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History and development of research on wildlife parasites in southern Africa, with emphasis on terrestrial mammals, especially ungulates

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ABSTRACT

The history of wildlife parasitology in South Africa, and to some extent southern Africa, is reviewed, giving a brief overview of the early years and following its development from the founding of the Onderstepoort Veterinary Institute in 1908 until the turn of the century. An emphasis is placed on game species. The main findings on protozoan parasites, including those of carnivores, are presented, starting in the 1890s and leading up to the first decade of the 21st century. Important developments with regard to the studies of arthropod and helminth parasites took place during a period of three decades, starting from the 1970s. Because of the sheer volume of work done by parasitologists during this time, this particular part of the overview concentrates on South African authors or authors working in South Africa at the time, and is limited to hosts that are members of the order Perissodactyla and the superorder Cetartiodactyla.

1. Introduction

The rich diversity of wildlife found in South Africa awakened the interest of parasitologists from an early stage onwards. Much of the initial work on wildlife parasites was based on incidental findings, but South African parasitologists soon realized the importance of investigating the parasite fauna of wildlife in order to complement their studies on parasites of domesticated animals. They perceived the interrelatedness of the two host groups regarding the potential of wildlife serving as reservoirs for the parasites of livestock and vice versa. From the 1970s on an attempt was made to systematically examine the helminth fauna of each game species and to obtain insight into the composition of their protozoan, arthropod and helminth fauna.

2. Protozoa

After an early start in the 1890s, research into protozoa of wildlife lagged behind the other parasitology disciplines. For the next few decades there were sporadic reports only, probably since veterinary research was focused on diseases affecting livestock. The first systematic investigations of wildlife parasites commenced in the 1960s, with large-scale surveys conducted in the Kruger National Park (KNP) and other conservation areas. Generally, parasites could only be identified to genus level. Real progress could only be made once molecular characterization techniques had become established.

2.1. Hemoprotozoa

2.1.1. Trypanosomes

Shortly after discovering that nagana is caused by *Trypanosoma* spp. and that tsetse flies (*Glossina* spp.) are the vectors, Bruce (1897) confirmed the occurrence of trypanosomes in African buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), greater kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*) and spotted hyaena (*Crocuta crocuta*) by subinoculation of blood into susceptible dogs. In 1914, impala (*Aepyceros melampus*) and plains zebra (*Equus quagga*) were added to the list (Neitz, 1931), while gray duiker (*Sylvicapra grimmia*) and warthog (*Phacochoerus aethiopicus*) followed in 1921 (Curson, 1928). Much later, a *Trypanosoma theileri*-like parasite was described from spleen smears of a nyala (*Tragelaphus angasii*) (Bigalke et al., 1972).

2.1.2. Piroplasms

Blood smears made from wild animals shot in tsetse-clearing operations in KwaZulu-Natal (KZN) during the 1920s were screened for the presence of piroplasms. *Theileria* spp. were reported from bushbuck, greater kudu, reedbuck (*Redunca arundinum*), mountain reedbuck (*Redunca fulvorufula*), common waterbuck (*Kobus ellipsiprymnus*), blue wildebeest, steenbok (*Raphicerus campestris*),

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gray duiker, warthog and aardvark (*Orycteropus afer*), while the presence of *T. equi* in plains zebras, first reported in 1909, was confirmed (Neitz, 1931, 1933). Although no formal description was made, the name *T. tragelaphi* was coined for the piroplasm occurring in bushbuck (Neitz, 1931). Four decades later a small piroplasm, possibly *T. tragelaphi* and a *Babesia* sp. were reported from a bushbuck (Bigalke et al., 1972).

In 1930 clinical babesiosis was reported from a wild-caught sable antelope (*Hippotragus niger*) transported to the Johannesburg Zoo, apparently the first ever report of this disease in a wild animal (Martinaglia, 1930). The parasite was later named *B. irvinesmithi*. Fatal babesiosis was also recorded in free-ranging sable antelope (Wilson et al., 1974; Thomas et al., 1982). Clinical babesiosis was reported from zoo-bred sable antelope imported into South Africa (McInnes et al., 1991), and a novel *Babesia* sp. from this host, possibly *B. irvinesmithi*, has been characterized molecularly (Oosthuizen et al., 2008).

A new genus name, *Cytauxzoon*, was coined when a hitherto unknown fatal infection in a gray duiker was described; the causative organism was named *C. sylvicaprae* (Neitz and Thomas, 1948). This was followed by the naming of *C. strepsicerosae* from greater kudu (Neitz, 1957). Piroplasmosis was incriminated in causing mortalities in sable and roan antelopes (*Hippotragus equinus*) in game reserves in the northern Transvaal (now Limpopo Province) (Wilson et al., 1974). A piroplasm isolated from a sable antelope carcass [now referred to as *Theileria* sp. (sable)] was successfully established and cultured *in vitro* (Stoltsz and Dunsterville, 1992). Subsequently, *Theileria* spp. associated with mortality in greater kudu, gray duiker, sable antelope and roan antelope were characterized molecularly (Nijhof et al., 2005). *Rhipicephalus appendiculatus* and *R. evertsi evertsi* have been identified as potential vectors of *Theileria* sp. (sable) (Steyl et al., 2012).

Fatal cytauxzoonosis was diagnosed in a young giraffe (*Giraffa camelopardalis*) translocated from Namibia to KZN, South Africa (McCully et al., 1970b). Both a *Theileria* sp. and a *Babesia* sp. have been reported from this host (Oosthuizen et al., 2009).

Fatal cytauxzoonosis was also reported in a tsessebe (*Damaliscus lunatus*) (Jardine and Dubey, 1996). Two novel *Theileria* 18S rRNA gene sequences which are phylogenetically very closely related to both *Theileria* sp. (sable) and *T. separata* have been identified in this antelope (Brothers et al., 2011). Hemoparasites prevalent in nyala in northern KZN included *Theileria* sp. (kudu), *T. buffeli, Theileri*a sp. (sable) and *T. bicornis* (Pfitzer et al., 2011)

East coast fever, caused by cattle-associated *T. parva*, was introduced into southern Africa in 1902 and finally eradicated in the mid-1950s (Lawrence, 1992). Shortly afterwards it was realized that African buffalo are natural hosts of *T. parva* that can be transmitted to cattle (Neitz, 1955). Due to its economic importance as a cause of Corridor disease in cattle, buffalo-associated *T. parva* is being studied intensively (*e.g.* Chaisi et al., 2011; Pienaar et al., 2011).

Between 1967 and 1969, thin blood smears were prepared from 106 healthy white rhinoceroses (*Ceratotherium simum*) in KZN immobilized for translocation. A *Babesia* sp. was seen in two animals (1.9%), while a small *Theileria* sp. was seen in 34 (32.1%) (Bigalke et al., 1970). Fatal babesiosis in black rhinoceros (*Diceros bicornis*) led to the characterization and description of *B. bicornis* and *T. bicornis* (Nijhof et al., 2003). Of 195 white rhinoceroses sampled in the KNP, 71 (36.4%) tested positive for *T. bicornis*, while 18 (9.2%) tested positive for *T. equi*; *B. bicornis* was not found (Govender et al., 2011).

Babesia thomasi was described from rock hyrax (*Procavia capensis*) (Jansen, 1952).

Despite early statements that black-backed jackal (*Canis mesomelas*) could not be infected with piroplasms from domestic dogs (Lounsbury, 1903), *B. canis* (*sensu lato*) was successfully transmitted from domestic dogs to black-backed jackal and African wild dog (*Lycaon pictus*) (Neitz and Steyn, 1947; Van Heerden, 1980). Using molecular techniques, the presence of *B. rossi* was confirmed in African wild dog (Matjila et al., 2008).

In the 1930s, a small piroplasm, now called *B. cynicti*, was described from yellow mongoose (*Cynictis penicillata*), one of the main vectors of the rabies virus on the central plateau of Southern Africa (Neitz, 1938). It was subsequently found to be quite prevalent in three mongoose populations studied (Penzhorn and Chaparro, 1994).

Piroplasms, first reported in lion blood smears from the KNP in 1975, were subsequently found to be quite prevalent (Young, 1975; Lopez-Rebollar et al., 1999). Although initially regarded as *B. felis*, molecular characterization revealed the presence of a hitherto unknown species, later named *B. leo* (Penzhorn et al., 2001). *Babesia lengau*, which was subsequently described from cheetah (*Acinonyx jubatus*), as well as *B. felis* and *B. leo*, were subsequently reported from various other wild felids (Bosman et al., 2007, 2010).

2.2. Coccidia

2.2.1. Intestinal coccidia

Coccidiosis is a disease of intensification due to the build-up of sporulated oocysts in accumulated feces, facilitating ingestion of large infective doses. A further factor is immunosuppression of the host, due to stress. This is particularly relevant in free-ranging wild animals brought into captivity, even temporarily. Reports of intestinal coccidia from wildlife are few and far between and systematic studies are lacking.

Eimeria impalae was incriminated as causing fatal coccidiosis in juvenile impala captured during autumn/winter and subsequently held in a boma (Bigalke, 1964; Pienaar et al., 1964). A rare, aberrant coccidian causing small intrauterine polyps, also developing in uterine glands of impala ewes and sporulating *in situ*, was named *E. neitzi* (McCully et al., 1970a).

At least six different *Eimeria* oocyst types have been recovered from African buffalo feces (Penzhorn, 2000), while fatal coccidiosis in springbok (*Antidorcas marsupialis*) was reported on a game ranch (Lopez-Rebollar et al., 1997).

2.2.2. Tissue-cyst-forming coccidia

Unidentified sarcocysts were reported at routine carcass inspection of African buffalo, impala, nyala and eland (*Taurotragus oryx*) (Young and Wagener, 1968; Young and Van den Heever, 1969; Basson et al., 1970; Keep, 1970, 1971, 1972). In virtually all cases the complete life cycle of the organisms is not known. It has been reported, however, that vultures *Gyps* spp. are definitive hosts of a *Sarcocystis* species, presumably *S. melampi*, from impala (Markus et al., 1985).

Detailed morphological studies of sarcocysts from various South African host species were carried out during the 1990s. The cyst wall of a sarcocyst from African buffalo was morphologically similar to that of *S. fusiformis*, but dimorphism of the cyst organisms, not known from *S. fusiformis*, was noted (Bengis et al., 1997). *Sarcocystis melampi* was described from impala, while a sarcocyst from greater kudu was structurally indistinguishable from *S. hominis*, which occurs in cattle (Odening et al., 1998). Three new species were described from giraffe: *S. giraffae, S. klaseriensis* and *S. camelopardalis* (Bengis et al., 1998). Two new species were described from warthog: *S. dubyella* and *S. phacochoeri* (Stolte et al., 1998). Two new species were described from the hippopotamus (*Hippopotamus amphibius*): *S. hippopotami* and *S. africana* (Odening et al., 1997).

During routine carcass inspection in KNP, *Besnoitia* cysts were found in greater kudu, blue wildebeest and impala (Basson et al., 1965b). Further investigation revealed that they were closely related to *B. besnoiti*, and a live vaccine against bovine besnoitiosis was developed from this isolate (McCully et al., 1966; Bigalke et al., 1967, 1974). *Besnoitia* cysts have also been reported from a warthog (Keep and Basson, 1973).

Clinical toxoplasmosis has been reported from free-living Chacma baboon (*Papio ursinus*) as well as a cheetah, while a *Toxoplasma*-like organism has been implicated in causing clinical disease in a young Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*) (McConnell et al., 1973; Van Rensburg and Silkstone, 1984; Jardine and Dubey, 1996). There is mounting evidence that many carnivores and herbivores are seropositive to *T. gondii* (Cheadle et al., 1999; Hove and Dubey, 1999; Penzhorn et al., 2002; Hove and Mukaratirwa, 2005). Clinical neosporosis has been confirmed in a white rhinoceros calf (Williams et al., 2002).

2.3. Other protozoa

Cryptosporidium spp. oocysts were recovered from fecal specimens of African elephant (*Loxodonta africana*), African buffalo and impala in the KNP (Abu Samra et al., 2011); molecular characterization revealed the presence of *C. ubiquitum* in two impala and one buffalo, and *C. bovis* in one buffalo (Abu Samra et al., 2013).

Developmental stages of *Hepatozoon* sp. were reported from lion, leopard and spotted hyaena, while a *Hepatozoon*-like parasite was also reported from impala (Basson et al., 1965a; McCully et al., 1975).

3. Metazoa

Investigations into the helminths of South African wildlife first started at the Onderstepoort Veterinary Institute (OVI) in 1908 with the appointment of L.A. Gough as zoologist, whose interests included avitelline cestodes of sheep and antelopes (Ortlepp, 1961). These studies gained momentum when Sir Arnold Theiler became the first director of Onderstepoort. Straight away, he realized the value of not only studying the helminths of domestic animals but those of the indigenous fauna as well. To this effect he initiated the collection of parasites from wild animals in the Pretoria vicinity (Ortlepp, 1961). Part of this collection was sent overseas for the identification of cestodes, but H.O. Mönnig, who was appointed as parasitologist at Onderstepoort in 1922, studied the nematodes and described four new species. Over and above his investigations into the pathology and treatment of helminthoses in livestock, he retained a vested interest in the helminths of wild animals. From an early stage on he realized their importance in relation to livestock: "The importance of studying the parasites of the wild fauna of a country like South Africa, where parasites play an important role in diseases of domesticated animals, is evident" (Mönnig, 1923).

He therefore not only described numerous new species of helminths from wild antelopes, but conducted a number of transmission experiments into the status of wild antelopes as carriers of nematodes of domestic ruminants (Mönnig, 1931a, 1932, 1933). Larvae harvested from fecal cultures of various antelope species were identified and used to infect lambs, whose feces at the time contained no or few helminth larvae. The success of cross-infection was determined either by subsequent culturing of the lambs' feces and/or during subsequent post mortem examinations. In this way, the following transmissions were accomplished: *Haemonchus contortus, Longistrongylus albifrons* (=*Bigalkea albifrons*), *Trichostrongylus falculatus* and, to a limited degree, *Impalaia nudicollis* from blesbok to sheep; *H. contortus, H. bedfordi, Cooperia fuelleborni, C. hungi* (=*C. fuelleborni* var. *hungi*) from waterbuck to sheep; *H. contortus, L. albifrons, T. falculatus, Nematodirus spathiger, Paracooperia serrata* and *Cooperioides antidorca* from springbok to sheep; *C. hungi* from impala to sheep; *H. vegliai* and *C. neitzi* from kudu to sheep; *H. bedfordi* from blue wildebeest to sheep; *H. contortus, T. deflexus* (=*T. instabilis*) and *Strongyloides papillosus* from sheep to springbok; *Teladorsagia* (=*Ostertagia*) *trifurcata, T. circumcincta* and *Oesophagostomum columbianum* from sheep to blesbok (Mönnig, 1931a, 1932, 1933).

In order to facilitate these studies, Mönnig, where possible, also described the larval stages of species of which the adults had recently been described, such as for *Bronchonema magna* from blesbok (Mönnig, 1932). He also produced illustrated descriptions for the infective larvae, obtained through fecal culture, of a number of nematodes from sheep, including keys for their identification (Mönnig, 1931b). Over the years these data were expanded, and, recognizing the value of this non-invasive technique, J.A. van Wyk, himself a prominent researcher at the OVI, refined the methodology (Van Wyk, 1977; Van Wyk et al., 2004). His work resulted in the most comprehensive guide to date on the morphological identification of nematode infective larvae in small ruminants and cattle (Van Wyk and Mayhew, 2013) some 80 years after Mönnig's initial publication.

P.L. Le Roux spent only a short time in South Africa (1929–1931) but described a number of helminths from wild animals during that period. Among others, he described *H. mitchelli* from eland, *H. vegliai* from kudu and *H. bedfordi* from buffalo (Le Roux, 1929). The last two were named after his OVI colleagues F. Veglia, still known for his pioneering work on *H. contortus* and *Oesophagostomum* spp., and G.A.H. Bedford, renowned arthropod taxonomist. He subsequently continued his work at the Department of Animal Health in the then Northern Rhodesia (Zambia), later including Malawi. Like his colleagues Mönnig and Ortlepp in South Africa, he emphasized the importance of investigating the diseases of the indigenous fauna and fish as well as farm stock (Le Roux, 1957).

In 1961, R.J. Ortlepp, one of South Africa's most productive and renowned helminth taxonomists, published an overview of the development of taxonomic helminthology in South Africa, with emphasis on helminths occurring in indigenous wild animals. To briefly summarize his statistics (published in Afrikaans) on newly described species, in the approximately 40 years of helminth research at Onderstepoort that lead up to his review, more than 150 new helminth species had been described. Thirteen of these were described by Le Roux, 46 by Mönnig, and Ortlepp himself had contributed over 100 new taxa. Not surprisingly so, more than 100 of the new species had been recovered from mammalian hosts, as these received the most attention from both zoologists and hunters at the time, thus increasing the availability of parasitic material from them. Another 30 new species were described from avian hosts, nine from reptiles and two from amphibians. Fish had not yet been studied at all. Ortlepp (1961) concluded his review with an appeal to zoologists and other interested persons to collect and study the parasites of wild animals that had hitherto not been given any attention, being well aware that much remained to be discovered.

In the years to follow, a number of South African parasitologists took up this challenge, often combining the efforts of various disciplines of parasitology, and with a slight shift in emphasis. Based on the ground work laid by earlier parasitologists in recording and describing the parasites of South African wildlife, in many instances based on incidental findings, they now followed a more structured approach, at the same time both increasing the host spectrum and complementing previous records. Studies were geared toward full parasite collections from a particular host species, including metazoan and blood parasites where possible, and hosts were examined in sufficient numbers to ensure detection of rarer parasite species. In many instances, examinations would be done over a period of 12 consecutive months or more, to account for parasites that may be plentiful but strictly seasonal, thus being easily missed in casual surveys, and to determine the seasonal abundance of parasites. Surveys of the same host species at different localities within South Africa would also provide an indication of the geographic distribution of its parasites. As a result, more and more data were accumulated that now allow us to gain insight into the ecology of parasites in at least some of the many and diverse hosts in South Africa and into the patterns and processes that shape their communities.

Because of the sheer volume of work done by parasitologists in South Africa during this period, the following overview is largely limited to South African authors or authors working in South Africa at the time, a period of 30 years following the early parasitologists, thus including research from 1970 to 2000. This overview is also limited to host members of the order Perissodactyla with the two families Rhinocerotidae (rhinoceroses) and Equidae (zebras), and the superorder Cetartiodactyla, comprising the three orders Whippomorpha (Hippopotamidae: hippopotamus), Suiformes (Phacochoerinae: warthog; Suinae: bushpig) and Ruminantia (Giraffidae: giraffe; Bovidae: buffalo and antelope). The classification of hosts follows that of Skinner and Chimimba (2005). Since the helminth composition of the various antelopes is largely determined by their feeding habits, their grouping as grazer, mixed feeder or browser is indicated when they are discussed.

3.1. Taxonomical works

While the emphasis of parasitology shifted, taxonomy nevertheless kept on playing an important role and it warrants placing the taxonomic developments in a broader context. Canaris and Gardner (2003) published a bibliography of helminth species that had been described from African vertebrate hosts during the period 1800–1967. It clearly illustrates the species diversity scientists addressing the parasite fauna of African hosts were faced with, posing a considerable challenge and providing endless opportunities at the same time. A total of 1392 helminth species, trematodes (n = 327), cestodes (n = 374) and nematodes (n = 691) were described from African vertebrates. Given its amphibian nature, it might not be surprising that the hippopotamus leads the list of mammals as type host for new trematode species with 24 new species described from it. The African elephant has 35 new nematode species to its credit, followed by the warthog with 16, the impala and springbok with 12 and nine new species, respectively, and black rhino with eight newly described taxa in the 167-year period (Canaris and Gardner, 2003). Horak (2009) reviewed a century of tick taxonomy in South Africa, compiling a list of the 80 ixodid tick species, 25 argasid tick species and *Nuttalliella namaqua* with special reference to South African authors or foreign authors that worked in South Africa when describing or adding to the description of a particular tick species. Despite the numerous taxonomic works published by the 1970s, the investigation of the parasite fauna of herbivores in South Africa still revealed a number of new species and provided much scope for taxonomic studies, as is evidenced in the over 20 taxonomic papers originating from large and medium-sized herbivores alone. As regards the ectoparasites, five new tick species of the genus *Rhipicephalus* have been described since 1970. Adults, nymphs and larvae of *R. lounsburyi* and *R. neumanni*, of which the adults parasitize the feet of sheep, were described by Walker (1990). Later all stages of development of *R. exophthalmos* were described, and the species, exclusive to Leporidae, with which it had formerly been confused, *R. oculatus* was redescribed (Keirans et al., 1993). Subsequently *R. oreotragi* was described from klipspringers and *R. warburtoni* from gemsbok and scrub hares, both of which are the hosts of the adults, while scrub hares are also the hosts of the immature stages (Walker et al., 2000). These descriptions are accompanied by detailed drawings and electron micrographs, life cycle data and host records. Studies of the fleas from warthog led to the erection of *Phacopsylla* as a new genus for the flea previously described as *Echidnophaga inexpectata* (Beaucournu and Horak, 1994). Adults of the louse fly *Lipoptena paradoxa* were redescribed by Visagie et al. (1992) from kudu in the KNP, together with a first description of the puparium of this parasite and notes on its biology. Studies on the parasites of blue wildebeest in the KNP provided the opportunity to provide the first description of the first-stage larvae of the oestrid fly *Kirkioestrus minutus*, a common parasite of the nasal passages and paranasal sinuses of these animals (Horak et al., 1980). Descriptions of the second- and third-stage larvae were included.

With regard to helminths parasitizing the Perissodactyla, a black rhino from the Umfolozi Game Reserve (GR) in KZN became type- and to date only host to a new nematode genus and species in the family Atractidae, *Diceronema versterae*, recovered in large numbers from its stomach (Gibbons et al., 1996). Its species epithet being a tribute to A. Verster, a South African helminthologist who is best known for her comprehensive works on taeniid cestodes (Verster, 1965, 1969), but who also contributed to the knowledge of the South African nematode fauna. An additional two trichostrongylid and two spirurid nematodes were described from zebras in this 30-year period. *Cylicostephanus longiconus* was first found in Hartmann's mountain zebra (*Equus zebra hartmannae*) in Namibia (Scialdo-Krecek, 1983b), and *Cylicodontophorus reineckei* was described from plains zebra in both Namibia and South Africa and Hartmann's mountain zebra from Namibia (Scialdo-Krecek and Malan, 1984). The latter species was named after another renowned South African parasitologist, R.K. Reinecke who headed Helminthology at Onderstepoort for a number of years. Descriptions and information on these Cyathostominae from zebras in southern Africa contributed to a comprehensive and annotated checklist for 51 recognized species of small strongyles of horses, asses and zebras of the world, including detailed drawings and light- and SEM photographs (Lichtenfels et al., 1998). Scanning electron microscopy studies of *Strongylus* species in zebra provided first-time data on their external ultrastructure and revealed further differences between *S. vulgaris, S. asini, S. equinus* and *S. edentatus*; at the same time the latter three species were reported for the first time from Hartmann's mountain zebra. The spirurid *Habronema malani* was described from the stomachs of plains zebra in the Etosha National Park (Etosha NP) and KNP, and from Hartmann's mountain zebra in Etosha NP (Krecek, 1989). The worms were named in honor of the vast contributions of F.S. Malan to parasitology in South Africa. *Habronema tomasi* was described from the small intestine of plains zebra in the KNP (Krecek, 1989), and after *H. zebrae* and *H. malani*, became the third *Habronema* species described by South African parasitologists from zebras in southern Africa.

All three orders in the Cetartiodactyla gave rise to further taxonomic studies. Boomker (1990) published the first description of the males of *O. mocambiquei*, originally described from female worms recovered from the large intestine of warthog from the northern parts of Mozambique. The description of the males was accompanied by a key to the six species of *Oesophagostomum* parasitizing warthogs in South Africa and Namibia (Boomker, 1990). From an ulcerated skin lesion observed on one of a number of hippopotami that had to be culled during a drought period in the KNP, *Stephanofilaria thelazioides* was described by Boomker et al. (1995). This parasite showed close affinities to its congener *S. dinniki* from a black rhino in Kenya. Based on the more primitive characters of the African species, it was assumed that the genus originated in Africa, from where it was introduced to Asia, and had only recently become adapted to domestic bovines (Boomker et al., 1995).

The attempt to identify specimens of the genus *Impalaia*, recovered during the autopsy of a giraffe that had died in the National Zoological Gardens, Pretoria, South Africa, and that were eventually assigned to *I. tuberculata*, led to the revision of this genus and to a revised host–parasite list for the four species considered valid (Boomker, 1977). Interestingly, unaware of the studies of his British colleagues, Boomker (1977) had embarked on the same project and came to the same conclusions as Gibbons et al. (1976), whose paper appeared some 3 months prior to that of Boomker (1977).

The majority of new taxa were described from the order Ruminantia, however, reflecting the main thrust of the parasitological surveys done in the years between 1970 and 2000. Without exception, these taxa belonged to the Trichostrongyloidea, one of the most common and species-rich superfamilies in domestic as well as wild ruminants, and represented five genera. *Cooperia connochaeti* was described from blue wildebeest in the KNP where it occurred in all but one of eight animals examined, and was also present in the same host in Botswana as well as in impala from the KNP (Boomker et al., 1979). A new genus and species, *Paracooperioides peleae*, was collected from the small intestine of gray rhebok from the Bontebok National Park (BNP) (Boomker et al., 1981). Two new species of the genus *Paracooperia* were found in tragelaphine antelopes: *P. devossi* in the small intestine of bushbuck in the KNP, where it was also present in kudu, and *P. horaki* was found in small numbers in nyala in the Mkuzi (type locality), Ndumu and Umfolozi GR in KZN (Boomker and Kingsley, 1984b; Boomker, 1986a). Interestingly, of the now recognized seven species of *Paracooperia* (Gibbons, 1978; Boomker and Kingsley, 1984b; Boomker, 1986a), five were described by parasitologists from southern Africa: *P. serrata, P. raphiceri, P. mazabukae, P. devossi* and *P. horaki*. Boomker and Kingsley (1984b) considered *P. devossi* a recent acquisition of bushbuck in the KNP, based on its low prevalence and intensity of infection. The authors assumed it had migrated together with its host from Mozambique, its spread being slow due to the browsing habits of its host.

During a parasite survey of, among others, gray rhebok and bontebok (*Damaliscus pygargus pygargus*; = *D. dorcas dorcas*) in the BNP, Boomker et al. (1983b) described specimens of *H. contortus* from the latter hosts which differed from typical representatives of this species by their much longer spicules. Specimens recovered from gray rhebok from this locality and possessing the same characteristics were subsequently described as a new species, *H. horaki* (Lichtenfels et al., 2001).

Four new species of the genus *Trichostrongylus* were collected from the small intestine of antelopes. Red duiker examined at Charter's Creek in the St. Lucia GR, KZN, are type host to *T. angistris* and *T. anomalus*, whereas *T. auriculatus* was described from a steenbok from the Kalahari Gemsbok National Park (now Kgalagadi Transfrontier Park, KTP), Northern Cape Province, and was also found in a gemsbok and a red hartebeest (*Alcelaphus buselaphus*) at the same locality (Boomker, 1986b; Boomker and Vermaak, 1986a, 1986b). A fourth species, *T. deflexus*, described from tsessebe from Nylsvley Nature Reserve (NR), Limpopo Province, as type-host, was also recovered from several antelope species from the KNP (Boomker and Reinecke, 1989).

By the end of the 20th century, a number of publications and check lists summarized information on the host and geographic distribution of some of the African ticks (Theiler, 1962; Arthur, 1965; Baker and Keep, 1970; Walker et al., 2000; Voltzit and Keirans, 2003), lice (Ledger, 1980) and flies (Zumpt, 1965), and ectoparasites in general (Bedford, 1932, 1936). Ortlepp (1961) listed the helminth species recorded at the time from giraffe, buffalo and antelope, indicating those that were common in domestic animals, those that had been used to experimentally infect sheep and those that were recorded from outside South Africa, Namibia, and Swaziland. To date the most comprehensive checklist of helminths of African mammals is that of Round (1968), updated by Bain (2003), and as mentioned, Canaris and Gardner (2003) published a bibliography of helminth species described from African vertebrates from 1800 to 1967.

3.2. Epidemiological studies

3.2.1. Order Perissodactyla

3.2.1.1. Rhinocerotidae. Round (1968) had recorded a total of eight helminth species from rhinoceroses in South Africa, *viz.* seven nematode species, six of which belonged to the genus *Kiluluma*, a common parasite genus of rhinos, and one *Oxyuris* species, from black rhinoceros (browser), and the cestode genus *Anoplocephala* from white rhinoceros (grazer). As part of a symposium on "Rhinos as Game Ranch Animals", Penzhorn et al. (1994) compiled a review of the protozoan, arthropod and helminth parasites that had been recorded from these two hosts throughout Africa. Approximately 40 tick species, three of which (*Amblyomma rhinocerotis, A. personatum* and *Dermacentor rhinocerinus*) are primarily rhino parasites, and at least 40 helminth species (including the trematodes *Brumptia bicaudata* and *Gastrodiscus aegyptiacus*, and the cestodes *A. diminuta* and *A. gigantea*) had by then been listed; flies were represented by *Glossina longipennis* and the two bot fly species *Gyrostigma rhinocerontis* (=*G. pavesii*) and *G. conjungens*, the latter from black rhinos in East Africa. Knapp et al. (1997) opportunistically studied the parasites of six black and three white rhinoceroses in South Africa and Namibia. Helminths and arthropods could be quantified from two black rhinos and one white rhino; from an additional four black and two white rhinos only the ticks could be counted. The diversity of internal and external parasites was greater in the black rhinos from South Africa than in the one from Namibia. Three nematode species, *K. rhinocerotis, Probstmyria vivipara* and *O. karamoja*, were recovered from a black rhinoceros from Etosha NP, of which *P. vivipara* was by far the most numerous as was also the case in a black rhino from South Africa. The latter host harbored an additional five nematode species: *K. goodeyi, K. magna, D. versterae, Draschia megastoma* and *Parabronema roundi*. The cestode *A. gigantea* was present in large numbers in black rhinos from both Namibia and South Africa, whereas the stomach bot *G. rhinocerontis* was only found in the rhino from South Africa. New host or geographic records were listed for six of the nematode species and the single cestode species from black and white rhinos. Based on previous lists drawn up by Theiler (1962) and Baker and Keep (1970), Knapp et al. (1997) amended the list of ixodid tick species from white and black rhinoceroses in South Africa and also presented Norval's (1985) list for Zimbabwe. The rhinoceros-specific tick *D. rhinocerinus*, originally recorded from KZN only (Theiler, 1962), was present on all rhinos from South Africa, excepting that from the Addo Elephant National Park, Eastern Cape. Knapp et al. (1997) speculated that this tick was introduced or re-introduced into the KNP together with its host.

3.2.1.2. Equidae. Three species or subspecies of zebras (grazer) occur in southern Africa and their parasites have been documented extensively. At the time these studies were conducted, the systematic position of the plains zebra was still somewhat uncertain and in the papers to listed later it was commonly referred to as 'Burchell's zebra', '*Equus burchellii*', or '*Equus burchellii antiquorum*'. The helminth and arthropod parasites of Hartmann's mountain zebra were studied in Namibia (Scialdo-Krecek et al., 1983; Horak et al., 1984a, 1992a; Krecek et al., 1987b), those of plains zebra in Namibia (Krecek et al., 1987a, 1994a; Horak et al., 1992a) as well as the KNP (Scialdo et al., 1982; Scialdo-Krecek, 1983a; Horak et al., 1984b; Krecek et al., 1987b) and in KZN (Mares et al., 1984), and those of Cape mountain zebra (*Equus zebra zebra*) in the Mountain Zebra National Park (MZNP), Eastern Cape (Young et al., 1973b; Horak et al., 1986a, 1991b; Krecek et al., 1994b). Some 19 new host–parasite and/or geographic records were listed during these studies (Els et al., 1983; Scialdo-Krecek, 1983b; Scialdo-Krecek et al., 1983; Scialdo-Krecek and Malan, 1984; Krecek et al., 1987a; Krecek, 1989).

The main nematode groups shared by the three zebras are the Cyathostominae, Strongylinae, Atractidae and Habronematidae. The following genera were reported from all three hosts: *Cyathostomum, Cylicocyclus, Cylicostephanus, Triodontophorus, Probstmyria, Crossocephalus, Habronema* and *Draschia*; a number of nematodes were recorded in plains zebra and Hartmann's mountain zebra, but were absent in Cape mountain zebra: *Cylicodontophorus, Cylindropharynx, Triodontophorus, Craterostomum, Oxyuris* and *Setaria*; the genera *Poteriostomum, Oesophagodontus, Strongylus, Trichostrongylus* and *Strongyloides* were recorded from the plains zebra only (Scialdo et al., 1982; Scialdo-Krecek et al., 1983; Krecek et al., 1987a, 1987b, 1994b). Two cestodes, *A. perfoliata* and *A. magna*, were reported from Cape mountain zebra (Penzhorn, 1984; Krecek et al., 1994b). The two atractids from the large intestine of zebras, *P. vivipara* and *C. viviparus*, are usually the most numerous helminths in zebras, although few *C. viviparus* were recovered from Cape mountain zebra (Krecek et al., 1994b). Intensities of *P. vivipara* often exceed several millions, with 104,120,467 recorded from a plains zebra in the KNP (Krecek et al., 1987a, 1994b). Individual Hartmann's mountain zebra in Namibia were infected with as many as over 60 million *Crossocephalus* sp. and over 42 million *P. vivipara* (Scialdo-Krecek et al., 1983). Scialdo-Krecek (1983a) also determined the predilection sites of small and large strongyles.

Comparing helminth burden and diversity of Hartmann's mountain zebra in Namibia *versus* plains zebra in the KNP, viviparous atractids, in which the entire life cycle is thought to be completed inside the host, appeared to be more successful in arid environments, whereas cyathostomes, in which free-living larval stages occur outside the host, were favored by wet climates (Scialdo et al., 1982; Scialdo-Krecek et al., 1983; Krecek et al., 1987a). Krecek et al. (1987b) compared the helminth fauna, including prevalence and mean burdens, of sympatric Hartmann's mountain zebra and plains zebra during the three climatic periods characteristic in the Etosha NP. The species composition of the helminth communities was similar in the two hosts, but, with the exception of two cyathostomine and two strongyline species, intensities in the plains zebra exceeded those in the Hartmann's mountain zebra. Survival strategies of cyathostomes infecting Hartmann's mountain zebra, which are less water-dependent than plains zebra, *i.e.* hypobiosis of fourth-stage larvae in the gut wall during the dry season, were discussed (Krecek et al., 1987b). Despite vastly different life cycle strategies, the seasonal abundance, recorded over a period of 11 months, of Atractidae, Cyathostominae and Spiruridae (indirect life cycle) in plains zebra in the KNP followed a similar pattern, with peak worm burdens in stallions being reached in November (Scialdo et al., 1982). For the same host and same locality, Krecek et al. (1987a), however, reported significantly higher intensities of the adult stages of nine of 14 cyathostome species in winter, together with an additional two cyathostome species that reached highest intensities in autumn.

The prevalence and seasonal abundance of arthropod parasites, including ticks, lice, and oestrid and gasterophilid fly larvae, of plains zebra were studied in the KNP during a long-term study with animals examined at irregular intervals over a 3-year period (Horak et al., 1984b). Ticks and gasterophilid flies of Cape mountain zebra from the MZNP were studied at irregular intervals over a 2-year period (Horak et al., 1986a), and ticks were collected as part of a long-term general survey of numerous small and large avian and mammalian hosts in this park (Horak et al., 1991b). The prevalence and seasonal abundance of ticks, oestrid fly and gasterophilid fly larvae were recorded from Hartmann's mountain zebra in Namibia during monthly intervals over a 1-year period (Horak et al., 1984a), and Horak et al. (1992a) investigated the tick parasites of plains and Hartmann's mountain zebra in the Etosha NP.

Of the ectoparasites recorded from zebras, ixodid ticks and gasterophilid stomach bot fly larvae were the most common. In addition, the nasal bot fly genus *Rhinoestrus* was reported from plains zebra in the KNP and from Hartmann's mountain zebra in Namibia, the first host harboring *R. usbekistanicus* and *R. steyni*, the latter being a new host record for *R. usbekistanicus* (Horak et al., 1984a, 1984b). Of these two oestrids, *R. usbekistanicus* was the commonest third-stage larva recovered. Two louse genera, *Damalinia* and *Haematopinus*, were collected from the plains zebra in the KNP, the latter being the more prevalent as well as the more abundant parasite (Horak et al., 1984b).

Gasterophilus ternicinctus was the most abundant bot fly larva in plains zebra from the KNP; of the remaining five congeners, *G. nasalis* and *G. pecorum* also occurred in both other zebra taxa, whereas *G. meridionalis* was only shared with Hartmann's mountain zebra in Namibia (Horak et al., 1984a, 1984b, 1986a). *Gasterophilus nasalis*, a parasite of horses and zebras, was numerous in plains zebra and Hartmann's mountain zebra, but occurred in such small numbers in Cape mountain zebra as to be suspected to be on the verge of extinction. *Gasterophilus pecorum*, on the other hand, was the most numerous of gasterophilids in Cape mountain zebra, its numbers even exceeding those in plains and Hartmann's mountain zebra (Horak et al., 1984a, 1984b, 1986a). The third member of the genus in Cape mountain zebra, *G. intestinalis*, is typically a parasite of horses and was thought to have originated from horses that were also kept in the park at the time (Horak et al., 1986a).

With 10 species recorded, Ixodid ticks were the most diverse external parasites of zebras. The tick community of the Cape mountain zebra was the most species rich (Young et al., 1973b; Penzhorn, 1984; Horak et al., 1986a). Three of these, *A. marmoreum, Ixodes* sp. and *R. arnoldi*, were classified as accidental infestations (Horak et al., 1986a).

The adults of *Hyalomma rufipes* (=*H. marginatum rufipes*), *H. glabrum* (=*H. marginatum turanicum*), *H. truncatum, R. evertsi evertsi* and *R. evertsi mimeticus* favor equids as hosts and representatives of all these species were found in all three zebra taxa, with subspecies varying according to the host (Horak et al., 1984a, 1984b, 1986a, 1991b, 1992a).

Rhipicephalus (*Boophilus*) *decoloratus* occurred only in plains zebra from the KNP, but at this locality it was the tick with the highest prevalence as well as abundance (Horak et al., 1984b), whereas *Margaropus winthemi*, occurred only in Cape mountain zebra in the MZNP, where in turn it was the most abundant tick (Horak et al., 1986a, 1991b). Both Horak et al. (1986a) and Horak et al. (1991b) found the one-host tick *M. winthemi* to be a winter tick which likely over summers off the host from spring until the following autumn/winter as engorged females or eggs.

3.2.2. Order Suiformes

3.2.2.1. Suidae. Little work has been done on the parasites of bushpigs (mixed feeders). Theiler (1962) and Baker and Keep (1970) listed their ticks, whereas Ledger (1980) listed their lice. Horak et al. (1991a) conducted the first study on the total numbers of arthropods harbored by these hosts in several game reserves in KZN. They recovered eight ixodid tick species, of which *R. maculatus* was the most abundant, and one louse species, *H. latus*, from the eight hosts examined. Round (1968) listed five helminth species from bushpigs in South Africa, but no detailed investigation into their helminth community has yet been conducted.

Van Wyk and Boomker (2011) recorded *Physocephalus sexalatus* and *Globocephalus versteri* from a single bushpig from the Soutpansberg forest in Limpopo Province.

3.2.2.2. Phacochoeridae. Thirteen helminths had been recorded from warthog (mixed feeders) when Round (1968) compiled his checklist. The first comprehensive survey of their helminth and arthropod parasites, however, was a study conducted in Namibia over a 13-month period (Horak et al., 1983a). Nine nematode species, one cestode species, six ixodid and one argasid tick species, a flea and a louse species and the larvae of a calliphorid fly were recovered from these warthogs. Warthog from the KNP examined at monthly intervals harbored 13 nematode species, one trematodes species, adults of one cestode species and larval stages of four taeniids, seven ixodid and one argasid tick species, three flea species, one louse species and nymphs of the pentastomid *Linguatula nuttalli* (Horak et al., 1988a), whereas warthog from Hoedspruit NR, Limpopo, were host to 11 nematode species, adults of one and larvae of two cestode species, eight ixodid and one argasid tick species, three flea species and one louse species. A total of 15 helminth species were listed as new parasites of warthog during these surveys (Horak et al., 1983a, 1988a; Boomker et al., 1991c). In these three surveys, adult cestodes were listed as '*Moniezia*/*Paramoniezia*'. Specimens from warthog collected at Hoedspruit (Boomker et al., 1991c) formed the basis of a redescription of *P. phacochoeri* and its transfer to the genus *Moniezia* as a new combination (Beveridge, 2014). Palmieri et al. (1985) reported microfilariae of *Setaria* spp. from warthog from the KNP. Seasonal patterns of abundance were found for the sucking louse *H. phacochoeri*, adults of the tick *R. simus*, and the nematodes *P. sexalatus, Oesophagostomum* spp. and *P. vivipara* (Horak et al., 1983a, 1988a; Boomker et al., 1991c). The species richness of the six warthogs from the Limpopo Province was less than that from the KNP, and considerably fewer worms were recovered, the maximum being 5920, excluding *Probstmayria* (Van Wyk and Boomker, 2011).

3.2.3. Order Whippomorpha

3.2.3.1. Hippopotamidae. Round (1968) listed four trematode species from the hippopotamus (grazer), two species each of *Gigantocotyle* and *Nilocotyle*; cestodes and nematodes were not recorded. There do not seem to be more recent papers on the parasites of this host in South Africa. Although not strictly within the set time frame, it is worth mentioning the paper by McCully et al. (1967), which might have coincided with Round's publication. The former authors surveyed the parasites, their infection sites and associated pathology, of 100 hippopotami culled during a drought in the KNP in 1964. The digenean genera *Schistosoma* and *Fasciola* were present in large numbers in numerous hosts, *Gigantocotyle* and *Nilocotyle* were found in the stomach, whereas *Ogmocotyle* was collected from the small intestine; the monogenean *Oculotrema hippopotami* adhered to the conjunctiva of all hippopotami, and larval stages of the taeniid cestode *Echinococcus* sp. were seen in the liver and lungs of a few animals; the filarial nematode *Dipetalonema* sp. was reported from the abdominal cavity and large numbers of the atractid *Cobboldina* sp. were present in the stomach of many animals. Swart (1961) had reported *G. gigantocotyle* and *G. duplicitestorum* from hippopotami in the KNP and described the new species *N. hepaticae* from the liver. Swart (1966) had redescribed *N. praesphinctris* from the stomach of a hippopotamus from South Africa.

3.2.4. Order Ruminantia

3.2.4.1. Giraffidae. Our knowledge on the parasite fauna of giraffe (browser) is still largely based on opportunities taken when and where they presented themselves. Horak et al. (1983c) and Boomker et al. (1986) recorded the tick burdens and helminth parasites of two giraffe in the KNP, and Krecek et al. (1990) and Horak et al. (1992a) surveyed the ticks and lice, and helminth parasites, respectively, of six giraffe shot in the Etosha NP. Although recovered from springbok, gemsbok and kudu during the same survey, lice were not recorded from giraffe in the Etosha NP. *Hyalomma rufipes* and *H. truncatum* were by far the most abundant ticks, with each of the giraffes carrying more than 200 adults. It was concluded that while large animals in general are the preferred hosts of these ticks, giraffe outrank them all (Horak et al., 1992a). In addition to *Hyalomma* spp., *R. evertsi mimeticus* and *R. longiceps* (a single adult male from one giraffe only) were present. Additional ticks recovered from giraffe in the KNP were *R. appendiculatus* (large numbers of larvae and nymphs) and *R. simus* (two males only). All developmental stages of *R.* (*B.*) *decoloratus* and *A. hebraeum* were found in large numbers. The large numbers of *A. hebraeum* recovered in winter seemed unusual, but confirmation would have necessitated examination of hosts at regular intervals which was not possible (Horak et al., 1983c). The very large numbers that were found on giraffe, and reported from eland and buffalo when compared to smaller hosts such as kudu, nyala and bushbuck again suggest that this tick prefers larger hosts (Horak et al., 1983c). The giraffe from the KNP harbored two helminth species only, the spirurid *P. skrjabini* and the hookworm *Monodontella giraffae*, a parasite of the bile ducts of giraffe. Both had previously been recorded from this host, and are two of the seven species of nematodes listed from giraffe in South Africa by Round (1968); Boomker et al. (1986) provided the first quantitative data. *Parabronema skrjabini* was also the most prevalent and abundant helminth in Etosha NP, followed by *Skrjabinema* spp., a new host–parasite record, *H. mitchelli* and larvae of the cestode *Echinococcus* (Krecek et al., 1990). Intensities of infection in animals from the Etosha NP were distinctly lower than those seen in the KNP, which was attributed to lower rainfall in the Etosha NP and consequently lower transmission rates of free-living larvae. The presence of *H. mitchelli*, albeit in low abundance, was seen as a consequence of the presence of its preferred host, eland, and subsequent cross-transmission (Krecek et al., 1990). *Skrjabinema* spp. are not considered nematodes of browsers (Boomker et al., 1989a), confirming observations that giraffe occasionally graze (Skinner and Chimimba, 2005). Because of the small host sample, the seasonal patterns of neither the ecto- nor the endoparasites of giraffe in Etosha NP could be evaluated (Krecek et al., 1990).

3.2.5. Bovidae

3.2.5.1. Buffalo. Boomker et al. (1996b) compiled an extensive list of the protozoan and metazoan parasites recorded from African buffalo (grazer) throughout the continent. For detailed references the reader is referred to this documentation. Nematodes were predominantly intestinal, excepting *Elaeophora* spp. in the blood vessels of the lung and coronary vessels, *Gongylonema* spp. from the esophageal mucosa and *Onchocerca* spp. in subcutaneous tissues. As with the nematodes, the majority of the few trematodes and cestodes occurring in buffalo are shared with domestic ruminants and with antelopes and the same is true for the ticks. Other ectoparasites recorded from buffalo are mites, flies, lice and pentastomes (Boomker et al., 1996b), the latter reaching prevalences of over 60% (Basson et al., 1970). Horak et al. (1983c) provided one of the few quantitative accounts of tick burdens, based on four buffalo shot in the Hluhluwe GR, KZN, in September 1978, reporting on large numbers of all developmental stages of *A. hebraeum* (a vector of *Ehrlichia ruminantium*), as well as *R. appendiculatus, R. maculatus* and *R. muehlensi* (vectors for *Theileria* spp.); *R. evertsi evertsi* and *R. simus* were also recovered and very few specimens of *R.* (*B.*) *decoloratus* and *H. silacaea* were collected, the former being a vector for *Babesia* spp. and *Anaplasma* spp. (Boomker et al., 1996b). Keet et al. (1997) for the first time reported the filarial worm *Parafilaria bassoni* (originally described from springbok in Namibia) from buffalo in the KNP, presented data on seroprevalence, which exceeded 30%, and described the lesions associated with this subcutaneous filarial parasite.

3.2.5.2. Greater kudu. Greater kudu (browser) are without doubt one of the best studied species of browsing antelope with respect to their parasite fauna. Excepting papers of a predominantly taxonomic nature, this antelope featured in 10 publications during 1970–2000, being the only host discussed in seven of these, four of which addressed the helminth parasites (Boomker et al., 1988, 1989a, 1991f; Pletcher et al., 1989), two the ticks (Knight and Rechav, 1978; Petney and Horak, 1997), and one the ectoparasite fauna, including ticks, lice and louse flies (Horak et al., 1992b). In three papers, kudu were one of several herbivores studied (Horak et al., 1983c, 1992a; Boomker et al., 1986). Boomker et al. (1988), in a long-term survey on kudu, examined at 2-month intervals over a period of 11 months in the Etosha NP, provided the first data on the composition of the helminth fauna of this host in Namibia, including data on the prevalence, total counts and parasite abundance with respect to age group and sex. No clear pattern of infection emerged with respect to age groups and, due to a bias toward females, no conclusions as to the influence of host sex on parasite burdens or composition could be drawn. *Cooperioides hamiltoni*, a common parasite of impala, was listed as a new host–parasite record, but several of the helminths collected from the kudu in the Etosha NP corresponded to those of other browsing antelope from other regions (Boomker et al., 1983a, 1984a, 1986). Of these, *H. vegliai* and *C. neitzi* were the most prevalent, the latter being the most numerous nematode as well. In addition to nematodes, fragments of the cestodes *M. expansa* and *Thysaniezia* spp. were found. Adults of the onchocercid *E. sagitta* (=*Cordophilus sagittus*) were seen in only two of the 23 kudus in the Etosha NP, but lesions of this parasite were seen in 31 of 42 kudus examined in the KNP (Pletcher et al., 1989), with only animals less than 1 year old being free of this filaria. This being a common parasite of tragelaphine antelopes, Boomker et al. (1988) attributed its low prevalence in the Etosha NP to either the parasite itself or its currently unknown vector being scarce. Another long-term study, based on a total of 96 kudus belonging to four age groups and culled at monthly intervals over 2 years, was conducted in the KNP (Boomker et al., 1989a). One trematode, three cestode and 10 nematode species/and or genera were added to the amended list of helminth parasites of kudu in South Africa. In addition, the total helminth burdens of male and female kudu in each age group were recorded. Similar to the kudu in Etosha, *H. vegliai* and *C. neitzi* were the most prevalent helminths, with *C. neitzi* followed by *T. deflexus* as being the most abundant. Neither adult nor fourth-stage larva of *H. vegliai* seemed to have a pattern of seasonal abundance in the southern part of the KNP. This and the absence of arrested development were likely due to mild winter temperatures. Composition of the nematode community varied according to the age of the hosts; certain nematodes were present in all age groups, whereas others, such as *T. falculatus, C. fuelleborni* and *S. papillosus*, occurred in calves only; *I. tuberculata*, on the other hand, seemed less prevalent in juveniles than in calves and adults (Boomker et al., 1989a). Older animals usually carried higher worm burdens and the mean worm burden of lactating females was twice that of quiescent or pregnant females. The original data from both the survey in the KNP and in the Etosha NP were subsequently used to analyze patterns of spatial and demographic variation in the parasite community assemblages (Fellis et al., 2003).

Boomker et al. (1991f) expanded the geographic range of parasite surveys in kudu to the Eastern Cape Province, including the Addo Elephant NP, the Andries Vosloo Kudu Reserve (AVKR) and the adjacent farm Bucklands. Other than in kudus in the KNP and Etosha NP, nematode species richness and prevalence were low, no trematodes or cestodes were recorded. More favorable climatic conditions for free-living larval stages in the KNP and a higher diversity of antelope species which can contribute to the pool of possible cross-infections in both the KNP and the Etosha NP were thought to be responsible for the discrepancies (Boomker et al., 1991f). The similar harsh and dry climate in the Etosha NP and the Eastern Cape localities likely resulted in the similar low parasite abundances. Two new parasites, both absent from kudu in the Etosha NP and the KNP, namely *O. ostertagi* and *Dictyocaulus* sp., were recorded as accidental parasites from the kudu in the Eastern Cape. Their presence, together with that of *N. helvetianus*, suggests that kudu might act as reservoir hosts for these worms that are predominantly parasites of cattle from which the infections were thought to originate (Boomker et al., 1991f).

Horak et al. (1992b) carried out surveys on the abundance of ectoparasites of kudus examined in the KNP, the Addo Elephant NP, as well as the AVKR and on the adjacent farm Bucklands. These animals had also been examined for their internal parasites (Boomker et al., 1989a, 1991f). The tick populations of kudu in the KNP and the AVKR/Bucklands complex showed a high degree of similarity not only with regard to species composition, but also with regard to prevalence and abundance. However, the one-host tick *R.* (*B.*) *decoloratus* was by far the most numerous ixodid on kudu in the KNP, but only occurred in low numbers in the AVKR/Bucklands complex. Conversely, *R. glabroscutatum* was one of the most abundant ticks in the latter locality, but was absent in the KNP. *Amblyomma hebraeum* reached high prevalences and numbers at both study sites. The seasonal abundance of the main tick species in the KNP and in the AVKR/Bucklands complex was recorded, and host preferences of the various tick species are discussed. The tick data obtained from the kudu in the AVKR/Bucklands complex were subsequently used in an analysis of the community structure of ticks on kudu in the Eastern Cape (Petney and Horak, 1997). The six tick species collected in the Addo Elephant NP coincided with those present on the kudu in the AVKR/Bucklands complex and the KNP, but *A. hebraeum* accounted for more than 90% of the entire tick population at this locality. Of the louse species, *L. taurotragi* occurred at all study sites, *H. taurotragi* was found in the KNP and in the AVKR/Bucklands complex, whereas *Damalinia* sp. infected kudu in the KNP and on the farm Bucklands. *Lipoptena paradoxa* was the only louse fly recovered and was present at all localities. Nymphs of *L. nuttalli* were recovered from over 60% of the kudu in the KNP, suggesting that they are even more susceptible than warthog and blue wildebeest to this pentastomid whose final host are lions (Horak et al., 1983c, 1988a).

3.2.5.3. Nyala. Studies on the parasites of nyala (browser) include opportunistic surveys of the ticks and helminths of two nyalas in the north of the KNP (Horak et al., 1983c; Boomker et al., 1986), the ticks of two nyalas in the Hluhluwe GR, KZN (Horak et al., 1983c), as well as three long-term studies conducted on arthropod and helminth parasites in KZN game reserves (Boomker et al., 1991e, 1996a; Horak et al., 1995). Nyala at all localities in KZN were infected with the lice *Damalinia* sp. and *L. angasi*, named after its host. Generally, louse burdens were low, and adult males harbored more *Damalinia* sp. than females (Horak et al., 1995). Higher burdens in male animals were also seen in *L. paradoxa*, not only on the nyala but also on kudu (Visagie et al., 1992; Horak et al., 1995). Similarly, certain developmental stages of several of the tick species occurred in significantly higher numbers on males than on females (Horak et al., 1995). Ticks were represented by largely the same species in the four game reserves in KZN, and to an extent overlapped with the species parasitizing nyala in the KNP. *Amblyomma hebraeum, R.* (*B.*) *decoloratus, R. appendiculatus* and *R. muehlensi* were the most dominant tick species on hosts in KZN, being present in almost all hosts examined, and of these *R. muehlensi*, followed by *R. appendiculatus, R. maculatus, A. hebraeum* and, to a lesser extent, *R.* (*B.*) *decoloratus* were the most numerous. Both *R. muehlensi*, for which nyala and bushbuck are preferred hosts, and *R. maculatus* appear confined in South Africa to the coastal regions of northern KZN (Horak et al., 1995). Interestingly, *R.* (*B.*) *decoloratus* was the most abundant tick on the nyala in the KNP, followed by *R. kochi*, a tick that was not recovered from hosts in KZN (Horak et al., 1983c, 1995). This was only the second report of *R. kochi* in South Africa, but its presence in high numbers on not only nyala but also on two additional tragelaphine hosts, kudu and bushbuck, in the Pafuri region of the KNP, suggest that it is a major species there (Horak et al., 1983c). Horak et al. (1983c) found the composition of the tick burdens to be influenced by the season during which animals were examined as well as host preference and host habitat. Kudu examined at Pafuri had more *A. hebraeum* and *R.* (*B.*) *decoloratus* than the nyala and bushbuck from the same locality and examined during the same week.

Despite its relative abundance, little is known about the helminth parasites of nyala in South Africa. Boomker et al. (1991e) summarized the listings of Dixon (1964), Round (1968), Vincent et al. (1968), Keep (1971), Boomker (1986a) and Boomker et al. (1986), and added another 12 new helminth records to the amended parasite list, which now includes five trematode, two cestode and 18 nematode species. To these, Boomker et al. (1996a) added the cestode *M. benedeni* and another four nematode species. The helminths from nyala from the Umfolozi, Mkuzi and Ndumu GR, KZN, differed little with respect to relative abundance and prevalence, and *O. harrisi* (in some papers named *Camelostrongylus harrisi*), *P. horaki* and *C. rotundispiculum* were the dominant parasites (Boomker et al., 1991e, 1996a). Paramphistomes, *Schistosoma mattheei*, and *Cotylophoron jacksoni* were the trematodes recovered, and the cestodes were *Taenia* sp., *Thysaniezia* sp. and *M. benedeni* (Boomker et al., 1991e, 1996a). No clear-cut trends in the seasonal abundance of any of the helminths were observed (Boomker et al., 1991e). Similar to the ectoparasite burdens (Horak et al., 1995), Boomker et al. (1991e) found male animals to harbor more worms than females, but conversely, Boomker et al. (1996a) subsequently recorded higher nematode burdens in female nyala. As in kudu in the KNP, no correlation existed between the total female or total helminth burdens and fecal nematode egg counts of nyala (Boomker et al., 1989a, 1996a).

The fact that the helminth community of nyala at False Bay, KZN, where few other antelope species occur, was species-poor (Boomker et al., 1991e), emphasizes the influence of cross-infection on helminth community patterns. Especially the presence of *I. tuberculata, Trichostrongylus* spp. and *Gaigeria pachyscelis*, which are more common in grazers (Boomker, 1977; Horak et al., 1983c; Boomker et al., 1989a), were attributed to the variety of antelope species present in the Umfolozi, Mkuzi and Ndumu GR (Boomker et al., 1991e).

3.2.5.4. Bushbuck. The ticks, lice, and helminth parasites of bushbuck (browser) were studied during a long-term survey in the Weza State Forest, KZN. As part of this survey, Boomker et al. (1987) drew up an amended list of the helminth parasites of bushbuck in South Africa, including references of the first records of the various worms. Horak et al. (1983c) and Boomker et al. (1986) listed the tick and helminth burdens of a total of 11 and 12 bushbuck, respectively, from two localities in the KNP, while Boomker et al. (1984a) recorded the helminths from two animals at Charter's Creek, KZN. Mares et al. (1984) listed *O. radiatum* from a single bushbuck from an unknown locality in the former Transkei region, Eastern Cape Province.

As with the nyala examined at the same time (see discussion earlier), *R. kochi* was present in large numbers on the bushbuck from the Pafuri region of the KNP, and constituted a new parasite record for this host, but was absent from eight bushbuck in the Skukuza area (Horak et al., 1983c). The remainder of the tick population of bushbuck in the Pafuri region was equally similar in the prevalence of the various developmental stages and their abundance to that parasitizing the co-occurring nyala. After *R. kochi, R.* (*B.*) *decoloratus* was the most abundant tick, represented by immature stages and adults, although its numbers remained clearly below those recovered from bushbuck in the Skukuza region. Larvae and nymphs of *R. appendiculatus* especially, but also of *R. zambeziensis*, were numerous, but adults were absent, which might be a reflection of the time during which the animals were examined, as peak adult abundance of *R. appendiculatus* is late summer (Horak et al., 1989). Larvae and nymphs of *A. hebraeum*, together with a few adults were collected as well (Horak et al., 1983c).

Bushbuck from the Weza State Forest harbored the louse-fly, *L. paradoxa*, which is common in tragelaphine antelope species and had a prevalence of nearly 50%. Two louse species, *D. natalensis* and *L. panamensis*, with a prevalence of nearly 50% and close on 80%, respectively, were also recovered (Horak et al., 1989). Ledger (1980) lists these lice as specific parasites of bushbuck. The bushbuck were infested with eight ixodid tick species. *Ixodes* sp. was the most prevalent and numerous, but no pattern of seasonal abundance emerged. The remaining tick species were *R.* (*B.*) *decoloratus, Haemaphysalis aciculifer, R. appendiculatus, R. evertsi evertsi*, typically a parasite of equids and probably due to the mules and horses that are kept as transport animals, and, in very small numbers, *R. follis* and *R. lunulatus*. While bushbuck in the KNP were found to be good hosts for *R.* (*B.*) *decoloratus*, the tick's prevalence and abundance in the Weza State Forest were low. Horak et al. (1989) attributed this to the habitat preference of *R.* (*B.*) *decoloratus* which is open grassland or savannah with an annual rainfall above 380 mm (Howell et al., 1978).

The abomasal nematodes *O. harrisi*, originally described from bushbuck, but also recorded from other browsers, such as red duiker in KZN (Boomker et al., 1984a), and nyala in game reserves in KZN and the KNP (Boomker et al., 1991e, 1996a), and *P. devossi* were the most abundant nematodes of bushbuck in the Weza State Forest and Charter's Creek (Boomker and Kingsley, 1984b; Boomker et al., 1984a, 1987). *Gongylonema* sp., *S. africana* and larvae of *Taenia* spp. were also recovered from hosts at Charter's Creek. In addition to these, but excepting the cestodes, bushbuck in the Weza State Forest harbored relatively large numbers of *Cooperia* sp. and *H. vegliai*, as well as low numbers of *Oesophagostomum* sp. and *Trichostrongylus* spp. (Boomker et al., 1984a, 1987). At both localities in KZN, the species richness as well as parasite burdens were much lower than those observed in bushbuck in the KNP (Boomker et al., 1986). Bushbuck in the KNP harbored not only all the helminths collected from these animals at Charter's Creek and Weza State Forest, but also *T. falculatus, T. instabilis, C. neitzi, Gaigeria* sp., the lung nematodes *D. viviparus* and *Pneumostrongylus calcaratus*, and, in the coronary and lung arteries, *E. sagitta* (Boomker et al., 1986). Lower host diversity, coupled with a reduced possibility of cross-infection, and a predominance of browsing antelope at Charter's Creek, which generally carry lower helminth burdens than grazers, were seen as reasons for the differences in the respective helminth assemblages (Boomker et al., 1987). The *Trichostrongylus* spp. as well as *C. neitzi* are common intestinal parasites of antelope in the KNP, whereas *H. vegliai* is considered the most common species of this genus in browsing antelope (Boomker et al., 1987).

3.2.5.5. Eland. Eland are mixed feeders, predominantly adapted to the drier regions in South Africa. Information on their tick and helminth fauna is largely based on opportunistic studies or animals that were irregularly examined over a period of years. Horak et al. (1983c) recorded the tick burdens of two elands in the KNP examined in September and October 1979 and of one eland each from the Thomas Baines Reserve and the AVKR, Eastern Cape Province, examined in April 1982 and March 1983, respectively. Horak et al. (1991b) investigated the ixodid ticks of a number of vertebrate hosts in the MZNP, and during this survey determined the prevalence and abundance of the ticks from 11 elands examined at approximately 3-month intervals from May 1983 to December 1985. A further two elands were examined in the KTP, Northern Cape Province, in October 1984 and another two in the West Coast National Park (WCNP) during February 1990 (Golezardy and Horak, 2007).

The composition of the tick population varied distinctly between eland from the KNP, the MZNP, the remaining Eastern Cape localities, the KTP and the WCNP. *A. hebraeum* and *R.* (*B.*) *decoloratus* were the most abundant tick species in the KNP, while a few nymphs of *R. appendiculatus* and some immatures and adults of *R. evertsi evertsi* were also present. *Amblyomma hebraeum* was the most abundant tick in the Eastern Cape, but contrary to the KNP, *R.* (*B.*) *decoloratus* was present in low numbers only, whereas all stages of *R. appendiculatus* and *R. evertsi evertsi* occurred in large numbers. *Haemaphysalis silacea*, absent on eland in the KNP and the MZNP, was abundant on especially the eland examined in the Thomas Baines Reserve. *Rhipicephalus* (*B.*) *decoloratus* was not collected from eland in the MZNP, and, excepting *R. evertsi evertsi* and *R. glabroscutatum*, which were shared between hosts from all Eastern Cape localities, all tick genera found in the MZNP were represented by species that differed from those in the KNP and the remaining Eastern Cape localities. For example, *A. marmoreum* and *R. follis*, *Hyalomma glabrum*, *H. truncatum* and *M. winthemi*, common and abundant ticks on large mammals of the MZNP, did not occur on eland in the other localities (Horak et al., 1983c, 1991b). In the MZNP, eland are among the preferred host of adults of *H. glabrum, H. truncatum, I. rubicundus* and *R. follis*, and of immatures and adults of *M. winthemi, R. evertsi evertsi* and *R. glabroscutatum* (Horak et al., 1991b). The eland examined in the KTP were infested with two tick species of which *H. truncatum* was the most numerous, while the two animals in the WCNP harbored six tick species with particularly large burdens of *H. truncatum* and *R. capensis* (Golezardy and Horak, 2007).

Data on the helminths of eland are scant. Round (1968) listed the cestode *Thysaniezia ovilla* (=*T. giardia)* and the five nematode species, *Bunostomum trigonocephalum, D. viviparus, H. mitchelli, H. vegliai* and *O. circumcincta*, from eland in South Africa. Mares et al. (1984) recorded two cestode genera, *Avitellina* and *Moniezia*, as well as *H. bedfordi* from two elands in the former Transkei, now part of the Eastern Cape Province. Boomker et al. (2000) studied the helminths of three elands from the MZNP, and two from the WCNP. Only nematodes were found. *Cooperia rotundispiculum* was the only worm shared between the two sites, and was the most common helminth at both. However, while more than a total of 30,000 specimens were recovered from the eland at the WCNP, total burdens from all eland at the MZNP did not exceed 5000, probably due to climate and stocking rates (Boomker et al., 2000). The only other helminth collected from eland in the WCNP was the lungworm *B. magna*, found in low numbers and likely acquired from co-occurring springbok, which are the preferred host. Eland in the MZNP harbored two additional nematodes, *N. spathiger*, a parasite well-adapted to semi-arid regions and occurring in large numbers, and *H. mitchelli*, which was less abundant. *Nematodirus spathiger* and *B. magna* were new parasite records for eland.

3.2.5.6. Black wildebeest. One trematode species, larvae of *T. hydatigena* and five nematode species are listed for black wildebeest (grazer) in South Africa in Round (1968). Young et al. (1973b) listed three nematodes, including *Trichinella spiralis*, the tick *R. glabroscutatum*, the louse-fly *L. sepiacea* and the nasal botfly *Gedoelstia* from this host in the MZNP. At the same locality, Boomker et al. (2000) recorded a single larva of *Taenia* sp. and fourth stage larvae and females of *Haemonchus* sp. from a single animal, and Horak et al. (1991b) recorded the ixodid tick burdens of nine black wildebeests examined between May 1983 and December 1985. Black wildebeest were not the preferred hosts of any of the ticks recovered from small and large mammals during the tick survey at the MZNP, but immatures and adults of *R. evertsi evertsi* and *R. glabroscutatum* had a high prevalence and occurred in relatively large numbers. Contrary to this, the remaining species, *Ixodes* sp., *M. winthemi, R. follis* and *R. lounsburyi*, generally infested a single host individual only, and their numbers were low (Horak et al., 1991b).

The most comprehensive survey on the helminth and arthropod parasites of black as well as blue wildebeest is that of Horak et al. (1983b), who examined seven black wildebeests in the Golden Gate Highlands Park (now Golden Gate National Park, GGNP), Free State and three in the Rietvlei NR, Gauteng. These animals harbored four nematode species (*H. bedfordi, O. columbianum, Trichuris* sp., *T. axei*), the cestode *Thysaniezia* sp., the larvae of five oestrid fly species, two louse species (*Damalinia* sp., *Lithognathus* sp.), four ixodid tick species [*R.* (*B.*) *decoloratus, R. capensis* group, *H. truncatum, R. evertsi evertsi*] and the mite *Chorioptes* sp. Species diversity as well as intensity of infection regarding both helminths and ticks was low and likely attributable to the cold climate at the two localities as well as to an inherent resistance of black wildebeest against parasites (Horak et al., 1983b). The latter might be supported by the fact that two black wildebeests in the Karoo National Park (NP) were free of worms (Boomker et al., 2000) and harbored only one tick species, *H. glabrum* (Golezardy and Horak, 2007). Only *H. bedfordi* was present in all hosts examined at the two localities and seemed well-adapted to colder climates. The presence of the oestrid flies *O. macdonaldi* and *K. minutus* at the Rievlei NR constitute new parasite records for black wildebeest. *Gedoelstia haessleri* was the only oestrid fly present at the GGNP, and *O. variolosus* was more common than *G. cristata* or *O. macdonaldi* at Rietvlei NR (Horak et al., 1983b).

3.2.5.7. Blue wildebeest. Round (1968) listed two trematode, two cestode and five nematode species from blue wildebeest (grazer) in South Africa, and Horak (1980) presented a list of eight nematode species, five ixodid tick species and five oestrid fly species as parasites of blue wildebeest. Mares et al. (1984) found blue wildebeest in the former Transkei (see discussion earlier) to be infected with *H. contortus* and *Avitellina* sp. *Haemonchus bedfordi* alone was recovered from a single blue wildebeest shot in the KTP in October 1984 (Boomker et al., 1986). Horak et al. (1983b) conducted an extensive survey of the internal and external parasites of 55 blue wildebeests in the KNP, shot at approximately monthly intervals during a period of 13 months. These animals harbored all helminth genera recorded by previous authors, excepting the trematode genus *Calicophoron* (Round, 1968). Of the 13 species of nematodes, *H. bedfordi* was the most prevalent, followed by *C. connochaeti, Agriostomum gorgonis* and *T. thomasi. Cooperia connochaeti* from the intestine was the most abundant worm, followed by the abomasal nematodes *H. bedfordi* and *T. thomasi*. Of the four cestode species, *Avitellina* sp. and larvae of *T. regis* were the most abundant; *M. benedenei* and *M. expansa* were confined to animals under 12 months of age. The seasonal prevalence of eight of the nematodes and two of the cestodes was determined and fecal egg counts were compared to actual worm burdens. The same genera and species of oestrid flies as found in the black wildebeest were present in the blue wildebeest, but *O. macdonaldi* was absent, whereas *O. aureoargentatus* was present (Horak et al., 1983b). Blue wildebeest in the KNP harbored three louse species: *D. theileri*, which was the most prevalent, *L. gorgonus*, which was the most abundant, and *L. spicatus*. Mites of the genus *Sarcoptes* were numerous but occurred in less than 5% of the animals. The pentastomid *L. nuttalli* was recovered from roughly a fifth of the hosts. Eight ixodid tick species were found on blue wildebeest in the KNP: *A. hebraeum, R.* (*B.*) *decoloratus, H. truncatum* and four species of *Rhipicephalus*. The seasonal prevalence of the first two species and of *R. appendiculatus* and *R. evertsi evertsi* was determined. Interestingly, with the exception of *R.* (*B.*) *decoloratus*, very few adult ticks were found on blue wildebeest. Generally, the burdens of all parasites were too low to produce readily detectable pathological changes, although *D. viviparus* produced fairly extensive pulmonary lesions in some animals (Horak et al., 1983b).

3.2.5.8. Red hartebeest. Helminth parasites of red hartebeest (grazer) were listed by Round (1968), and Mares et al. (1984) who examined eight adult animals in game reserves in the former Transkei. *Impalaia nudicollis* and *Parabronema* sp. were new parasite records from a single red hartebeest in the KTP (Boomker et al., 1986). Together with *H. bedfordi* these were the most abundant nematodes. In addition, *Trichostrongylus* spp. and *Cooperia* spp. were present (Boomker et al., 1986).

3.2.5.9. Bontebok. Early works on the parasites of bontebok (grazer) include lists of their helminths (Round, 1968; Verster et al., 1975), their oestrid larvae (Zumpt, 1965), and their lice (Ledger, 1980). Further studies were to add eight additional helminth species, three tick species and one oestrid fly species to these lists (Horak et al., 1982a, 1986b; Boomker and Horak, 1992; Horak and Boomker, 1998; Boomker et al., 2000). An amended list of the helminths of bontebok in the BNP, with reference to the first record, can be found in

Boomker and Horak (1992), to which *C. rotundispiculum* from bontebok in the WCNP should be added (Boomker et al., 2000). One trematode, two cestode and 20 nematode species have been recorded from this host.

Verster et al. (1975) gave a brief overview of historical and more recent listings of worms associated with bontebok, concluding that only the helminths listed by Ortlepp (1961, 1962) should be considered authentic. Based on the helminths of four bontebok, which died upon transfer from the BNP, Western Cape, to the National Zoological Gardens, Pretoria, Gauteng, and other diagnostic specimens, Verster et al. (1975) added the larvae of *T. hydatigena* and six nematode species as new host–parasite records. The lung worm *B. magna* was only recorded from bontebok after the park had been resited at Swellendam. They seemed to have picked up the new lung worm from springbok, which were introduced shortly after the bontebok and are a well-known host of *B. magna* (Verster et al., 1975). In contrast, the bontebok appeared to have lost their infection with *Protostrongylus cornigerus* and *P. capensis* in the new habitat, possibly due to the absence or low density of the snail intermediate host (Verster et al., 1975). The latter parasite was, however, recorded during subsequent surveys in the BNP (Horak et al., 1982a; Boomker and Horak, 1992). Both these worms had originally been described from bontebok (Ortlepp, 1962) and *P. capenis* occurs in bontebok only (Boomker and Horak, 1992).

Based on 33 bontebok examined at irregular intervals in the BNP, Horak et al. (1982a) were able to give a more complete picture of the composition of the arthropod and helminth assemblages of this antelope, as well as on prevalence, abundance and seasonal variation thereof. Horak et al. (1986b), Boomker and Horak (1992), and Horak and Boomker (1998) reported on a long-term survey conducted in the BNP, during which two animals were examined at two-monthly intervals from February 1983 to February 1984, and thereafter every February for 8 years. Horak et al. (1997) compared the tick infestations of these bontebok to those of gray rhebok examined during the same 10-year survey and found that the diversity of tick species found on the two hosts had not changed during the decade despite the introduction of additional host species to the park. Boomker et al. (2000) expanded the geographic range of the helminth surveys by examining two bontebok from the WCNP.

Longystrongylus curvispiculum and *N. spathiger* were the most prevalent and by far the most abundant nematodes in bontebok in the BNP and also in the WCNP. *Cooperia rotundispiculum, H. contortus, T. circumcincta* and *T. thomasi* were absent in bontebok in the BNP, and probably acquired from co-occurring springbok, eland or gemsbok in the WCNP (Boomker et al., 2000). While *M. expansa* was recovered from a single host in the BNP, cestodes were not recovered from the bontebok in the WCNP (Boomker and Horak, 1992; Boomker et al., 2000).

Bontebok from the BNP harbored 10 species of ixodid ticks, two louse flies, *Damalinia* sp. and *Linognathus* sp, and larvae of two oestrid fly species, *Gedoelstia* sp. and *Strobiloestrus* sp. (Horak et al., 1982a, 1986b; Horak and Boomker, 1998). Of the ticks, *R. nitens* was the most prevalent and abundant, followed by *R. glabroscutatum*. Immature stages of *Ixodes* sp. (near *Ixodes pilosus*) were collected from nearly all animals in moderate numbers, but adults were few. These three ticks were collected from bontebok, vaal ribbok and scrub hares in the BNP (Horak et al., 1986b). Four larvae of *Rhipicephalus* (*B.*) spp. were recovered from a single bontebok only (Horak and Boomker, 1998).

3.2.5.10. Blesbok. Young et al. (1973b) found *H. contortus* and *N. spathiger*, larvae of the cestode *T. hydatigena* and the ectoparasites *R. glabroscutatum* and *O. variolosus* in blesbok (*Damaliscus pygargus philippsi*; = *D. dorcas philippsi*) (grazer) during a disease survey in the MZNP. Mares et al. (1984), examining blesbok from the former Transkei, added *O. ostertagi, Cooperia* sp. and *M. expansa* to the list of helminths. A checklist of the nematodes, ixodid ticks and oestrid larvae of blesbok was included in a paper on the control of the parasites of antelope in small game reserves (Horak, 1980). Long-term studies on the oestrid fly larvae of these antelope were presented by Horak and Butt (1977), who examined 34 blesbok shot at approximately monthly intervals over a period of 18 months in the Percy Fyfe NR, Limpopo Province, and who examined four blesbok culled in the Rietvlei NR, Gauteng, during a single occasion during May 1972. The helminth fauna of the same two sets of animals was studied by Horak (1978a). Additional geographic localities from which information on the helminth and arthropod parasites of blesbok could be obtained were the GGNP, Free State (n = 8), the MZNP, Eastern Cape (n = 8), Rob Ferreira NR, Mpumalanga Province (n = 28), and the Rietvlei NR (n = 3) (Horak et al., 1982a).

Together with blue and black wildebeest, red and Lichtenstein's hartebeest and tsessebe, blesbok are considered the natural host of the nasal botfly genus *Gedoelstia* (Zumpt, 1965; Basson, 1966). In the natural hosts infection with these parasites seems to be largely asymptomatic, but the deposition of larvae in the eyes of notably sheep causes specific oculo-vascular myiasis, commonly referred to as 'uitpeuloog' (Basson, 1962). In an attempt to evaluate possible control strategies and to indicate seasons during which game and domestic livestock could be grazed together with comparative safety, Horak and Butt (1977) established the patterns of seasonal abundance of infestation of blesbok with *G. haessleri*, and of *O. variolosus* and *O. macdonaldi*, which were also present. They presented life cycle data as well.

Three of the nematode species, four of the ixodid tick species and two of the oestrid flies reported by Horak et al. (1982a) were considered new host–parasite records. The composition of the arthropod fauna of blesbok varied according to locality, and only the louse *D. crenelata* was present at all four study sites (Horak et al., 1982a). The second louse parasitizing blesbok, and actually described from bontebok and blesbok, was only found on one of two animals in the GGNP. Larvae of the oestrid fly genera *Gedoelstia, Kirkioestrus* and *Oestrus* were found. While black wildebeest were infested with *G. haessleri* at the GGNP, blesbok carried larvae of *G. cristata* (Horak et al., 1982a, 1983b). *Kirkioestrus minutus* is typically a parasite of blue wildebeest, and since only first-stage larvae were recovered, it is possible that this parasite might not complete its life-cycle in blesbok (Horak et al., 1982a).

Of the seven ixodid tick species recovered from blesbok, *R.* (*B.*) *decoloratus* was the only species on hosts in the GGNP, whereas usually at least two or more tick species were recovered at the remaining localities. *Rhipicephlaus evertsi evertsi* had the widest geographic range and generally was the most abundant tick on blesbok (Horak et al., 1982a). Ectoparasite abundance seemed especially low in the GGNP and the MZNP.

Horak (1978a) listed *H. bedfordi*, only present in the Rietvlei NR, *Skrjabinema alata* and *A. centripunctata* as new helminth records for blesbok. In addition, *H. contortus, T. axei, T. falculatus* and *I. nudicollis* were recovered at both localities. Seasonal fluctuation in worm burdens was determined for the blesbok in Percy Fyfe NR. Blesbok were also new host records for *L. curvispiculum, L. sabie* and *N. helevtianus* (Horak et al., 1982a). Of the 21 nematode and two cestodes species that were collected from blesbok in the four parks studied by Horak et al. (1982a), only *H. bedfordi* and *T. axei* were present in each region. *Nematodirus helvetianus* was the most abundant nematode in hosts in the GGNP, whereas *N. spathiger* was the most abundant in the MZNP, but the genus was not present at the other two localities. A similar picture was observed for *Impalaia*, with *I. nudicollis* being the most abundant nematode in blesbok in Rietvlei NR, and *I. tuberculata* the most abundant worm in the Rob Ferreira NR. However neither worm was present at the other localities. The lungworm *B. magna* infected blesbok in all regions except in the Rietvlei NR (Horak et al., 1982a). The highest species richness and overall worm burdens were associated with blesbok from the Rob Ferreira NR, probably resulting from high stocking rates and the presence of a variety of antelope (Horak et al., 1982a).

3.2.5.11. Tsessebe. Round (1968) listed 10 helminths from this host in South Africa, and Boomker et al. (1986) added *C. yoshidai, L. schrenki, T. instabilis* and *T. thomasi* as new parasite records from a single tessebe (grazer) examined in the KNP. Additional helminths were *H. contortus* and *Skrjabinema* sp., which together with *C. yoshidai* were the most abundant, as well as *I. tuberculata* and *Parabronema* sp. Reinecke et al. (1988) recovered helminths from the gastrointestinal tracts of 11 tsessebes in the Nylsvley NR. Two animals were examined bi-monthly between May 1985 and March 1986. The nematode genera *Agriostomum, Cooperia, Habronema, Haemonchus, Impalaia, Oesophagostomum, Ostertagia, Skrjabinema, Setaria, Strongyloides* and *Trichostrongylus* were present, together with the cestodes *Thysaniezia* and larvae of a *Taenia* sp., as well as the trematode genus *Paramphistomum*. The most prevalent and abundant nematodes were *C. hungi, I. tuberculata* and *T. falculatus.* The authors attributed the relatively low worm burdens to a low population density of hosts, and a drier than normal summer which reduced numbers of viable infective stages on pasture (Reinecke et al., 1988).

3.2.5.12. Gemsbok. Originally confined to the more arid regions of southern Africa, gemsbok (*Oryx gazella*) (mixed feeder) have been introduced to many regions in southern Africa and are now widely distributed (Fourie and Vrahimis, 1989). Round (1968) listed six helminth species from this host in South Africa. Horak et al. (1983c) reported on the ixodid ticks recovered from two gemsbok in the MZNP, and Boomker et al. (2000) recorded worm burdens from two animals from the WCNP, and Golezardy and Horak (2007) the tick burdens of the same two animals. During a long-term survey over a 12-month period, Fourie et al. (1991) studied the tick, louse and helminth assemblages of 24 introduced gemsbok in the Willem Pretorius NR, Free State, and reported seasonal variation in parasite abundance. One calf or sub-adult and one adult were examined at each sampling occasion. Seven tick species were found on the two gemsbok in the MZNP, of which *R. glabroscutatum* and *M. winthemi* were the most abundant, followed by *R. evertsi evertsi* (Horak et al., 1983c). The latter two species were also the most prevalent and abundant ticks on gemsbok in the Willem Pretorius NR, whereas *R. glabroscutatum* was absent in the Free State (Horak et al., 1983c; Fourie et al., 1991). The majority of tick species recovered in the MZNP were also found in the Free State, together with an additional four species. *Margaropus winthemi* peaked during the winter months and was the only tick for which a clear pattern of seasonal abundance could be determined. Gemsbok were also infected with two louse species, *Damalinia* sp. and *L. oryx*, the latter occurring in large numbers and being more abundant on calves and sub-adults than on adults (Fourie et al., 1991). *Ixodes rubicundus*, found in very small numbers on three of the gemsbok, can cause tick paralysis. Its low prevalence as well as intensity of infection suggests, however, that the study region in the Free State represents a marginal distribution area for the tick (Fourie et al., 1991). The two animals examined in the WCNP were infested with six ixodid tick species of which fairly large numbers of *H. truncatum, R. capensis* and *R. evertsi evertsi* were recovered and very large numbers of *R. glabroscutatum* (Golezardy and Horak, 2007).

The helminth assemblage of gemsbok in the Free State was species-rich. Albeit in generally low numbers, 17 nematode species and two cestodes species were recovered. As in blue wildebeest, *Moniezia* sp. occurred exclusively in calves (Horak et al., 1983c; Fourie et al., 1991). *Trichostrongylus falculatus, H. contortus, C. yoshidai* and *C. fuelleborni* had the highest prevalence, and *T. falculatus* and *C. fuelleborni* were also by far the most abundant worms. None of the helminth species presented a clear pattern of seasonal abundance (Fourie et al., 1991). Helminth burdens were significantly lower in younger animals than in adults, possibly influenced by the fact that some of the calves had still been suckling at the time of examination. Helminth burdens were generally small, however, with the low number of fourth-stage larvae recovered indicating that veld contamination was low. Rainfall during the larger part of the survey had been low (Fourie et al., 1991). Fourie et al. (1991) pointed out that a number of the nematodes infecting the gemsbok likely originated from other hosts present in the reserve or adjacent areas, and they listed these as well as their assumed primary hosts.

The most remarkable finding with regard to the helminths of gemsbok in the WCNP was the presence of five species of *Trichostrongylus*. One of these, *T. rugatus*, was the overall most abundant helminth at this site, followed by *N. spathiger* and *O. ostertagi*. In addition, *L. curvispiculum* and *B. magna* were collected (Boomker et al., 2000).

Of the three gemsbok collected at Musina, Limpopo Province, one harbored a small number of *C. hungi*, primarily a parasite of impalas, and the other *S. hornbyi*. The animal from the Kerneels Young Trust harbored only *Taenia* spp. larvae (Van Wyk and Boomker, 2011). These numbers are even lower than those recovered from the gemsbok from the Kalahari, possibly indicating a lack of host diversity, even though the climate is similar to that of the Kalahari (Van Wyk and Boomker, 2011).

3.2.5.13. Blue duiker. Blue duiker (*Philantomba monticola*) (browser) are the smallest antelope occurring in southern Africa and are found only in dense forest. In South Africa their distribution is confined to a narrow coastal strip extending from KZN to the Eastern Cape Province. They are exclusively browsers and closely associated with water (Boomker et al., 1991b). According to Boomker et al. (1991b), *M. expansa* was the only parasite recorded from this antelope in 1986, when Boomker et al. (1986) recovered *T. axei* from a single blue duiker from the Tsitsikama Forest NP, Eastern Cape. Boomker et al. (1991b) examined three blue duikers from three nature reserves in KZN that died due to unrelated causes and reported eight new helminth species for this antelope. The amended list of the helminth parasites of blue duikers, presented in Boomker et al. (1991b), comprises the cestodes *M. expansa*, larvae of *T. hydatigena*, and the following nematodes: *C. rotundispiculum, Gongylonema* sp., *Setaria* sp., *T. angistris, T. anomalus, T. axei, T. falculatus* and *T. rugatus*. Three blue duikers from the eastern part of Zimbabwe harbored *C. chabaudi, H. lawrenci, T. axei, Trichuris* sp., *M. expansa* and *S. hepatica* (Jooste, 1984; Boomker et al., 1991b). Because of their selective feeding habits, blue duiker do not seem to harbor a large variety of worms or a great abundance of them (Boomker et al., 1991b).

3.2.5.14. Red duiker. The habitat of the rare red duiker (*Cephalophus natalensis*) (browser) is limited to the thick shrub and evergreen forests of the eastern parts of KZN and a small area of the Soutpansberg in northern Limpopo. They are shy and secretive browsers, found near permanent surface water (Skinner and Chimimba, 2005). Round (1968) listed no parasites for this antelope in South Africa. Previous records of ticks and lice infesting red duiker are referenced by Horak et al. (1991a). Boomker et al. (1984a) recorded the abundance of helminth species from two red duikers examined at Charter's Creek in March 1983, whereas Horak et al. (1988b) recorded their tick burdens as well as those of an additional duiker examined in July 1984. Subsequently, an additional 25 animals from three game reserves in KZN became available for examination at irregular intervals. Boomker et al. (1991d) reported on their helminth parasites, whereas Horak et al. (1991a) examined 20 of these to determine their ixodid tick and louse populations.

Studies on the helminth parasites of red duiker in South Africa resulted in a total of 20 new host–parasite records (Boomker et al., 1984a, 1991d). An amended list of the helminth species infecting red duiker in KZN with reference to the first record can be found in Boomker et al. (1991d). Boomker et al. (1984a) had tentatively assigned specimens of *Trichostrongylus* to *T. vitrinus* and *T. capricola*, but emphasized certain discrepancies between the morphology of their specimens and descriptions of these two species. Boomker and Vermaak (1986a, 1986b) transferred all specimens of *Trichostrongylus* from these two red duikers to the two new species *T. angistris* and *T. anomalus*. Together with *C. rotundispiculum* and *O. harrisi*, they were the most prevalent and abundant nematodes of red duiker (Boomker et al., 1984a, 1991d). Paramphistomes were recovered in large numbers from some of the hosts at Charter's Creek and *M. benedeni* was not uncommon. *Setaria scalprum* and *S. cornuta* were collected from the abdominal cavity (Boomker et al., 1991d). Interestingly, *Hyostrongylus rubidus*, a stomach parasite of pigs, was very prevalent and quite abundant. Its presence in the red duiker can probably be explained by its presence in bushpigs in the area (Boomker et al., 1991d). Other helminths present were *S. hepatica, C. yoshidai, D. viviparus, H. contortus, I. tuberculata, L. schrenki, T. circumcincta, S. papillosus, T. axei, T. thomasi* and *Trichuris* sp. The survey was not conducted on a strictly seasonal basis and therefore seasonal patterns could not be established. However, large numbers of nematodes were consistently found in red duiker shot during November of each year (Boomker et al., 1991d). The larger worm burdens observed in duiker from Charter's Creek were ascribed to a larger variety and population density of other antelope species, as well as a high density of red duiker themselves, facilitating the possibility of cross-infection (Boomker et al., 1991d).

Red duiker harbored eight ixodid tick species, *A. marmoreum, H. leachi, H. parmata, R. appendiculatus, R. maculatus, R. muehlensi, R. evertsi evertsi* and *Rhipicephalus* sp. (near *R. oculatus*), as well as the two louse genera, *Damalinia* and *Linognathus* (Horak et al., 1988b, 1991a). Of the two, *Linognathus* was the more prevalent as well as abundant one. All duiker were infested with *H. parmata* and the nymphs of *R. muehlensi*. Due to the irregularity of the intervals it was not possible to study seasonal patterns. While the immature stages of all tick species were quite abundant, only adults of *H. parmata* occurred in large numbers, adults of the remaining species were largely absent on red duiker. Horak et al. (1991a) attributed this to the small size and habitat preference of this antelope, thus catering only for the immature stages of many tick species, as adult ticks, however, appear to prefer larger animals as hosts (Horak et al., 1983c). Red duiker as well as bushbuck were considered preferred hosts of *H. parmata*. A shared habitat preference with nyala, the favored host of all stages of *R. muehlensi*, was seen as the reason for the large numbers of immatures of this tick on red duiker (Horak et al., 1991a).

3.2.5.15. Common duiker. Common duiker or gray duiker (browser) occur in Africa south of the Sahara in a wide range of habitats, excepting desert and dense forest. While some authors list these small antelope as browsers (see Boomker et al., 1983a), Keep (1969) stated that common duiker in KZN are mixed feeders, feeding on grass and leaves, similar to impala. An overview of several records and checklists of the helminth and arthropod parasites of these antelope in Africa, and South Africa in particular, is given by Boomker et al. (1983a). Boomker et al. (1983a) studied the helminths, ticks, lice and flies of 16 common duikers culled on the farm Riekert's Lager, Limpopo Province, at irregular intervals from May 1979 to March 1981, and listed 10 new helminth records for this host. Boomker et al. (1986) reported on the helminth species composition and helminth burdens of four common duikers in the KNP, adding one new helminth record to its parasite list. Helminth parasites of a total of 12 common duikers were collected monthly during a 1-year survey on the farm Brakhill, Eastern Cape, from February 1983 to January 1984. Similarly, one common duiker was examined each month from May 1983 to May 1984 in the Weza State Forest, KZN (see also bushbuck), and their helminth and arthropod parasites studied. The study yielded two new helminth records for the common duiker.

Six ixodid tick species, three louse species and a single louse-fly species, *L. paradoxa*, were recorded from common duiker in Limpopo. Of the ticks, *A. hebraeum* followed by *R. appendiculatus* were the most prevalent and abundant, especially their immature stages. Immatures as well as adults of *R.* (*B.*) *decoloratus* and *R. evertsi evertsi* occurred in low numbers; one female of *R.* (*B.*) *microplus* and one *Haemaphysalis* sp. larva were found on one animal only. Generally few adults were collected during all seasons, suggesting that common duiker are poor hosts for adult ticks. The lice *D. lerouxi* and *L. breviceps* were more prevalent than *L. zumpti zumpti* (Boomker et al., 1983a).

The composition of the arthropod assemblage on common duiker in KZN largely resembled that of bushbuck at the same locality, but numbers were lower (Horak et al., 1989). *Lipoptena paradoxa*, which was present on the bushbuck in Weza Forest and on the common duiker in Limpopo, was not collected from common duiker in KZN (Boomker et al., 1983a; Horak et al., 1989). The louse genus *Linognathus* was found on bushbuck as well as common duiker in KZN; it was represented by the bushbuck-specific *L. panamensis* in the former host and *L. breviceps*-complex in the common duiker, similar to *L. breviceps* found on common duiker in Limpopo (Boomker et al., 1983a; Horak et al., 1989). The genus *Damalinia* was present at both localities. *Ixodes pilosus* and *Ixodes* sp. (near *I. pilosus*) made up the majority of ticks recovered from the common duiker in KZN, but *R. appendiculatus, R. evertsi evertsi, R. lunulatus, H. aciculifer* and *R.* (*B.*) *decoloratus* were present as well (Horak et al., 1989).

Amended lists of helminths of the common duiker, including references to the first records, are presented in Boomker et al. (1983a, 1987). According to Boomker et al. (1986), the mean helminth burdens and species composition of helminth parasites recovered from common duiker in the KNP and the Limpopo Province were similar. However, certain parasites present in the animals on the farm in Limpopo that are common helminths of domestic ruminants, such as *T. axei* and *C. pectinata*, were replaced in the KNP by worms such as *T. thomasi, C. hungi* and *C. neitzi*, which are almost exclusive parasites of wild antelope (Boomker et al., 1986). Comparatively speaking, helminth species richness in the common duiker in Weza Forest was low and consisted of five nematode species, one cestode species and paramphistomid trematodes (Boomker et al., 1987). In contrast, hosts in the KNP and Limpopo harbored more than 10 helminth species. Similar to what was observed in bushbuck, this might reflect the higher chance of cross-infection at the sampling sites in the KNP and Limpopo Province (Boomker et al., 1983a, 1986). Seven nematodes and the cestode genus *Thysaniezia* were listed from common duiker in the Eastern Cape, and worm burdens were comparable to those seen in KZN. Boomker et al. (1989c) attributed the relatively low abundance to climatic conditions in the study area, concluding that frequently high temperatures and low rainfall in the summer months, combined with scarce grass cover, were not conducive to the survival of free-living nematode larvae.

3.2.5.16. Southern reedbuck. Southern reedbuck, also referred to as common reedbuck (grazer), are medium-sized, grazing antelope, occurring in southern Africa. Their distribution is patchy, however, due to their specialized habitat requirements, including permanent water and long grass, reedbeds or rocks for cover (Skinner and Chimimba, 2005). Ixodid ticks infesting common reedbuck in and outside South Africa were listed by Theiler (1962), Baker and Keep (1970), and Walker (1974). The louse species were listed by Ledger (1980). Round (1968) listed the helminths of southern reedbuck, and Boomker et al. (1989b) compiled an amended helminth parasite list for this host, including references to the first record of each parasite in South Africa.

During a long-term study of the diversity and seasonal abundance of the tick, lice and helminth species of southern reedbuck, a total of 25 animals were examined at monthly intervals from May 1983 to May 1984 in the Himeville region, KZN. In addition, 27 reedbuck from three localities in the greater St. Lucia area, KZN, were examined at less regular intervals (Horak et al., 1988b; Boomker et al., 1989b).

Reedbuck in the Himeville region harbored four ixodid tick species, those in St. Lucia 10. The composition of the tick population was largely similar at the three game reserves in the St. Lucia area, and differed from that of reedbuck in Himeville, the only overlap being the presence of *Rhipicephalus* (*B.*) sp. and *R. evertsi evertsi* in both regions. The two additional ticks present in Himeville were *Ixodes* sp. and *Rhipicephalus* sp., whereas hosts in St. Lucia harbored *A. marmoreum, A. hebraeum, Haemaphysalis* sp., *R. appendiculatus* and *R. muehlensi. Rhipicephalus evertsi evertsi* was the most abundant and prevalent tick in Himeville as well as in the Eastern Shores GR in St. Lucia. Contrary to this, *R. appendiculatus* was the most abundant tick in Charter's Creek NR and St. Lucia Game Park in St. Lucia. The lice *D. reduncae* and *L. fahrenholzi* were present on the reedbuck in each locality (Horak et al., 1988b).

Ten nematode species, two cestodes, *M. benedeni* and *T. hydatigena*, and one paramphistomid trematode were recovered from reedbuck in the Himeville region. *Cooperia yoshidai* was both the most prevalent and most numerous helminth. Between four and 11 nematode species, *M. benedeni* and one paramphistomid trematode were recovered from reedbuck shot at different localities in St. Lucia (Boomker et al., 1989b). *Cooperia yoshidai* was also the most prevalent and abundant nematode in the St. Lucia area. *Haemonchus contortus, D. viviparus* and *L. schrenki* were common and abundant in both the Himeville and St. Lucia regions. The former two are typical parasites of sheep, goats and cattle, but have been recorded from a large variety of antelope (Horak, 1981; Horak et al., 1982b, 1983c; Boomker et al., 1983a, 1984a). The genus *Longistrongylus* is considered a typical parasite of wild antelope (Gibbons, 1977). While not occurring in large numbers, the genus *Setaria*, mainly represented by *S. bicoronata*, was present at all localities at which reedbuck were examined and can be considered a definitive parasite of this host (Boomker et al., 1989b).

3.2.5.17. Mountain reedbuck. Round (1968) listed six helminth species for this antelope. Baker and Boomker (1973) recorded the helminths from several mountain reedbuck (grazer) in the Loskop NR, Mpumalanga, and in the MZNP, including 10 new host–parasite records. Young et al. (1973b) examined mountain reedbuck in the MZNP and recorded the helminths *Haemonchus* sp., *N. spathiger, S. boulangeri*, and *M. expansa*, the ixodid tick *R. glabroscutatum* and the lice *L. reduncae* and *D. trabeculae*. Boomker et al. (2000) surveyed the helminth parasites of 18 mountain reedbuck shot at approximately 3-monthly intervals from November 1983 to November 1985 in the MZNP, and examined two animals from the Karoo NP, Western Cape. Horak et al. (1991b) and Golezardy and Horak (2007) examined the same animals for ticks. The two animals from the Karoo NP were not infected with helminths. Only four helminths were present in the animals in the MZNP, of these *M. benedeni* and *T. falculatus* were new host–parasite records. *Nematodirus spathiger* was by far the most prevalent and numerous of the helminths (Boomker et al., 2000). To date the following helminths have been listed from mountain reedbuck: Paramphistomidae (see comment Boomker et al., 2000), larvae of *Taenia* sp., *M. expansa, M. benedeni, C. hungi, C. oncophora, C. pectinata, C. punctata, C. yoshidai, Cooperia* sp., *Gongylonema* sp., *H. contortus, H. krugeri, Haemonchus* sp., *I. tuberculata, N. spathiger, O. columbianum, S. boulangeri, Skrjabinema* sp. and *T. falculatus*.

The 18 animals examined in the MZNP harbored a total of eight ixodid tick species, of which *R. glabroscutatum* was the most numerous (Horak et al., 1991b). Three tick species were recovered from the two animals examined in the Karoo NP, with *R. glabroscutatum* again the most numerous (Golezardy and Horak, 2007).

3.2.5.18. Waterbuck. Boomker et al. (1986) and Van Wyk and Boomker (2011) recorded the helminth parasites and their abundance in one waterbuck (grazer) each in the KNP and Limpopo Province. Six nematode species, *H. bedfordi, C. hungi, C. yoshidai, C. fuelleborni, I. tuberculata* and *O. columbianum*, and one cestode, *S. hepatica*, infected the waterbuck in the KNP (Boomker et al., 1986). Of these the *Cooperia* species were the most abundant. The waterbuck in Limpopo harbored three nematodes, *C. curticei, Trichuris* spp. and *O. columbianum*, as well as the cestodes *Avitellina* sp. and *S. globipunctata* (Van Wyk and Boomker, 2011). Helminth abundance in the animal in Limpopo was distinctly lower than that in the waterbuck in the KNP, possibly due to the arid climate at the former study site and the lower variety of co-occurring antelope.

3.2.5.19. Gray rhebok. The medium-sized gray rhebok or vaal ribbok (*Pelea capreolus*) (browser) is exclusive to South Africa, Lesotho and Swaziland, where it inhabits hilly country and plateaux with good grass cover, seemingly independent of a water supply. Despite its wide distributional range, this browsing antelope seldom occurs in large numbers (Horak et al., 1982b; Boomker and Horak, 1992). Parasites listed for this host were three nematode species (Round, 1968), a louse (Ledger, 1980), and larvae of a warble fly (Zumpt, 1965). Quantitative figures on the helminth and arthropod parasite communities of gray rhebok were first presented from five rhebok examined in the BNP during December 1979 (Horak et al., 1982b). A total of 30 animals, collected at the same locality at 2-monthly intervals from February 1983 to February 1984, were examined for their arthropod parasites (Horak et al., 1986b), and their parasite burdens compared to sympatric bontebok and springbok. The helminth fauna of 25 of these rhebok was studied by Boomker and Horak (1992). Following the initial survey, another three to four gray rhebok were examined every February for another 8 years, and the abundance of ixodid ticks and botfly larvae was recorded (Horak et al., 1997; Horak and Boomker, 1998).

Horak et al. (1982b) recovered 10 nematode species, the louse *D. peleae*, which is specific for gray rhebok, and the two ixodid ticks *I. pilosus* and *R. nitens*. Lesions that suggested the prior presence of larvae of *Strobiloestrus* sp. and *Gedoelstia* sp. were also seen. The nematode *L. namaquensis* was originally described by Ortlepp (1962) from a sheep. However, its presence in gray rhebok and also in springbok and bontebok in the BNP confirms that this is a parasite of wild ruminants as stated by Gibbons (1977), and that it might be an accidental parasite in sheep (Horak et al., 1982b). Immature *Ixodes* sp. were more abundant on gray rhebok than *Rhipicephalus* sp., but the reverse was true for bontebok, which Horak et al. (1982b) attributed to the habitat preferences of the two hosts.

The long-term survey of Horak et al. (1986b) confirmed the presence of the larvae of three botfly species, those of *Strobiloestrus* sp., *Gedoelstia* sp. and *O. ovis*, the former being the most prevalent as well as abundant. *Linognathus peleus* was added as a second louse species, but its relative abundance made up less than 1% of the louse population. All ticks recorded by Horak et al. (1982b) were seen during the long-term survey, and in addition the following tick species were recovered: *A. marmoreum, Rhipicephalus* (*B.*) sp., *H. aciculifer, R. evertsi evertsi, R. gertrudae, R. glabroscutatum* and *Rhipicephalus* sp. More specimens of *R.* (*B.*) *decoloratus* and *R.* (*B.*) *microplus* were collected from a single gray rhebok run over by a car just outside the park, and that had been grazing in close proximity to cattle, than on animals shot inside the park, emphasizing the possibility of parasite exchange between domestic and wild ruminants (Horak et al., 1986b). Horak et al. (1997) illustrated the relative abundance of the major tick species *I. pilosus, R. glabroscutatum* and *R. nitens* on gray rhebok, over the 10-year period that had been surveyed. In addition, two animals were examined for ticks in the Karoo NP during February 1991 (Golezardy and Horak, 2007) and four species were recovered of which *R. glabroscutatum* was the most abundant.

The helminths recovered from gray rhebok during the long-term survey corresponded to those listed by Horak et al. (1982b), except for the absence of *T. pietersi*, and the presence of *L. schrenki* (Boomker and Horak, 1992). An amended list of the helminths of gray rhebok with reference to the first record is presented by Boomker and Horak (1992) and contains the trematode *Fasciola hepatica*, and 12 nematode species. Specimens listed as "*Haemonchus contortus*, long spicule type" (Boomker et al., 1983b) were subsequently described as *H. horaki* (Lichtenfels et al., 2001). *Ostertagia hamata*, followed by *P. peleae* and *H. horaki*, were the most abundant and prevalent nematodes. No clear pattern of seasonal abundance was apparent for any of the helminths (Boomker and Horak, 1992).

Boomker and Horak (1992) found that the helminth community of gray rhebok differs from that of other browsers, in that common worms for the latter, such as *H. vegliai, C. rotundispiculum, O. harrisi, C. neitzi* and *E. sagitta*, are not present in gray rhebok. They ascribed this to the vegetation and climatic conditions in the BNP.

3.2.5.20. Springbok. Several authors have listed the helminth and arthropod parasites found in springbok (mixed feeder) in Africa and particularly South Africa (Theiler, 1962; Zumpt, 1965; Round, 1968; Young et al., 1973a; Horak, 1980; Ledger, 1980). Young et al. (1973a) examined 10 live and eight dead springbok in the MZNP as part of a disease survey and recorded their helminth, arthropod and protozoan parasites. Horak et al. (1982c) recorded the helminth burdens of eight springbok examined near Lichtenburg, NorthWest Province, during May and June 1977, nine springbok examined in the Krugersdorp GR, Gauteng, from June to August 1977, and four animals examined in the BNP during December 1979. All the springbok in NorthWest and four in the BNP were also examined for arthropod parasites. From July 1979 to December 1980, 48 springbok were examined during an ecto- and endoparasite survey near Kimberley, in the Northern Cape Province (De Villiers et al., 1985). Boomker et al. (1986) provided data on the helminth species composition and abundance of two springbok in the KTP, two springbok in the MZNP, and seven springbok at three localities in the Western Cape (four in the Karoo NP, two in the WCNP and one near Bredasdorp) (Boomker et al., 2000). Horak et al. (1991b) added information on the ticks infesting of 18 springbok examined in the MZNP between November 1983 and December 1985. A total of 48 springbok were examined at approximately bi-monthly intervals from May 1983 to June 1984 in the Etosha NP and Hardap NR in Namibia. Total counts and prevalence of their tick and louse species were recorded (Horak et al., 1992a).

Springbok in Namibia harbored few ticks and the two species present, *R. evertsi mimeticus* and *R. exophthalmos* [= *Rhipicephalus* sp. (near *R. oculatus*)] were neither prevalent nor abundant. Species richness of the lice was higher, and *D. antidorcus, L. antidorcitis, L. armatus, L. bedfordi* and *L. euchore* were recovered, with *L. antidorcitis* being the most prevalent and abundant, followed by *L. euchore*. Three of the ticks were also the most abundant and prevalent ticks collected from springbok in Kimberley (De Villiers et al., 1985). While Horak et al. (1992a) observed no seasonal pattern of abundance in Namibia, the four major louse species at Kimberley reached peak burdens in September (De Villiers et al., 1985). De Villiers et al. (1985) recorded second and third stage larvae of the nasal botflies *R. antidorcitis* and *R. vanzyli* during winter.

A total of seven tick species were recovered from the springbok in the MZNP (Horak et al., 1991b). However, the majority of these were collected from single host individuals and occurred in low numbers. Only *R. evertsi evertsi* and *R. glabroscutatum* reached a high prevalence. Many larvae and few adults were recovered of the former, whereas few immatures but more than 150 adults of the latter were found. Springbok were not considered to be a preferred host of any of these ticks (Horak et al., 1991b). Excepting *L. armatus*, which occurred in half the springbok examined near Lichtenburg, but was absent in the BNP, the same lice were present at the two localities (Horak et al., 1982c), and were also found during other surveys. As in the MZNP, *R. evertsi evertsi*, represented mostly by larvae, was the most common tick on animals near Lichtenburg (Horak et al., 1982c, 1991b). The remaining two ticks, *R. appendiculatus* and *Rhipicephalus* (*B.*) sp., were present on single animals and in very low numbers. Only two tick species infested springbok in the BNP, *I. pilosus* group, found on a single animal and *R. nitens* found on all four springbok (Horak et al., 1982c).

A total of 27 nematode species were recovered from springbok examined at various localities in South Africa (Horak et al., 1982c; De Villiers et al., 1985; Boomker et al., 2000). Many genera, such as *Haemonchus, Longistrongylus* and *Nematodirus*, were present at all the localities surveyed, albeit represented by different species. *Cooperiodes antidorca, P. serrata* and *T. falculatus* were consistently abundant and found at all localities (Horak et al., 1982c; De Villiers et al., 1985; Boomker et al., 2000). The lungworm *B. magna* was widespread, but usually occurred in low numbers. It was not found in the KTP. Fewer species and lower worm burdens were found in hosts in the KTP than in the surveys conducted by Horak et al. (1982c), De Villiers et al. (1985) and Boomker et al. (2000), probably reflecting the extremely arid conditions in the KTP (Boomker et al., 1986). The filarial nematode *Skrjabinodera kuelzii* has been collected from springbok in Namibia, where it was mainly found in the pelvic cavity fascia, muscle fascia and renal fat (Magwedere et al., 2012), but was not found in any of the previous surveys, although it has also been listed as a parasite of springbok by Round (1968). To date it is the only filaria recorded from this host in South Africa/Namibia. The only cestode recovered during the surveys listed earlier was *Avitellina* sp. in two hosts near Lichtenburg (Horak et al., 1982c). Round (1968) also listed larvae of *Taenia* sp. and *T. hydatigena*, as well as the trematode *C. calicophoron* from springbok in South Africa.

3.2.5.21. Oribi. Round (1968) only listed *S. scalprum* from oribi (*Ourebia ourebi*) (grazer) in South Africa. The parasites of a single male oribi, which died on a farm near Pietermaritzburg, KZN, were collected and counted, and *T. falculatus, T. colubriformis*, a new parasite record, and *C. yoshidai* were recovered (Boomker et al., 1984a).

3.2.5.22. Steenbok. Round's (1968) list of helminth parasites of steenbok (browser) comprises 17 species. Boomker et al. (1986) added the helminth data, including the counts, of one steenbok each at Riekert's Lager, the KNP and the KTP. A paramphistome, *H. krugeri, L. meyeri, L. sabie* and *T. instabilis* were considered new parasite records. The steenbok in the KTP harbored only *Skrjabinema*, which was found at all localities, and *P. serrata* as well as a *Trichostrongylus* species. *Paracooperia serrata* was likely acquired from sympatric springbok which is the type host of this species. The *Trichostrongylus* sp. was subsequently described as *T. auriculatus* (Boomker, 1986b).

Between 1982 and 1993 four steenbok were examined for ticks in the KNP, one in the MZNP and one in the KTP (Golezardy and Horak, 2006). Five tick species were collected from the animals in the KNP and all stages of development of *A. hebraeum, R.* (*B.*) *decoloratus* and *R. evertsi evertsi* were recovered. The animal in the MZNP harbored two species of which *R. glabroscutatum* was the most numerous, and the steenbok in KTP was infested only by the adults of *R. exophthalmos* (Golezardy and Horak, 2006).

3.2.5.23. Cape grysbok. Cape grysbok (*Raphicerus melanotis*) (predominantly browsers) are endemic to the Eastern and Western Cape Provinces in South Africa. Little is known about their parasites and only the nematodes *H. contortus* and *I. tuberculata* were listed by Round (1968), but see comments in Boomker et al. (1989c). During a long-term study on the helminths and ixodid ticks of grysbok, conducted on the farm Brakhill in the Eastern Cape, one grysbok was shot each month from February 1983 to January 1984 (Boomker et al., 1989c; MacIvor and Horak, 2003). Two cestode species, *Thysaniezia* sp. and larvae of *T. hydatigena*, and 10 nematodes were collected. Of these, *Skrjabinema* spp. was the most prevalent and abundant, followed by *T. pietersei, T. rugatus* and *N. spathiger*. Also present were *Haemonchus* sp., *L. sabie, T. circumcincta, T. deflexus, T. falculatus*, and *Trichuris* sp. (Boomker et al., 1989c). Due to the small sample size, seasonal patterns of abundance could not be established.

Five ixodid tick species were recovered from the grysbok: *A. hebraeum, H. silacea, R. evertsi evertsi, R. glabroscutatum* and *R. oculatus*. The most abundant tick was *R. glabroscutatum*, mostly represented by immatures. The remaining tick species occurred in low numbers only (MacIvor and Horak, 2003).

3.2.5.24. Impala. Impala (mixed feeder) are well studied in South Africa as regards the composition and abundance of their parasite communities. A literature review of previous studies on the helminth parasites of impala is given by Heinichen (1973), who also listed the trematodes, cestodes and nematodes recorded by various authors from impala in Kenya, Malawi, South Africa, Swaziland, Tanzania and Zambia. During a long-term study conducted in the Nylsvley NR, Limpopo, two to four impala were culled each month from February 1975 to February 1976, and their arthropod and helminth parasites studied, including prevalence and abundance (Horak, 1978b, 1982). Anderson (1983) published the results of a 2-year study on the helminths of impala on a game ranch close to Empangeni, KZN, and added an updated host–parasite list for the countries listed earlier. She also presented helminth data from different localities in South Africa, including the Hluhluwe GR and the KNP, accumulated by various researchers. Helminths from both impala and domestic animals that had been recorded from experimental or natural infections in South Africa were listed. The prevalence and mean intensity of infection of the various helminths was recorded for 46 impalas, and the seasonal abundance and the effect of host age were discussed. The most prevalent nematodes were *T. colubriformis, S. papillosus* and *C. fuelleborni*. No marked pattern of seasonal fluctuation in helminth burdens was found, probably because of the equable climatic conditions at the time. Contrary to this, Horak (1978b) observed seasonal patterns for *H. placei, L. sabie* and *I. tuberculata*, with adult worms being present during November to February and hypobiosis, as evidenced by the large number of fourth-stage larvae recovered, from April to September; hypobiosis was less obvious in *C. hungi, C. hamiltoni* and *C. hepatica*. Horak (1978b) found that worm burdens increased with the age of animals and reached a peak when impala were 1 year of age, reflecting increased exposure to worm infection as lambs make the transition from suckling to feeding on their own and a gradual increase in resistance as animals matured. In addition, Anderson (1983) reported a decrease in resistance against helminth infections in animals approaching old age. Total worm burdens of 30 000–50 000 were judged to be able to seriously affect the condition of impala and to lead to death.

The helminth burdens of five impalas from the St. Lucia GR were distinctly lower than those of co-occurring reedbuck, suggesting that mixed feeders such as impala are less likely to pick up helminth larvae while feeding than their strictly grazing counterparts such as reedbuck (Boomker et al., 1989b). Because of their feeding habits, however, impala are also exposed to the helminths of both browsers and grazers, and this, combined with a considerable overlap between their helminth assemblages and that of sheep, goats and cattle (Horak, 1978b), results in a diverse helminth fauna (Horak, 1978b; Anderson, 1983; Boomker et al., 1989b; Van Wyk and Boomker, 2011). The composition of the helminth assemblages at the various study sites was largely similar, and a number of species of different genera had a high prevalence and occurred in large numbers (Horak, 1978b; Anderson, 1983; Boomker et al., 1989b; Negovetich et al., 2006). In contrast, the prevalence and mean abundance of 10 helminth species and two cestodes species recovered from 10 impala studied at three localities in Limpopo were quite low, probably because of the dry climate and relatively low diversity of other antelopes (Van Wyk and Boomker, 2011). The following are the most common and abundant worms collected at the respective study sites: *H. placei, L. sabie, T. colubriformis, C. hungi, C. hamiltoni* and *I. tuberculata* at Nylsvley (Horak, 1978b); *H. bedfordi, T. colubriformis, S. papillosus, C. fuelleborni, I. tuberculata* close to Empangeni (Anderson, 1983); *H. contortus, C. yoshidai* and *I. tuberculata* at St. Lucia (Boomker et al., 1989b); *T. deflexus, C. hungi, C. hamiltoni* and *I. tuberculata* in the KNP (Negovetich et al., 2006); *C. hungi, I. tuberculata, O. columbianum* and *T. deflexus* in Limpopo (Van Wyk and Boomker, 2011). In addition, in a number of studies the lungworm *P. calcaratus* is reported as a typical parasite of impala (Anderson, 1983), but Van Wyk and Boomker (2011) did not find these nematodes in impala in the semi-arid northern regions of Limpopo Province.

Impala in the Nylsvley NR harbored six species of ixodid ticks and four louse species (Horak, 1982). Listed in order of abundance the lice were *D. aepycerus, L. aepycerus, D. elongata* and *L. nevilli*. A fifth louse species was later described as *L. weisseri* (Durden and Horak, 2004). The ticks recovered were *R. evertsi evertsi, R. appendiculatus, A. hebraeum, R.* (*B.*) *decoloratus, I. cavipalpus* and *H. rufipes*. Two additional tick species were present on cattle in the same reserve, *H. truncatum* and *R. simus*. Only 2.8% of ticks from impala (from total of 12 757) were adults, but 32.9% of ticks from cattle (from total of 14 186). Horak (1982) concluded that impala are inefficient hosts for adult ticks but serve as reservoir hosts for the immature stages of ticks of cattle. Clear seasonal patterns were seen in certain tick species.

Horak et al. (1995) studied the burdens of ixodid ticks and lice collected during two droughts in the KNP. They emphasized the importance of climate conditions in years preceding a drought, concluding that a mat of decaying vegetation persisting from a previous year of good rainfall, can be a microhabitat in which eggs can be laid, develop and newly hatched larvae can shelter even during drought. Although larvae of *A. hebraeum* and *R. zambeziensis* were the more abundant ticks on the vegetation, *R.* (*B.*) *decoloratus* was the most abundant tick on various ruminants, including impala, and zebra in the KNP. Horak et al. (1995) ascribed this to the fact that *R.* (*B.*) *decoloratus* is one-host tick that can complete its life cycle within 3 weeks and can thus complete more than one life cycle per year. The peak abundance of this tick on vegetation and on hosts during September to November also coincides with the time of greatest nutritional stress for the impala and other antelope in the KNP, which might render them especially susceptible (Horak et al., 1995). Matthee et al. (1997) studied the predilection sites of attachment of six ixodid tick species collected from impala on a ranch in the Northern (Limpopo) Province, and studied their seasonal abundance. Different models to predict total counts from counting selected sites were compared and the predilection sites of five different louse species were also determined (Matthee et al., 1998). Horak et al. (2003) collected 13 ixodid tick species, five louse species and two species of hippoboscid flies from impala from four different localities in the KNP. Parasite burdens were analyzed in relation to locality, sex, age class, month and drought.

3.2.5.25. Suni. Boomker et al. (1991a) examined four sunis (*Neotragus moschatus*) (browser) from the Tembe Elephant Park, KZN that had died during translocation procedures. At the time the parasites of these animals were practically unknown and first records had only been provided by Khalil and Gibbons (1976), who had collected 10 helminth species from six sunis in Kenya (Boomker et al., 1991a). Except for *Megacooperia woodfordi*, none of the worms found in suni from the Tembe Elephant Park were present in the animals in Kenya. *Trichostrongylus anomalus* and *H. vegliai* were the most common and abundant helminths of suni, the remaining species being *C. hungi, C. rotundispiculum, S. cornuta, Skrjabinema* sp., *S. papillosus* and *T. deflexus*. Cestodes and trematodes were not present.

Ticks were collected from three of the sunis examined by Boomker et al. (1991a). Five species were recovered, including larvae and adults of *H. parmata* and the immature stages of both *R. maculatus* and *R. muehlensi* (Golezardy and Horak, 2006). The collection of *R. kochi* from these animals constitutes a new locality record for this species.

4. Conclusion

Many of the findings of wildlife parasitologists discussed earlier have found their way into the applied control of parasites as part of livestock farming and game ranching as well as the management of conservation areas (Malan et al., 1997). Given the increased economical importance of game ranching in South Africa and the ever expanding interface between wildlife and domestic livestock, a thorough understanding of the host–parasite relationships of the two is necessary.

Conflict of interest

The authors declared that there is no conflict of interest.

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