Rh. appendiculatus*; *Rh. (B.) decoloratus*; *Rh. (B.) microplus*; *Rh. evertsi evertsi*	Morphological and molecular	Tonetti et al. (2009)
Free State	White rhinoceros (*Ceratotherium simum*); Guinea fowl (*Numididae*); African buffalo (*Syncerus caffer*); rock elephant shrew (*Elephantulus myurus*)	135	ND	*Am. hebraeum*; *Ha. silaceae*; *Rh. appendiculatus*; *Rh. (B.) decoloratus*; *I. rubicundus*	Morphological	Horak et al. (2015)
Free State	Common warthog (*Phacochoerus africanus*)	46	ND	*Hy. truncatum*; *Rh. gertrudae*; *Rh. simus*	Morphological	Matthee et al. (2013)
Eastern Cape	Four-striped grass mouse (*Rhabdomys pumilio*) and murid rodents	286	ND	*Am. hebraeum*; *Ha. leachi*; *I. alluaudi*; *I. bakeri*; *Ixodes* sp.; *Rh. follis*; *Rh. simus*; *Rh. simus* group	Morphological	Petney et al. (2004)
Eastern Cape	Black rhinoceros (*Diceros bicornis*)	12	*Babesia bicornis* (*n* = 6; 50.0%); *Theileria bicornis* (*n* = 7; 58.3%)	ND	Molecular	Nijhof et al. (2003)
Kwa-Zulu Natal	Four-toed elephant shrew (*Petrodromus tetradactylus*)	9	ND	*Ha. elliptica*; *Ha. silacea*; *Rh. appendiculatus*; *Rh. maculatus*; *Rh. muehlensi*	Morphological	Horak et al. (2011b)
Kwa-Zulu Natal	Nyala (*Tragelaphus angasii*)	97	*Theileria* sp. (kudu) (*n* = 87; 89.7%); *T. buffeli* (*n* = 85; 87.6%); *Theileria* sp. (sable) (*n* = 57; 58.8%); *T. bicornis* (*n* = 51; 52.6%); *Anaplasma* sp. "Omatjenne" (*n* = 32; 33.0%); *A. marginale* (*n* = 13; 13.4%); *A. bovis* (*n* = 11; 11.3%)	ND	Molecular	Pfitzer et al. (2011)
Various provinces (FS, LP, MP)	Leopard (*Panthera pardus*)	17	Haemoparasites (*Hepatozoon luiperdjie* and/or *H. ingwe* (*n* = 8; 47.1%)	ND	Molecular	van As et al. (2020)
Various Provinces (MP, GP, LP, KZN, NC, FS)	Giraffe (*Giraffa camelopardalis*); roan antelope (*Hippotragus equinus*)	8	*Babesia* sp. (*n* = 4; 50.0%); *Theileria* sp. (*n* = 3; 37.5%)	ND	Molecular	Oosthuizen et al. (2009)

Table 1 (*continued*)

Province	Host species	N	Pathogens (*n*; Prevalence)	Tick species[a]	Diagnostic method	Reference
Various provinces (MP, LP, NW)	Greater kudu (*Tragelaphus strepsiceros*); giraffe (*Giraffa camelopardalis*); impala (*Aepyceros melampus*); sable antelope (*Hippotragus niger*); blue wildebeest (*Connochaetes taurinus*); black wildebeest (*Connochaetes gnou*); springbok (*Antidorcas marsupialis*); blesbok (*Damaliscus pygargus phillipsi*); gemsbok (*Oryx gazella*); African buffalo (*Syncerus caffer*); common eland (*Taurotragus oryx*)	64	ND	*Am. hebraeum*; *Ha. silacea*; *Hy. marginatum rufipes*; *I. rubicundus*; *M. winthemi*; *Rh. appendiculatus*; *Rh.* (*B.*) *decoloratus*; *Rh.* (*B.*) *microplus*; *Rh. evertsi evertsi*; *Rh. gertrudae*; *Rh. warburtoni*; *Rh. zambeziensis*	Morphological	Berggoetz et al. (2014)
Various provinces (LP, NW)	African wild dog (*Lycaon pictus*)	301	*Babesia rossi* (*n* = 16; 5.3%); *Hepatozoon* sp. (*n* = 2; 0.7%)	ND	Molecular	Matjila et al. (2008b)
Various provinces (EC, KZN, MP, NC NW, WC)	Giraffe (*Giraffa camelopardalis*); African buffalo (*Syncerus caffer*); eland (*Taurotragus oryx*)	58	ND	*Am. hebraeum*; *Am. marmoreum*; *Ha. aciculifer*; *Ha. silacea*; *Hy. marginatum rufipes*; *I. pilosus* group; *M. winthemi*; *Rh. appendiculatus*; *Rh.* (*B.*) *decoloratus*; *Rh. evertsi evertsi*; *Rh. exophthalmos*; *Rh. follis*; *Rh. glabroscutatum*; *Rh. lounsburyi*; *Rh. maculatus*; *Rh. muehlensi*; *Rh. pravus* group; *Rh. simus*	Morphological	Horak et al. (2007)
Various provinces (EC, FS, GP, KZN, MP, NC, NW, WC)	Black-backed jackal (*Canis mesomelas*); hunting dog (*Lycaon pictus*); bat-eared fox (*Otocyon megalotis*); Cape fox (*Vulpes chama*); cheetah (*Acinonyx jubatus*); caracal (*Caracal caracal*); African wildcat (*Felis silvestris lybica*); feral cat (*Felis catus*); lion (*Panthera leo*); leopard (*Panthera pardus*); yellow mongoose (*Cynictis penicillata*); slender mongoose (*Galerella sanguinea*); small grey mongoose (*Galerella pulverulenta*); white-tailed mongoose (*Ichneumia albicauda*); banded mongoose (*Mungos mungo*); meercat (*Suricata suricatta*); spotted hyena (*Crocuta crocuta*); brown hyena (*Parahyaena brunnea*); aardwolf (*Proteles cristatus*); ratel (*Mellivora capensis*); zorilla (*lctonyx striatus*); civet cat (*Civettictis civetta*); small-spotted genet (*Genetta genetta*); large-spotted genet (*Genetta tigrina*); genet (*Genetta* sp.)	111	ND	*Am. hebraeum*; *Am. marmoreum*; *Ha. aciculifer*; *Ha. leachi*; *Ha. leachi/Ha. zumpti*; *Ha. spinulosa*; *Haemaphysalis* sp.; *Hy. truncatum*; *I. pilosus* group; *I. rubicundus*; *Ixodes* sp.; *Rhipicentor nuttalli*; *Rh. appendiculatus*; *Rh.* (*B.*) *decoloratus*; *Rh. evertsi evertsi*; *Rh. kochi*; *Rh. maculatus*; *Rh. simus*; *Rh. theileri*; *Rh. turanicus*; *Rh. warburtoni*; *Rh. zambeziensis*	Morphological	Horak et al. (2000)
Various provinces (LP, NW)	Cheetah (*Acinonyx jubatus*); murid rodents (*Aethomys* sp., *Graphiurus murinus*, *Mastomys* sp., *Mus minutoides*, *Saccostomys campestris*, *Tatera leucogaster*)	247	ND	*Am. hebraeum*; *Am. marmoreum*; *Ha. elliptica*; *Rh.* (*B.*) *decoloratus*; *Rh. simus*; *Rh. zambeziensis*	Morphological	Golezardy et al. (2016)
Various provinces (FS, LP, MP)	Tree squirrel (*Paraxerus cepapi*); short-tailed pouched mouse (*Saccostomys campestris*); bushveld gerbil (*Tatera leucogaster*); red veld rat (*Aethomys chrysophilus*); Namaqua rock mouse (*Aethomys namaquensis*); single-striped mouse (*Lemniscomys rosalia*); multimammate mouse (*Mastomys coucha*); Natal multimammate mouse (*Mastomys natalensis*); pigmy mouse (*Mus minutoides*); black rat (*Rattus rattus*); four-striped grass mouse (*Rhabdomys pumilio*); Angoni swamp rat (*Otomys angoniensis*); swamp rat (*Otomys irroratus*); spring hare (*Pedetes capensis*); Cape hare (*Lepus capensis*); scrub hare (*Lepus saxatilis*)	225	ND	*Am. hebraeum*; *Am. marmoreum*; *D. rhinocerinus*; *Ha. leachi*; *Hy. marginatum*; *Hy. truncatum*; *I. rubicundus*; *Ixodes* sp.; *M. winthemi*; *Rh. appendiculatus*; *Rh.* (*B.*) *decoloratus*; *Rh. evertsi evertsi*; *Rh. gertrudae*; *Rh. lounsburyi*; *Rh. simus*; *Rhipicephalus* sp.; *Rh. warburtoni*; *Rh. zambeziensis*	Morphological	Horak et al. (2005)

Table 1 (*continued*)

Province	Host species	N	Pathogens (n; Prevalence)	Tick species[a]	Diagnostic method	Reference
Various provinces (EC, FS, KZN, LP, MP, NC)	Reptiles, birds, small mammals; large herbivores; carnivores	3201	ND	*Am. marmoreum*	Morphological	Horak et al. (2006)
Various provinces (EC, MP)	Caracal (*Felis caracal*); small-spotted genet (*Genetta genetta*); bat-eared fox (*Otocyon megalotis*); aardwolf (*Proteles cristatus*); black-backed jackal (*Canis mesomelas*); side-striped jackal (*Canis adustus*); wild dogs (*Lycaon pictus*); spotted hyena (*Crocuta crocuta*); serval (*Felis serval*); African civets (*Civettictis civetra*); leopards (*Panthera pardus*); lion (*Panthera leo*)	69	ND	*Am. marmoreum*; *Ha. leachi*; *Ha. leachi/spinulosa*; *Hy. marginatum*; *I. rubicundus*; *M. winthemi*; *Rh. arnoldi*; *Rh. (B.) decoloratus*; *Rh. distinctus*; *Rh. evertsi evertsi*; *Rh. glabroscutatum*; *Rhipicephalus* sp. (near *Rh. capensis*); *Rhipicephalus* sp.	Morphological	Horak et al. (1987)
Various provinces (EC, FS, GP, KZN, LP, MP, NC, NW, WC)	Black rhinoceros (*Diceros bicornis bicornis*; *Diceros bicornis minor*)	156	*Theileria bicornis* (n = 37; 23.7%); *T. equi* (n = 3; 2.0%); *Babesia bicornis* (n = 14; 9.0%)	ND	Molecular	Zimmermann et al. (2021)

Abbreviations: *N*, number of samples; *n*, number of positive samples; ND, not determined; *A.*, *Anaplasma*; *Am.*, *Amblyomma*; *D.*, *Dermacentor*; *Ha.*, *Haemaphysalis*; *Hy.*, *Hyalomma*; *I.*, *Ixodes*; *M.*, *Margaropus*; *N.*, *Nuttalliella*; *Rh.*, *Rhipicephalus*; EC, Eastern Cape; FS, Free State; GP, Gauteng; LP, Limpopo; KZN, Kwa-Zulu Natal; MP, Mpumalanga; NC, Northern Cape; NW, North-West; WC, Western Cape.
[a] Adults, nymphs, larvae.

in carnivores while that of *Theileria* spp. was higher in bovids and rhinoceros.

3.3. Host-vector relationships

Ticks of the genera *Amblyomma*, *Haemaphysalis*, *Hyalomma*, *Ixodes* and *Rhipicephalus* were observed to be generalists as they infested a wide range of host animals regardless of locality (Fig. 3). *Amblyomma marmoreum* was observed to be associated with a wide range of hosts such as the black-backed jackal, African wild dog, lion, leopard, spotted hyena, civet cats, mongoose, leopard tortoise and a wide range of wild bovids (buffalo, black wildebeest, blesbok, springbok, mountain reedbuck, impala, kudu, gemsbok, grey reebok, eland and zebra) (Fig. 3). Adults and immature stages of *Am. hebraeum* were recorded infesting large bovids and carnivores while the nymphs and larvae were found to infest small ruminants, carnivores, ground-frequenting birds, reptiles
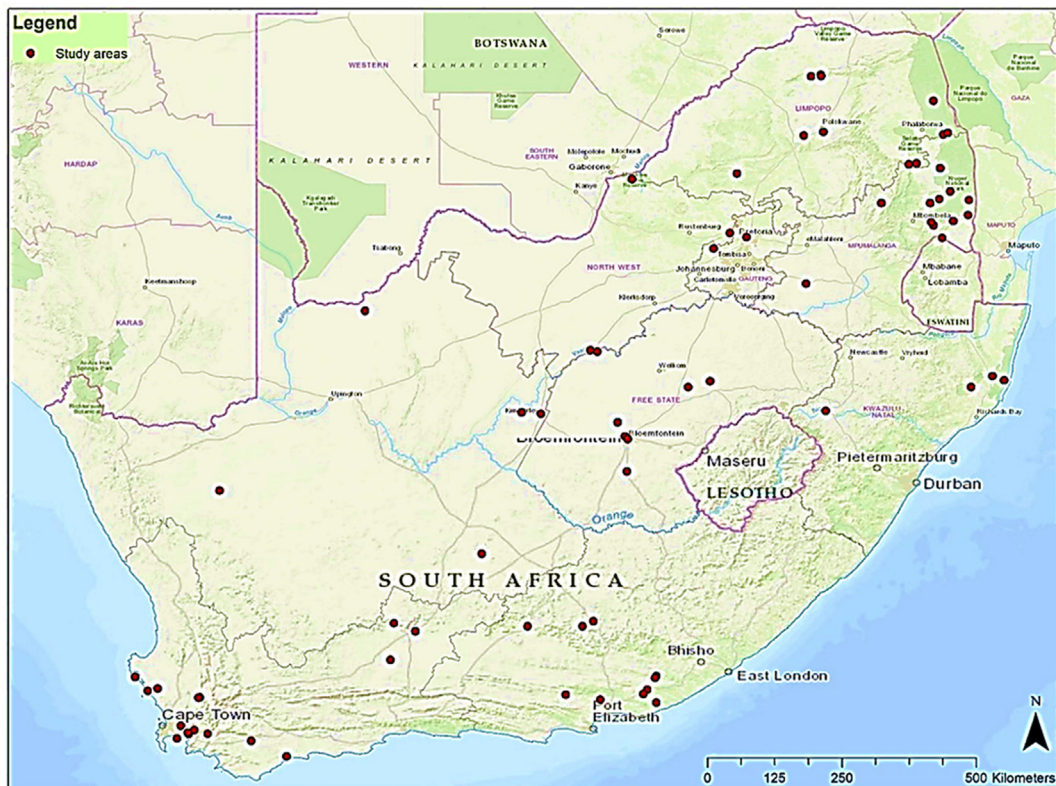

Fig. 2. Sampling localities indicated in the studies included in the review.
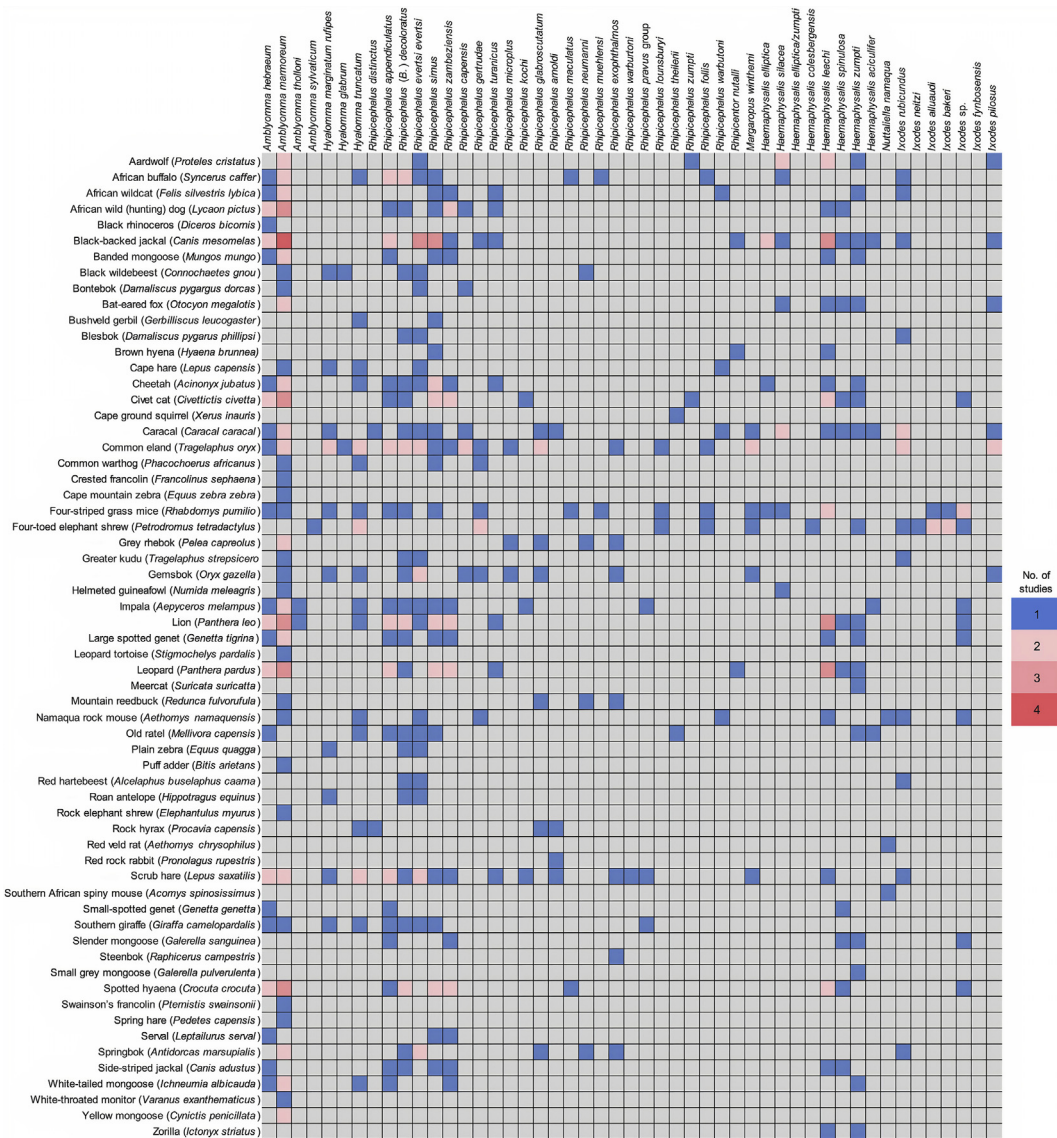
Fig. 3. Host-vector associations according to the studies included in the review.

and hares. Amongst species of *Ixodes* reported, both *I. rubicundus* and *I. pilosus* were the most common species identified in close association to bovids and carnivores, while *I. alluaudi*, *I. bakeri* and *I. rubicundus* were mainly associated with rodents, elephant shrews and scrub hares (Fig. 3). Results further showed that species of the genus *Haemaphysalis* were mostly found on species of the families Felidae, Canidae and Viverridae. *Haemaphysalis leachi* was harboured by most carnivores and hares.

Some tick species appeared to be host-specific; for instance, *Am. tholloni* was only identified in impalas whereas *Am. sylvaticum* was only identified in the red rock rabbit and leopard tortoise. Additionally, *N. namaqua* was only reported on murid rodents while *Ha. spinulosa* showed a noticeable preference to hosts of the carnivorous families such as Felidae, Canidae and Viverridae. Only three species of the genus *Hyalomma* (*Hy. glabrum*, *Hy. marginatum rufipes* and *Hy. truncatum*) were identified in this study and they are all related to a wide range of hosts such as bovids, felids, leporids and murids (Fig. 3). Species of *Rhipicephalus* (*Rh. appendiculatus*, *Rh. evertsi evertsi*, *Rh. simus* and *Rh.* (*B.*) *decoloratus*) were also associated with a wide range of host animals belonging to the families Bovidae, Canidae, Felidae, Muridae and

Leporidae. *Rhipicephalus evertsi evertsi* is widely distributed and associated with a wide range of host species, which are mainly ungulates as well as lagomorphs, carnivores and rodents. *Rhipicephalus simus* was mainly associated with carnivores while *Rh.* (*B.*) *decoloratus* was mostly linked to bovids, felids and leporids (Fig. 3). *Rhipicentor nuttalli* was related to carnivores only and *Rh.* (*B.*) *microplus* was identified from the grey rhebok, common eland and gemsbok.

Species of *Babesia* and *Hepatozoon* were reported in hosts of the families Felidae, Canidae and Giraffidae (Fig. 4). Wild bovids were mostly affected by *Theileria* spp. and *Anaplasma* spp. Furthermore, infections with *Babesia leo* and *B. felis* were mainly found in felines whereas infections with *Babesia rossi* were reported in canids. Additionally, infections with both *B. leo* and *B. felis* were also observed in caracals, whereas *B. rossi* was identified from African wild dogs and black-backed jackals. *Theileria* spp. were reported from various animal hosts but mainly from bovids. Species of the Rhinocerotidae and Herpestidae were infected with *B. bicornis*, *T. bicornis* and *T. equi*.

Hepatozoon canis was isolated from black-backed jackals while the recently described *H. ingwe* and *H. luiperdjie* were both isolated from leopards. *Hepatozoon felis* was isolated from almost all felids.
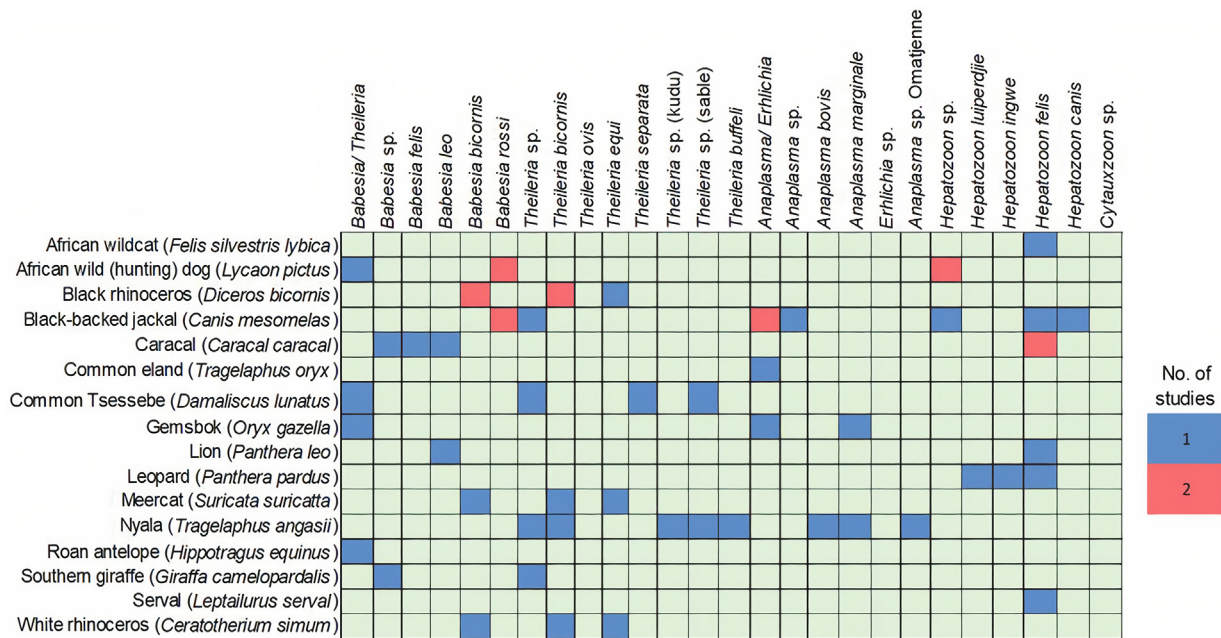
Fig. 4. Host-pathogen associations according to the studies included in the review.

Furthermore, *Anaplasma marginale*, was isolated from the gemsbok and nyala while *A. bovis* was isolated from nyala only. *Anaplasma* sp. "Omatjenne" was reported from the nyala in a study by Pfitzer et al. (2011). This host was also associated with the following pathogens: *A. marginale*; *A. bovis*; *T. bicornis*; *T. buffeli*; *Theileria* sp. (kudu); and *Theileria* sp. (sable).

3.4. Vector-pathogen relationships

Of the reported pathogens, *Am. hebraeum* was associated with *Rickettsia africae* while *R. massiliae* were associated with *Am. sylvaticum* and *Rh. simus*. Furthermore, most *Rhipicephalus* spp. were associated with *Theileria* spp. except for *Rh. warburtoni*, which was associated with *A. marginale*, *A. centrale* and *Ehrlichia ovina*. *Rhipicephalus appendiculatus* was also associated with the latter pathogens in addition to *T. bicornis* and *Theileria* sp. (Fig. 5).

3.5. Diagnostic assays employed

Morphological keys were used to identify the tick species and only a few studies combined morphology and molecular assays for species identification (Table 1). Moreover, molecular assays (PCR and reverse line blot (RLB)) and sequencing have been employed for the identification and characterization of tick-borne pathogens. The two studies that combined morphology and molecular assays used DNA samples isolated from vectors as compared to other studies which isolated DNA from hosts.

4. Discussion

This review shows that wild animals in South Africa harbour a diverse range of tick species. It further indicates that environmental conditions in all nine provinces in South Africa are conducive for the survival of
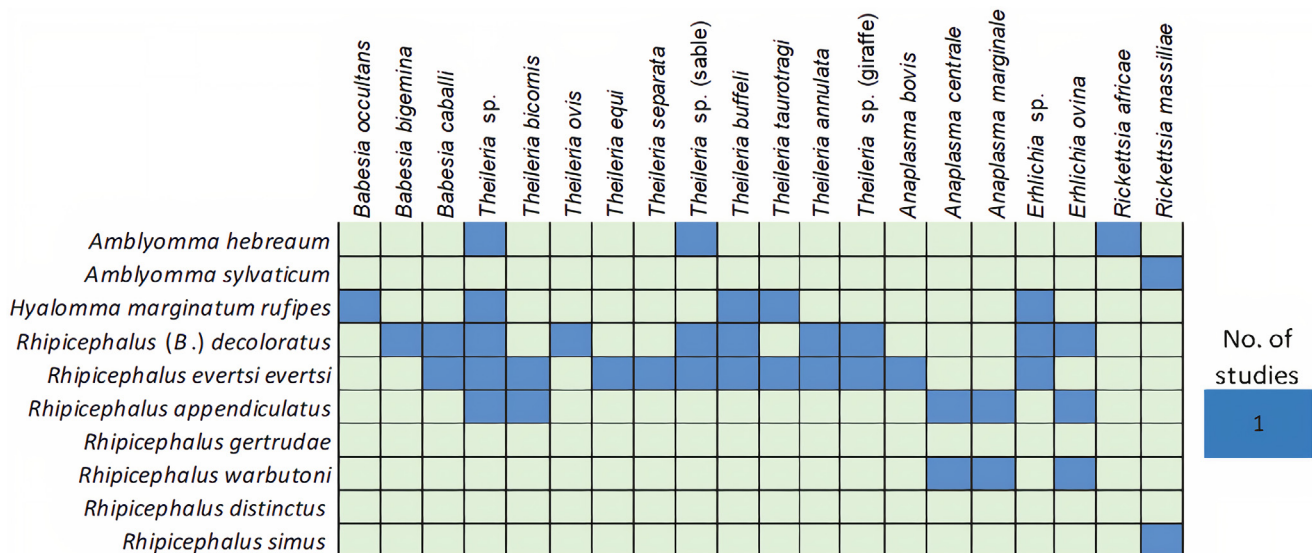

Fig. 5. Vector-pathogen relationships according to the studies included in the review.

multiple tick species. Previous reports indicated that *Am. hebraeum, I. rubicundus, Rh. appendiculatus, Rh. decoloratus* and are the indigenous tick species harbored by domestic and wild animals in South Africa (Horak et al., 2015). Varying host preference shown in most ticks is basically due to different tick life stages, environmental conditions and sometimes host availability.

4.1. Tick-host associations

The aspect of host preference is crucial to the survival of ticks because when a preferred host becomes extinct, ticks that cannot adjust to the available host will not persist (Koh et al., 2004). Hoogstraal & Aeschlimann (1982) previously indicated that majority of the ticks of the superfamily Ixodoidea have a strict host preference. Thus, most tick species are restricted to the geographical regions where their preferred host are found.

Amblyomma marmoreum and *Am. hebraeum* are the two most recorded tick species. Horak et al. (2006) showed that the scrub hare is the preferred host of *Am. marmoreum* as compared to other small mammals. Moreover, the study indicated that this tick occurs in all provinces of South Africa; even though its population in some provinces is low. We also observed that *Am. hebraeum* is widespread in Limpopo, Mpumalanga, North-West, Kwa-Zulu Natal and Eastern Cape provinces, thus corroborating previous reports which highlighted that this tick species prefers warmer, moist regions (Jongejan & Uilenberg, 2018). *Ixodes rubicundus* and *I. pilosus* were the most frequently reported species of the genus *Ixodes*. Walker et al. (2003) indicated that both species are well represented in South Africa. *Ixodes rubicundus*, also referred to as the Karoo paralysis tick, is associated with bovids (buffalo, gemsbok, red hartebeest, common eland and blesbok), felids (caracal and African wildcat) as well as rabbits and mice. This tick occurs in hilly or mountainous regions especially in the Karoo vegetation of South Africa. Hence, adults of this tick species are associated with most ruminants dwelling or visiting mountainous, rocky areas whereas the nymphs and larvae affect the elephant shrews and red rock rabbits while caracals are affected by the larvae, nymphs and adults (Horak et al., 2015). Horak et al. (1986) also indicated that *I. pilosus* is widely distributed in the eastern and southern coastal regions of South Africa where it parasitizes various wild hosts including the bushbuck, bontebok, eland, common duiker and scrub hare as their preferred hosts (Horak & Boomker, 1998).

Nuttalliella namaqua, the sole species of the genus *Nuttalliella*, is regarded as the species closest to the ancestral lineage of ticks as it has characteristics that are respectively distinctive to hard and soft ticks. Horak et al. (2012) reported that murid rodents are the natural hosts of the larvae of this tick species. Nymphs and adults of this tick are reported to be generalists affecting numerous hosts including burrowing mammals and reptiles, especially lizards (Krasnov et al., 2010). Previous studies have shown that this tick species occurs mainly in the Kalahari and Namaqualand (Northern Cape), the Karoo (Eastern Cape, Northern Cape, Western Cape) and the Soutpansberg regions in the Limpopo Province (Mans et al., 2011a; Horak et al., 2012). Although *Ha. leachi* was reported to be the most common species of the genus *Haemaphysalis* in South African wild animals, Apanaskevich and Horak (2007) indicated that this species only occurs in the northern regions of Africa. Thus, all ticks that were identified as *Ha. leachi* in previous studies in the southern regions of Africa may actually belong to *Ha. elliptica*, a species associated with carnivores (Horak et al., 1987, 2000). Furthermore, Penzhorn et al. (2020), indicated that *Ha. elliptica* is the most prevalent species infesting the black-backed jackal population occurring in South Africa, especially in the eastern and north-eastern areas with moderate rainfall. Matthee et al. (2010) also reported that this tick species is prevalent in South African domestic dogs. Thus, identification of *Ha. elliptica* in livestock is assumed to be due to their close interaction with domestic dogs (Walker et al., 2014). Another species of the genus *Haemaphysalis*, *Ha. spinulosa*, was reported as a potential host specialist, which mostly prefers carnivores (Cumming, 1998). However, Hoogstraal (1964) has indicated that

the species was originally collected from a lesser cane rat (*Thryonomys gregorianus*) in Uganda.

The review indicated that species of *Hyalomma* are generalists as they parasitize a wide range of hosts. Walker et al. (2003) reported that large domestic and wild herbivores are preferred hosts of the adults of *Hyalomma* spp. while immature stages parasitize on scrub hares, gerbils, rodents and ground-frequenting birds; these authors regarded felids as occasional hosts of *Hyalomma* spp. Walker et al. (2003) also indicated that *Hy. marginatum rufipes* is widely distributed in most areas of South Africa, and all its life stages are found throughout the year with high abundance of immature stages and adults in the dry and wet seasons, respectively. *Hyalomma truncatum* and *Hy. glabrum* were also shown to parasitize ungulates, leporids and ground-frequenting birds.

Most *Rhipicephalus* spp. were associated with a wide range of hosts except for *Rh. warburtoni* that prefers scrub hares and *Rh. distinctus* which seems to prefer caracals and rock hyraxes. Walker (1991) indicated that *Rh. appendiculatus*, commonly known as the "brown ear tick" is associated with an extensive range of hosts predominantly bovids whereas *Rh. evertsi evertsi* is associated with a wide range of hosts, including ungulates, lagomorphs, carnivores and rodents. The author further indicated that both species are widely distributed in South Africa as evident in this review. Furthermore, the abundance of most *Rhipicephalus* spp. especially *Rh. simus* and *Rh. (B.) decoloratus* is influenced by rainfall as they survive well in warm, moist regions of South Africa (Braack et al., 1996; Jongejan & Uilenberg, 2018). Adults of *Rhipicentor nuttalli* were collected from a leopard and a brown hyena in Gauteng Province, and from a black-backed jackal in the Free State (Horak et al., 2000; Baauw et al., 2019). This tick is reported to affect wild carnivores (Horak et al., 2010), domestic dogs and hedgehogs (Fourie et al., 2002) with felids, especially leopards, as the preferred hosts.

4.2. Host-pathogen relationships

Based on the results, the prevalence of *Hepatozoon canis* among the populations of African wild dogs and black-backed jackal in South Africa is very high. Although *Hepatozoon* spp. are transmitted by ticks, their mode of transmission is ingestion of either an infected tick vector or a host carrying *Hepatozoon* oocysts rather than a tick-bite as compared to other protozoan parasites (Baneth et al., 2003). Van Heerden et al. (1995) reported a prevalence of 89.7% for *Hepatozoon* spp. in the blood smears obtained from wild dogs in the Kruger National Park. However, the prevalence of *H. felis* was also shown to be high in caracals, lions, cheetahs, servals and leopards (Harris et al., 2020; Viljoen et al., 2020), thus indicating that *Hepatozoon* spp. are abundant in hosts of carnivore families presumably due to their feeding behavior that coincides with the transmission route of *Hepatozoon* spp. van As et al. (2020) also reported a prevalence of 56% for the recently described species, *H. luiperdjie* and *H. ingwe*, in the captive and free-ranging leopard populations in Mpumalanga, Free State and Limpopo provinces of South Africa.

In addition to *Hepatozoon* spp., *Babesia* spp. were shown to be prevalent in the population of the free-ranging black-backed jackal as well. Species of *Babesia* and *Theileria* are tick-transmitted protozoan parasites affecting a wide range of hosts globally and are the causative agents of babesiosis and theileriosis, respectively. Penzhorn et al. (2017) previously reported *B. rossi* in subclinical infections of black-backed jackals and these animals were regarded as the natural hosts of this pathogen. A high prevalence of *B. bicornis* was recorded in black rhinoceros from different provinces of South Africa (Nijhof et al., 2003). Although *B. leo, B. felis* and *B. rossi* were described from lions (Penzhorn et al., 2001), domestic cats (Davis, 1929) and side-striped jackals (Nuttall, 1910), respectively, they can successfully infect other felids. Generally, most pathogens of these genera are given names in accordance with either their area of origin or host (De Vos et al., 2004). The identification of *B. leo* and *B. felis* from caracals and *B. rossi* from African wild dogs and black-backed jackals, in addition to their initial hosts, is consistent with

reports that these are parasites of wild and domestic felids and canids, respectively.

Theileria spp. affect various hosts but are mostly associated with bovids. *Theileria parva*, transmitted mainly by *Rh. appendiculatus*, is the most economically important species of the genus in sub-Saharan Africa especially in cattle farming as it causes potentially fatal theileriosis, Corridor disease, East Coast fever and January disease in cattle and buffalo (Lawrence, 1992, 2004a; Mbizeni et al., 2013). Corridor disease (buffalo-derived theileriosis) is a controlled disease in South Africa and is mainly transmitted by *Rh. appendiculatus*. Several studies have identified *T. parva* in African buffalo and cattle in southern Africa using molecular-based assays. However, the African buffalo is reported as the natural wild animal reservoir of Corridor disease (Sibeko et al., 2008; Chaisi et al., 2011; Mans et al., 2011b; 2015; Pienaar et al., 2014). *Theileria parva* commonly co-occurs with other *Theileria* spp., namely, *T. buffeli, T. mutans, T. taurotragi, T. velifera, Theileria* sp. (bougasvlei) and *Theileria* sp. (buffalo) (Sibeko et al., 2008; Mans et al., 2011b; Chaisi et al., 2013, 2014; Pienaar et al., 2014). In another study, Oosthuizen et al. (2009) identified *Babesia* spp. and *Theileria* spp., grouped within the *Babesia* (*sensu stricto*) and *Theileria* (*sensu stricto*) clades, respectively from giraffes and roan antelopes. Furthermore, Nijhof et al. (2003) reported the presence of *B. bicornis* and *T. bicornis* from samples collected from rhinoceros in Tanzania and South African game reserves.

Anaplasma spp. affect a wide range of hosts from various taxa and cause considerable losses in the livestock and game farming. Stoltsz (1994) and Potgieter & Stoltsz (1994) indicated that the most prevalent species within the genera *Anaplasma* and *Ehrlichia* in domestic and wild ruminants in South Africa include *A. bovis, A. centrale, A. marginale, A. ovis, E. ovina* and *E. ruminantium*. *Anaplasma marginale*, the causal agent of bovine anaplasmosis is widespread in South Africa (Potgieter & Stoltsz, 1994). Low prevalence of *A. marginale* in wild ruminants was reported previously in the Free State (Tonetti et al., 2009). Despite this low prevalence in wild animals, infection caused by *A. marginale* in cattle has been reported in eight provinces of South Africa (Hove et al., 2018). Cattle are regarded as the main hosts but *A. marginale* has also been isolated from the gemsbok (Tonetti et al., 2009) and nyala (Pfitzer et al., 2011). *Anaplasma* sp. "Omatjenne", initially described in cattle (Du Plessis, 1990) has been reported from the nyala (Pfitzer et al., 2011) and the African buffalo (Debeila, 2011) thus indicating that this pathogen can infect wild animal species as well. However, its distribution in South Africa is still unknown.

4.3. Vector-pathogen relationships

Numerous tick-borne pathogens have been reported from tick species in South Africa. Recently, Halajian et al. (2016) reported the occurrence of *R. africae* and *R. massiliae* in *Am. sylvaticum* and *Rh. simus* ticks collected from a leopard tortoise. *Rickettsia africae* is the causal agent of African tick bite fever, a zoonotic disease frequently reported among travelers visiting African countries including South Africa (Angerami et al., 2018). This pathogen is transmitted by ticks of the genera *Amblyomma, Haemaphysalis, Hyalomma* and *Rhipicephalus*, which are known to transmit numerous zoonotic pathogens in the Eastern Cape Province of South Africa (Iweriebor et al., 2017). In the present review most *Rhipicephalus* spp. are linked to *Theileria* spp.; however, *Rh. appendiculatus* and *Rh. warburtoni* are also linked to *A. marginale* and *A. centrale*. In contrast, other studies (Potgieter & van Rensburg, 1987; Hove et al., 2018) have indicated that in South Africa, *A. marginale* and *A. centrale* are transmitted by *Rh. simus, Rh. microplus, Rh. decoloratus, Rh. evertsi evertsi* and/or *Hyalomma marginatum rufipes*. Almost half of the studies included in the review did not identify pathogens in the identified ticks; therefore, the role of these ticks in the epidemiology of vector-borne diseases in South Africa is still unknown. Consequently, a significant number of transmission experiments is required to clarify the vectoral capacity of some of the identified ticks. Additional studies are required to determine the possible role of wild animals and ticks in the transmission of zoonotic

tick-borne pathogens such as *Babesia microti, Borrelia burgdorferi, A. phagocytophilum, C. burnetii* and other *Rickettsia* spp.

4.4. Diagnostic tests

Definite identification of tick is a crucial aspect in the detection of tick-borne diseases and pathogens, and it is of great benefit in their control and possible eradication. Morphology has been used for the identification of ticks in most studies (Horak et al., 2000, 2006; Matthee et al., 2013; Penzhorn et al., 2020) and has often been applied in combination with other tests (Tonetti et al., 2009; Halajian et al., 2016; Viljoen et al., 2020, 2021). However, this method has its own limitations as it is labour-intensive and the results are sometimes subjective, especially with morphologically similar taxa, damaged specimens and immature tick stages (Couper & Swei, 2018). Molecular methods such as PCR, RLB, quantitative polymerase chain reaction, NGS etc., have contributed greatly to detecting novel pathogens that cannot be isolated using traditional culture-based methods and have allowed for the characterization of species to the genus or species level. Moreover, sequencing also provides a platform for generation of high-throughput data to explore the composition, distribution and taxonomic classification of pathogens, as well as discovering new pathogens (Grada & Weinbrecht, 2013).

4.5. Limitations and recommendations for future studies

The majority of the studies considered in this review investigated host-pathogen relationships and only a few studies investigated vector-pathogen associations. Nonetheless, the determined tick distribution and the associations between the host-vector-pathogen can serve as the foundation for future investigations, especially in monitoring the spread of alien and invasive tick species. Although the use of molecular-based assays in the detection of tick-borne pathogens is preferred over serology due to improvements in their sensitivity and specificity, several serology tests still exist for diagnostics of economical important *Theileria* spp. and the indirect fluorescent antibody test (IFAT) is still the gold standard assay recommended by the World Organisation for Animal Health (OIE) for most economically important parasites (reviewed by Mans et al., 2015). The exclusion of serological methods in the search criteria may have limited the number of pathogens identified. Additionally, South Africa has different styles for the management of wild animals, which include captive, semi-captive/managed wild animals and wild/free-ranging populations (Swanepoel et al., 2021) and these were not considered in our methodology. Lastly, this study excluded surveys of tick-borne viruses such Crimean-Congo haemorrhagic fever virus, the causative agent of Crimean-Congo haemorrhagic fever in southern Africa (Chitanga et al., 2014). Future studies should focus on addressing these shortfalls. Most of the studies on tick-borne pathogens in South African wild animals focus on the identification of tick-borne piroplasms of veterinary importance. Studies on tick-borne zoonoses in South African wild animals and human populations are under-represented and should be included in future epidemiological surveys, especially in the light of climate change and emergence of novel pathogens.

The research question in future studies should preferably be narrow so that quantitative data can be obtained from similar studies to allow quantitative synthesis (meta-analysis) of the data. Given the fact that potential vectors of zoonotic pathogens like *R. africae* were identified from wild animals in some of the studies included in this review, it is necessary for game parks to provide information and awareness programmes about the prevention and control of zoonotic diseases to visitors.

5. Conclusions

The present review has demonstrated that South African wild animals habour a wild range of tick species across the nine provinces of South

Africa and some of these ticks are competent vectors of pathogens of veterinary and medical importance. Ticks have a reciprocal beneficial coexistence with a wide range of hosts, and are significant vectors that transmit bacterial, viral and protozoan pathogens to animals and humans. The review also emphasized the host preference of the ticks and the pathogens they transmit. Most of the adult and immature (larvae and nymphs) ticks collected in the studies considered in this review mainly feed on larger animals as well as on crawling and ground-dwelling small mammals respectively as shown in various previous reports. It is expected that this review will contribute to the management of ticks and tick-borne pathogens in South African wild animals.

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Declaration of competing interests

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Appendix A. Supplementary data

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