

Wildlife parasites: Lessons for parasite control in livestock

F.S. Malan ^a, I.G. Horak ^{b,*}, V. de Vos ^{b,c}, J.A. van Wyk ^d

^a *Hoechst Roussel Vet Research Farm, PO Box 124, Malelane 1320, South Africa*

^b *Department of Veterinary Tropical Diseases, Faculty of Veterinary Science, University of Pretoria, Private Bag X04, Onderstepoort 0110, South Africa*

^c *National Parks Board, Private Bag X402, Skukuza 1350, South Africa*

^d *Division of Helminthology, Onderstepoort Veterinary Research Institute, Onderstepoort 0110, South Africa*

Abstract

For sustainable livestock production it is suggested that the parasitologist take a leaf out of Nature's book in the search for solutions to the mounting problems concerning parasite control. While the farmer has come to regard all parasites affecting livestock as entirely without benefit, indigenous parasites and diseases are normal and play an essential role as interacting components of a natural environment in an ecosystem such as the 19000 km²-sized Kruger National Park, Republic of South Africa. The parasites help to select their hosts for fitness and are assisted by predators and intra-species territorial aggression which continually eliminate the weak individuals from the system. It is essential to guard against the introduction of foreign parasites or infectious agents which have no real ecological niche or role in an established ecosystem, however, as they cause untoward interactions, sometimes of a violent nature. The policy must be to block off or, failing that, to control or eliminate these foreign parasites and diseases as far as possible. Often, when Man intervenes in an ecosystem, it leads to stress, overcrowding and stagnation and predisposes to disease and death. Intensification of the system, as in farming units, denies Nature the chance to manage on its own, because of clashing interests with Man. Frank parasitism and disease should almost invariably be seen as indicators of an imbalance in the ecosystem and should be rectified. Chemicals and vaccines should be used to produce sufficient food for all, but without exploiting Nature, or else Nature will be unable to continue catering for Man's needs.
© 1997 Elsevier Science B.V.

Keywords: Wildlife; Balance of Nature; Parasite role; Host selection; Survival of the fittest; Sustainable production; Host resilience; Host resistance

* Corresponding author.

1. Introduction

The knowledge acquired by studying the interactions between wildlife parasites, their hosts and their environment may hold the key to successful cost-effective livestock farming in the future. The aim of this paper is to stimulate thinking towards discovering novel methods or rediscovering old existent knowledge, so as to enable sustainable livestock production in the face of problems such as resistance to parasiticidal drugs.

The prevalence of anthelmintic resistance is increasing to such an extent that Waller and Larsen (1996) sounded the following warning ‘...the problem of anthelmintic resistance amongst nematode parasites is rapidly reaching a state of crisis....’ Better use of the available anthelmintics is essential, preferably in combination with management strategies, because new drugs with different mechanisms of action or novel means of control are unlikely to appear on the market within the foreseeable future (Borgsteede et al., 1996).

In addition, more than 500 species of arthropods are known to be resistant to one or more groups of pesticides (Georghiou and Lagunes, 1991). Resistance to virtually every kind of widely used toxicant has been documented, including insect growth regulators and the insecticidal crystals produced by *Bacillus thuringiensis* (Georghiou and Lagunes, 1991; McGaughey and Whalon, 1992). Because of cross-resistance, populations are often resistant to novel insecticides even before they are introduced (Roush, 1993).

In situations where remedies have become ineffective it could be worthwhile to study the role parasites play in an ecosystem where mankind has not interfered materially. Thus insight can be gained from the natural interactions taking place between the elements, hosts and parasites, and adapted as possible alternative strategies for parasite control in production animals.

2. Nature

‘Then God commanded, ‘Let the earth produce all kinds of animal life: domestic and wild, large and small’—and it was done. So God made them all, and he was pleased with what he saw’ (Genesis 1: 24–25).

The question is often asked whether Nature can manage on her own.

An area in the world where natural conditions still prevail today is the Kruger National Park (KNP) situated in the Mpumalanga Lowveld of the Republic of South Africa (RSA). The KNP encompasses 19 000 km² and is 350 km long and up to 90 km wide.

When tourists visiting the KNP report animals with conditions such as mange, skin infections, wounds and emaciation, their general expectation is that the animals will be caught and treated. Many ask whether they may see the ‘hospital’ where sick animals are treated. The truth is, however, that very seldom will veterinarians intervene, the reason being that it is not in accordance with the principles of nature conservation as applied in the numerous national parks of the RSA (Fig. 1).

One of the primary objectives of a national park is to conserve all biotic and abiotic components of the ecosystem in their natural state and, while having to accommodate

National Parks of South Africa

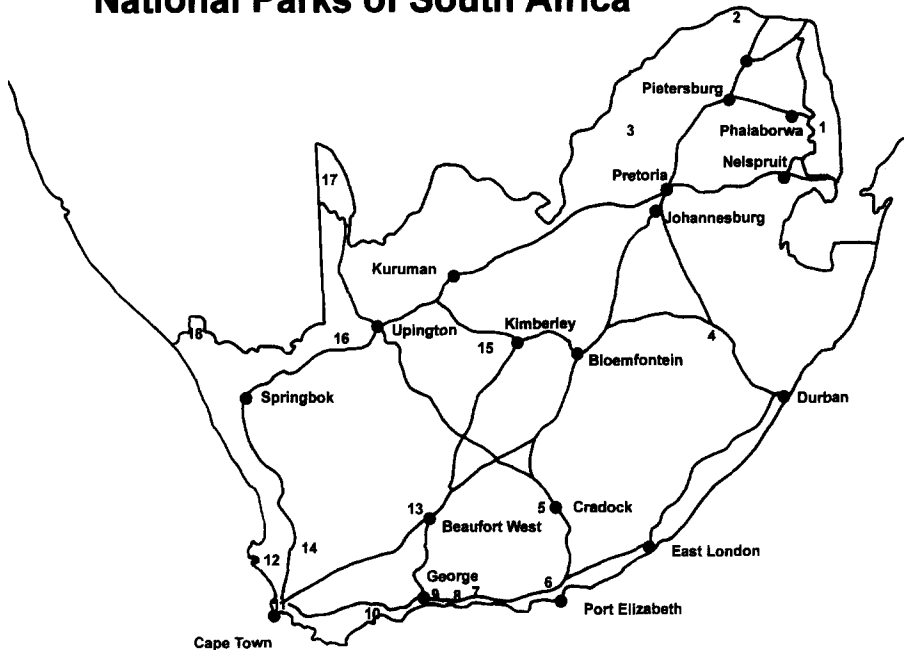


Fig. 1. National parks of South Africa ((from a National Parks Board brochure. Key: The figures on the map denote the following national parks: 1—Kruger; 2—Limpopo Valley; 3—Marakele; 4—Golden Gate; 5—Mountain Zebra; 6—Addo Elephant; 7—Tsitsikamma; 8—Knysna; 9—Wilderness; 10—Bontebok; 11—Table Mountain; 12—West Coast; 13—Karoo; 14—Tankwa Karoo; 15—Vaalbos; 16—Augrabies Falls; 17—Kalahari Gemsbok; 18—Richtersveld).

tourists for financial reasons, to combat all foreign elements, including foreign parasites and infectious organisms.

A schematic representation of the ecosystem will help us visualise the interactions that take place in the KNP (Fig. 2).

Indigenous parasites and infectious agents are normal and essential interacting components of a natural environment and have to be conserved together with the other elements of the ecosystem. On the other hand, foreign parasites, infectious agents and hosts and other elements which are not indigenous to the ecosystem are considered alien and should as far as possible be debared.

Indigenous, or naturally occurring parasitic or infectious life forms have had a common evolutionary history with their hosts in a specific habitat and this has led to a reduction, or a cessation in detrimental effects such as the virtual absence of nodules cause by *Oesophagostomum columbianum* in impala, *Aepyceros melampus* as opposed to domestic sheep (Horak, 1981). The co-evolutionary trajectory followed by any particular parasite-host association will depend on the manner in which the virulence and the production of transmission stages of the parasite are interlinked and on the costs to the host of evolving resistance (May and Anderson, 1983), coupled with (often involuntary) evasive habits of the host, e.g. seasonal migration.

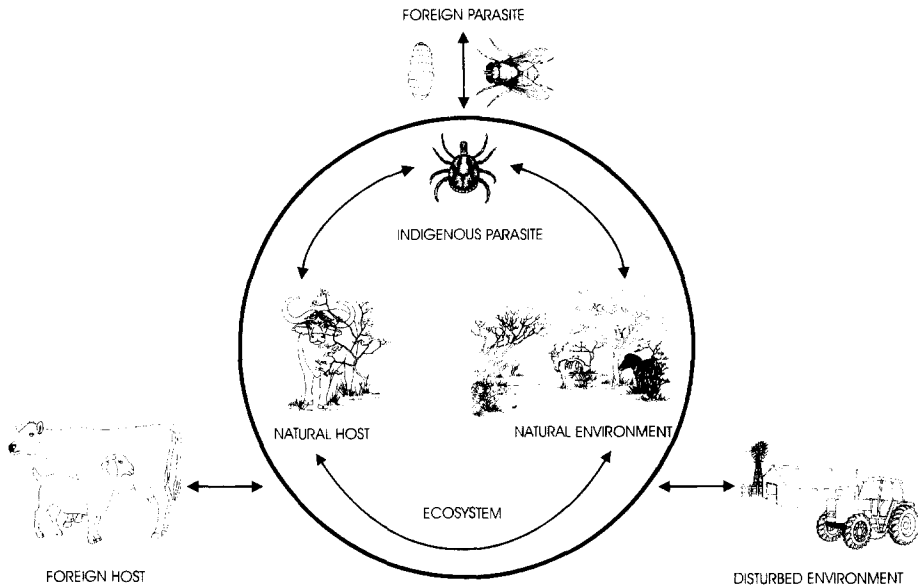


Fig. 2. A schematic representation of interactions taking place in an ecosystem such as the Kruger National Park (* Foreign parasites, such as *Theileria parva*, *Hypoderma* spp. and *Glossina* spp.).

The more complex and diverse the components of the association between host, parasite and environment are, the more stable the relationship can be expected to be. A multiple host-species situation provides the benefits of predation and scavenging, a better 'vacuum cleaner' effect of each other's parasites and ensures better and wider utilisation of the habitat without the domination and resultant over-abundance of any single species.

The diversity of the habitat in a nature reserve such as the KNP also ensures an abundance of associated life forms, a mosaic of species providing natural barriers or buffer areas to the spread of disease.

In large ecosystems free from human interference, parasites and predators fulfil an important role in the selection of host populations for fitness and by their effect upon the natural intrinsic growth rate of their host populations (Anderson and May, 1978; Anderson, 1979; Holmes, 1982). Young animals, usually until the age of 12–18 months, are often subject to large parasite infections (Horak et al., 1983), causing weaker individuals and those that have neither innate resistance nor the ability to mount an effective immune response, to succumb to predators before they can contribute to the gene pool.

Parasites may also have an effect on each other or the particular niche of a parasite might already have been occupied by another. For example, in the abomasum of the blue wildebeest, *Connochaetes taurinus*, peak burdens of *Haemonchus bedfordi* were followed by peak burdens of *Trichostrongylus thomasi*. *H. bedfordi* reached its maximum numbers during April and October in the 1–12-month-old animals and only during April

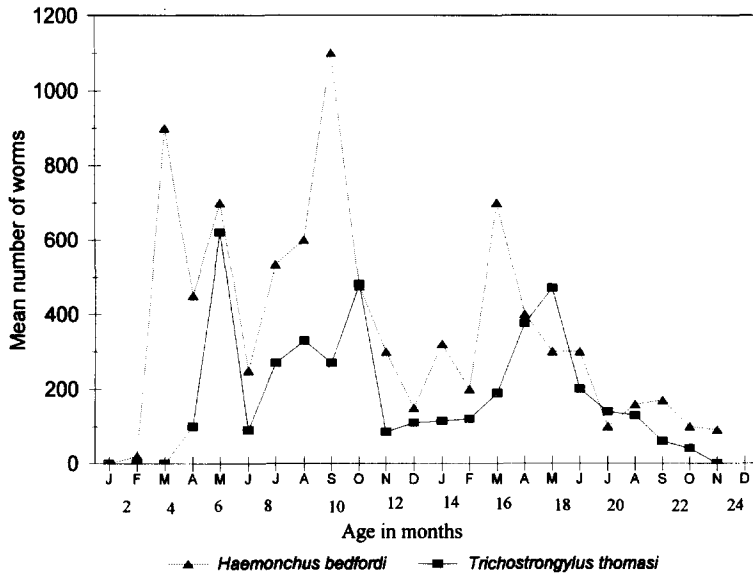


Fig. 3. Seasonal occurrence of *Haemonchus bedfordi* and *Trichostrongylus thomasi* in blue wildebeest, *Connochaetes taurinus* (Horak et al., 1983).

in the older animals. *T. thomasi* followed a similar pattern to *H. bedfordi* but its peaks were always later than those of the latter worm, namely, June and November in the younger animals and only June in the older ones (Fig. 3) (Horak et al., 1983). While there are also other possibilities, such as seasonal preferences, the staggered peaks of *H. bedfordi* and *T. thomasi* might be due to such competition. Large burdens of *Haemonchus contortus* and *Trichostrongylus axei* compete in the abomasa of sheep to the detriment of the former species (Reinecke, 1974).

Except for a few helminth species, such as *T. thomasi*, *Trichostrongylus deflexus*, *Trichostrongylus falculatus* and *Nematodirus spathiger* which occur in a wide variety of wild animals, the nematodes of wildlife are generally host specific, or infect animals within a particular genus or within a grouping of generically related animals (I.G. Horak, unpublished observations, 1996).

Lesson: For meaningful parasite control, establish the various parasite interactions taking place within the farming unit. Alternate use of pasture for animals of different species which are not susceptible to one another's worm parasites (Morley and Donald, 1980; Van Wyk, 1990), or even alternate susceptible and more resistant animals of the same species (Michel, 1969, 1976; Brunsdon, 1980).

In healthy diverse ecosystems, such as the KNP, a dynamic balance between these components has been attained. Some of the parasitic life forms may, however, be dormant at times, and flare up to cause disease only when the habitat is altered by conditions such as droughts and veld fires.

3. Drought

Droughts have been shown to have a dramatic effect on parasitic disease. For example, when a sudden drought occurred after a period of good annual rainfalls, the tick and louse burdens rose (Horak et al., 1995). Impalas, *Aepyceros melampus*, harboured a mean of 7461 ticks during such a sudden drought period, compared with 678 during a prolonged period of drought (Horak et al., 1995).

Repeated high annual rainfalls give rise to a mat of decaying vegetation under the standing grass, from which the ticks quest for their hosts. This mat supplies an ideal habitat for the survival of the ticks, even in a drought year, hence the high numbers of ticks.

In contrast, when the annual rainfall is relatively low in the years preceding a drought, there is a severe depletion of the standing grass and the mat of dead and decaying material virtually disappears. Consequently the micro-habitat, in which the female ticks lay their eggs and in which the eggs develop and hatch and the newly hatched larvae can shelter, is progressively lost.

Under natural conditions excessive infections of endoparasites seldom occur. However, in drought situations nutritional stress is severe and the immune status of hosts is compromised, and animals concentrate near water holes, leading to temporary local overpopulation and acceleration in parasite and disease transmission. Combined with the increased stress through social interactions and insufficient food, the stage is set for disease to emerge and act as a culling factor.

Worm burdens stay remarkably constant in healthy animals but rise significantly in cases where animals are under stress (such as during drought periods), or are suffering from disease or injuries. In the KNP, the total worm burdens of impalas rose from below 20 000 under normal conditions, to more than 60 000 during a drought period (Boomker, Horak and de Vos, unpublished observations, 1996).

Such a disease is density-dependent, however, and will abate when the animals scatter and develop immunity to reinfection after rain or after a certain number have been eliminated. This culling role of the parasitic life-forms is one of Nature's ways of relieving excessive pressure on the habitat, in turn ensuring maintenance of the quality and quantity of grazing that is essential for the survival of hosts and parasites.

Lesson: During and immediately after periods of drought be aware of sudden outbreaks of disease and parasitoses and be proactive in managing the problem. For instance, during a drought the bovine faecal pat, and to a lesser extent the sheep pellet, offer the free-living worm stages protection in the form of moisture and shade. With the advent of the first good rains after the drought, very large numbers of larvae may be set free within a short period of time, often with dire consequences (Barger et al., 1984; Reinecke, 1960; Van Wyk, 1990).

4. Veld fires

Veld fires originating from lightning or human intervention may influence the ecology.

The abundance of 13 ixodid tick species detected by drag-sampling of a burnt zone in the KNP was compared with that in an adjacent unburnt area over a 2-year period (Spickett et al., 1992). While numbers of ticks were reduced after the burn, they soon rose again, and there appeared to be little practical benefit from veld-burning during spring as a method of tick control.

Lesson: The effects of fire are influenced by the amount of vegetation; by the species and developmental status of the tick population at the time of the burn; by subsequent host influx or exclusion from the burnt area; and by the ecoclimatic suitability of the region for tick species. Nevertheless, burning may be effective if aimed at specific tick species, either tenuously adapted to an area or with populations already reduced by chemical control. Efficacy could be enhanced by the exclusion of major hosts for a critical period after the burn to prevent or delay population recovery, a strategy advocated by Minshull and Norval (1982). An additional potential effect is that the numbers of free-living stages of parasitic nematodes could be reduced by the heat of burning as larvae apparently migrate up and down the vegetation in the presence of moisture and light (Barger, 1978).

5. Base-line values of parasite burdens

In order to appreciate the role of indigenous parasitic life-forms in our southern African national parks, surveys have been directed at establishing parasitic and pathological norms or base-line values for many host and parasite species under different environmental conditions. In this way deviations from levels that the host can tolerate can be evaluated. Without this base-line knowledge, how would a total count of over 124 million internal parasites in a single host be judged, without knowing that this burden of *Probstmayria vivipara* was recovered from a fat zebra, *Equus burchelli antiquorum*, that was obviously unaffected by the vast numbers? Indeed, now we also know that this was no exception; ‘impossible’ figures of many millions of *P. vivipara* still fall within the acceptable range for zebras of that particular sex and age, under environmental conditions such as those reigning at the time the particular necropsy was performed (Krecek et al., 1987).

At no stage of a study in which two to four impalas were culled each month for a period of a year, did it appear as if the worm burdens harboured by the impalas affected them adversely (Horak, 1978). Subsequently, monthly necropsies over two consecutive years on impalas indicated that lambs up to 9 months have fewer parasites than 1 to 2-year-old impalas and that selection for the fittest animals seems to occur during the second year of life (Boomker, Horak and de Vos, unpublished observations, 1996).

While impala males have the highest parasite burdens during the mating season, possibly as a result of the stress of fighting, the burdens of the ewes peak during the lambing season.

Lesson: Without base-line values concerning parasite burdens it is impossible to evaluate the effect of the parasites on their hosts (Gordon, 1981).

6. Species diversity

Diversity appears to bring stability into natural systems. Different animals sharing the same habitat ingest and in this way help to control one another's parasites, granted that their susceptibility to the various parasites differs.

Despite regular rabies outbreaks in black-backed jackal, *Canis mesomelas*, (Mansvelt, 1956; McKenzie, 1993) and domestic dogs in the areas adjacent to the KNP, with a regular overflow of rabid dogs into the park (Swanepoel et al., 1993), rabies has never been diagnosed in the wild animal populations in the KNP. Can it be that this phenomenon is due to the fact that the rich variety of life forms within the KNP provides an adequate buffer to suppress any small outbreak which may occur? (V. de Vos, unpublished observations, 1991). Compare this situation to Namibia where poor host diversity and an over-abundance of a single species have, by horizontal transmission, caused the death of about 10 000 kudus, *Tragelaphus strepsiceros*, from rabies over a 6-year period (Barnard and Hassel, 1981). This phenomenon of stability in diversity is accepted by the National Parks Board, which aims as far as possible to re-establish the historical life forms in all the parks in the RSA, even in the so-called species parks such as the Mountain Zebra and Bontebok National Parks.

Lesson: Alternation of animals of different species may contribute to parasite control (Barger and Southcott, 1975; Southcott and Barger, 1975; Jordan et al., 1988; Nansen et al., 1990).

7. Overcrowding and stagnation

In the KNP it has been shown that elephant, *Loxodonta africana*, buffalo, *Syncerus caffer*, and to a lesser extent, hippo, *Hippopotamus amphibius*, populations have the potential to outgrow natural reduction mechanisms and enter an exponential or population explosion growth phase. History has shown that such growth is usually associated with habitat destruction and an eventual population crash through hunger and disease. Being afraid of the dimensions that this might attain, the National Parks Board has opted for control procedures, which have been successfully executed since 1970 (De Vos et al., 1983).

A predator-proof enclosure of 256 ha was erected in roan antelope, *Hippotragus equinus*, and sable antelope, *Hippotragus niger*, habitat in northern KNP for the propagation of these species. Predators and other antelopes were excluded. In the ensuing years a correlation was found between climatic factors, density of animals and the outbreak of diseases such as dermatophilosis (Senkobo disease), (De Vos and Imes, 1976), papillomatosis, cytauxzoonosis and excessive tick burdens in these animals. With the exception of low tick burdens, none of these conditions have ever been found in roan or sable antelope outside the enclosure. Significantly, at the onset of a disease outbreak, the roan antelopes usually had reached a density of about one animal per 0.1 km² as opposed to one animal per 14.5 km² for comparable habitats outside the enclosure.

Nature is largely left alone to look after other animal populations within the extensive ecosystems of the KNP and Kalahari Gemsbok National Park. Climatic factors, preda-

tors and natural parasites keep these animals in a dynamic balance. In the process, outbreaks of diseases such as mange occur sporadically and claim the lives of some animals, probably from stress, or perhaps insufficient nutrients or over-population, all of which are in time rectified by Nature. The policy is therefore not to treat these animals, but only to monitor and assess their role in the ecosystem context. There have been exceptions, however, one of which being a pride of lions, *Panthera leo*, with white cubs that were treated for mange. It is debatable whether this should have been done, however, even for white lions. By intervening, man is wittingly favouring the survival of one component over another (V. de Vos, unpublished observations, 1991).

Smaller national parks in the RSA (such as Bontebok National Park) are all fenced and have no large predators. Thus, as overflow into neighbouring areas is prevented, a tendency towards overpopulation is created, resulting in habitat destruction and disease outbreaks. As stated by Lightfoot and Norval (1981) regarding eland, *Taurotragus oryx*, which they classified as relatively susceptible to tick infestation: 'No serious tick problems have arisen in eland whose movements have been unrestricted over a large range. A common factor in almost all cases where tick problems have been encountered with eland has been the restriction of the animals within relatively small fenced areas'. Similarly, Padaiga and Marma (1970) demonstrated in Lithuania that the extent of infection of roe deer, *Capreolus capreolus*, with strongylids and coccidia correlated directly with the population density of the hosts.

Lesson: Excessively high stocking rates usually go hand in hand with a deterioration of pasture quantity and quality, and thus an increased incidence of parasitism and disease. To prevent this, ensure that grazing pressure is optimal (Morley and Donald, 1980; Van Wyk, 1990).

8. Stress

In coincidental studies in the KNP it was found that individual animals that had a previous history of stress, such as a wound or bone fracture, would invariably harbour a parasite burden far in excess of the usual levels, counts being up to 100 times higher than in healthy animals. Such animals that act as reservoirs and disseminators of parasites are rare in the KNP, as they are predator-prone. In the absence of large predators, however, they could be expected to be more common and play a much more important role in excessive contamination of grazing.

For example, a 6-month-old blue wildebeest, which had broken a leg ca. 4 weeks previously, harboured 575 adult *Strongyloides* spp. and 175 adult *T. falculatus* when shot. In contrast, a healthy calf of similar age and shot at the same time, harboured neither of these helminth species. Furthermore, while the stressed calf housed 2071 *Boophilus decoloratus*, of which more than 24% were adults, the healthy calf and 2 others (which were 12 months older when shot) were infested with only 390–805 of this tick species, only 4–12% of which were adults (Horak et al., 1983).

These results support the surmise of Grootenhuis (1979) that stress may lead to fatal infections. It has been shown in cattle in Australia that stress can decrease resistance to *Boophilus microplus* (Utech et al., 1978).

Lesson: Prevent stress, and isolate and/or cull diseased animals. The farmer must take over the role of the predator and attend to stressed animals before the parasites they harbour can bring about excessive contamination of pastures or spread diseases.

9. Fitness

Predators play the role of hatchet men in the ecosystem, but parasites have the last word by also helping to test predators for fitness.

While some hosts have an innate resistance to primary infection, others are susceptible yet able to mount a very effective immune response to secondary infection. Yet others have the ability to retain high levels of fitness and production despite heavy parasite infections. These are termed resilient hosts (Bisset and Morris, 1996).

Lions in the KNP have been shown to harbour no fewer than five infectious disease agents and 18 different parasite species, some of which have been shown to act as selection agents for lions and other predators (Young, 1975). For example, while paralysis resulting from *Trichinella spiralis* infection was recorded in lions and civets, *Civettictis civetta*, the spotted hyena, *Crocuta crocuta*, is obviously resilient as no untoward effects of trichinosis have been observed, despite an infection rate of 85% in hyena frequenting the surroundings of the Skukuza tourist camp in the KNP. Young and Kruger (1967) pointed out that overcrowding of rodents or carnivores may result in an increase in cannibalism, which may present '... favourable conditions for the transmission of trichinosis which may, depending on its lethal effect... play some part in the natural regulation of numbers of wild carnivores...'. Similarly, an unknown *Dirofilaria* spp. was the cause of paraplegia in a lion.

Sarcoptic mange, caused by *Sarcoptes scabiei*, has an extremely wide host range, but most wildlife species develop only sub-clinical mite infestations. It is only when the hosts are stressed that clinical signs are seen—and then usually only in individual animals in a herd or group. Skin lesions have been found in lions, buffalo, blue wildebeest, impalas, springbok, *Antidorcas marsupialis*, and red hartebeest, *Alcelaphus buselaphus*, often affecting the general condition of the hosts that are clinically affected (Young, 1969). Severe infestations may even result in mortality, particularly in young lion cubs. Young (1975) stated that '... in one year one pride of lions in the KNP is known to have lost all of their cubs due to a particularly severe outbreak of sarcoptic mange'. He also reported that *Linguatula serrata* has been the cause of necrotic rhinitis in lions and that *Hepatozoon* spp. may contribute to seasonal mortalities in spotted hyenas in the KNP.

Heavy tick infestation, often in association with nutritional stress, is a common direct or indirect cause of mortality and other deleterious effects, such as a low calving rate in eland and other wild ungulates (Lightfoot and Norval, 1981). Ticks are not only important parasites in their own right, but transmit a large variety of pathogenic and benign tick-borne diseases and can also lead to metabolic debilitation, tick toxicosis and secondary infection with bacteria, maggots and other organisms. Secondary bacterial infection, although not yet recorded as a direct cause of death in wild ungulates, has

been reported to lead to the death of eland calves, after tick damage to the teats of their mothers had made it impossible for them to suckle (Harthoorn, 1977).

It is important for game wardens to take note of considerable variations in susceptibility to ticks among wild ungulate species. Square-lipped rhino, *Ceratotherium simum*, warthog, *Phacochoerus aethiopicus*, blue wildebeest and tsessebe, *Damaliscus lunatus*, are apparently the most resistant to tick infestation, and can therefore be translocated almost anywhere without any consideration to ticks as a cause of morbidity. Tick species composition is of paramount importance to other ungulates such as eland, sable, and kudu, however, and these animals should not be introduced to regions where *Rhipicephalus appendiculatus* occurs in large numbers (Lightfoot and Norval, 1981).

Lice, like mange, also cause considerable debility, but likewise only in certain individuals within a herd. Impala comb their haircoat with their incisor teeth to control external parasites, such as lice (McKenzie, 1990), but as the animals age, their incisor teeth become worn, causing an explosion in their louse populations.

Lesson: In the absence of predators on a farm unit the owners should take over the responsibility for selecting for fitness. They should use Nature as a partner, by allowing parasites to help with selecting the fittest individuals in the face of parasite challenge (Bisset and Morris, 1996). In the case of helminths and ticks, farmers ignore this advice at their peril: practically unmanageable resistance to parasitocides has developed, and in certain countries especially sheep farming is almost at the crossroads for want of anthelmintics effective against some extreme cases of resistance (Van Wyk et al., 1997; Waller and Larsen, 1996).

10. Foreign parasites

A close watch should be kept for foreign or aberrant parasites or diseases in every ecosystem. Aberrance in host-parasite relationships indicates the invasion by a parasite or disease of a new host or ecosystem, usually giving rise to instability in the system and manifesting itself in the form of a disease epidemic, often of a violent nature. A classic example is the rinderpest pandemic which swept through Africa at the turn of the century, killing millions of cattle and all but wiping out the buffalo population in the Lowveld of Mpumalanga and Northern Province (Stevenson-Hamilton, 1912; Stevenson-Hamilton, 1929; Stevenson-Hamilton, 1947). Eland, kudus, warthogs and bushpigs, *Potamochoerus porcus*, were also severely affected. The area now encompassing the KNP was devastated to such an extent that a recurrence of that magnitude would today be considered a national disaster.

At least 21 species of exotic arthropods have become established in the KNP, although fortunately without serious consequences to date. Danger arises when parasites or other infectious agents are translocated on or in their hosts to places where they did not occur previously, and affect other hosts that have never previously come into contact with them. A recent example is a serious outbreak of *Mycobacterium bovis* infection in buffalo in the KNP, probably as a result of contact with infected cattle (Bengis et al., 1996). It appears that the bacterium has entered a naïve population, leading to a prevalence of 92% in certain buffalo herds (V. de Vos, unpublished observations, 1996).

and also invading other hosts, such as lions, cheetahs, baboons, *Papio ursinus*, (Keet et al., 1996) and kudus (Bengis, pers. com., 1996). After post mortem examination of affected buffaloes it was estimated that at least 10% of animals in the worst-affected herd would have died of tuberculosis within a year.

Among the ticks, *Amblyomma variegatum* is a cause for concern, because, having invaded the Caribbean islands, (with *Cowdria ruminantium* ‘in tow’), is now posing a threat to the USA (Barré et al., 1987). Similarly a rhino tick, *Rhipicephalus maculatus*, has established itself in the KNP, probably having been introduced on rhinoceroses or nyalas, *Tragelaphus angasii*, from KwaZulu-Natal, and *Hyalomma marginatum turanicum*, previously confined to the more arid zones of the RSA, was brought in probably on a migratory bird (Braack et al., 1995).

Lesson: Adopt rigid control measures to minimise the risk of passive transport of other organisms, not only internal and external parasites, but also the immature stages of beetles, flies and other organisms often present in faeces contaminating transport crates used for wildlife.

11. Foreign hosts

Parasites protect the environment against foreign host species. The gemsbok, *Oryx gazella*, prefers the relatively dry regions of southern Africa. When introduced to the Free State and large areas of the Cape Province, approximately 50% of sub-adult gemsbok suffered tick-induced paralysis and subsequent mortality caused by *Ixodes rubicundus* during 1987 and 1988 (Fourie and Vrahimis, 1989).

Lesson: Do not introduce species into an area which is not suitable for them, even if there are apparently sufficient chemicals to be able to keep metazoan parasites at bay.

12. Human intervention

The main lesson that can be learnt from Nature is that it can manage on its own, except if foreign or aberrant parasites, infectious diseases, or highly susceptible hosts are introduced into the ecosystem (Lawrence and Norval, 1979), in which case artificial control measures have to be adopted to achieve Man’s objectives. Nature cannot manage on its own if the ecosystem is intentionally altered by Man to suit his requirements.

Human intervention frequently severely jeopardises the delicate balance between the host, the parasite and the environment. Man alters and often rapes the natural environment by erecting fences, by placing bore-holes and dams in places where Nature did not intend water to be, by indiscriminate veld-burning, or other farming practices. Often sustainable production then becomes an impossibility, as a relative over-abundance of animals results firstly in a situation in which the habitat cannot sustain them, and, secondly, in ideal conditions for a flare-up of diseases—again Nature’s way of relieving the pressure which Man has forced upon it.

Nature has provided effective methods for managing ticks, such as the voracious red-billed oxpecker, *Buphagus erythrorhynchus*. In a laboratory trial oxpeckers were able

to reduce the numbers of adult *Boophilus decoloratus* by 95.7% (Bezuidenhout and Stutterheim, 1980). Oxpecker populations have become markedly reduced in stock farming areas, however, probably because of Man's interference by intensive dipping of livestock with arsenicals and organophosphorus drugs and less wildlife in farming areas.

Man is also not innocent regarding the negative effects of anthelmintics on Nature, as exemplified by mounting evidence of deleterious effects of ivermectin on dung beetles and other fauna inhabiting dung (Sommer et al., 1993; Gunn and Sadd, 1994). On the other hand, Man has slowly been awakening to the possibility that organisms such as dung beetles can be allies in the struggle to produce sufficient food for the global population. For instance, dung beetles were introduced to Australia—albeit in an attempt to restore the balance after the problems created by having introduced cattle into an environment where Nature was not geared to receive them!

The results of Man's interference with the ecosystem can be summarised by the letters SOS, which are often also symbolically indicative of Natures' apparent desperate cry for help—to be left to its own devices:

Stagnation: Vast areas are divided by fences into smaller units that restrict hosts and parasites from moving at will, thus interfering with the normal seasonal nomadic flow of animals that usually occurs in Nature from nutritional factors and water needs. Amongst other effects stagnation often exerts undue pressure on water and grazing resources.

Overpopulation: Livestock farmers tend to overpopulate their properties with wild animals or livestock, with consequent malnutrition and greater susceptibility of the hosts to parasites. The reasons for this could be the fallacy of financial gain or plain ignorance. The result is that parasites and diseases increase as it is seemingly their task to counteract this overpopulation by taking individuals out of the system, so as to ensure survival of both parasite and host.

Stress: The effect of stagnation and overpopulation on the host is that of stress which results in a host with a lowered ability to withstand disease.

That this SOS is of great practical significance is evident from the toll taken among captured wildlife, such as deaths from coccidiosis in buffalo calves and impalas in captivity, and salmonellosis which is common in penned elephants and Lichtenstein hartebeest, *Sygmoceros lichtensteinii*. Internal parasites have made some farmers in South Africa give up sheep farming (Van Wyk et al., 1989; Van Wyk et al., 1991). Crowding of animals in feedlots and dog kennels, etc., lead to a plethora of diseases, such as viral and bacterial respiratory diseases that are relatively rare elsewhere. It is well-known that humans in overpopulated areas are prone to outbreaks of cholera, influenza and typhoid fever, which are major global diseases.

13. Conclusion

Unfortunately Man does not have a proud track-record regarding the use of the bounties of Nature. However, when studying the ecosystem in the KNP many answers are to be found to our questions relating to parasite and disease control:

Carefully observe the hosts within the ecosystem for conditions such as weight loss, mange, ticks and internal parasites, as these point to an underlying shortcoming in the

system, and attempt as far as possible to restore the natural balance. An outbreak of disease in Man in urban areas points to underlying causes such as overpopulation, improper water supply and sewage disposal. On the farm, select animals indigenous to the ecosystem, e.g. *Bos indicus* and Nguni breeds that are more resistant to ticks than *Bos taurus* (Spickett et al., 1989; Rechav and Kostrzewski, 1991).

Do not bring heartwater-susceptible cattle, eland, springbok, blesbok, *Damaliscus pygargus phillipsi*, and bontebok, *Damaliscus pygargus dorcasi*, into heartwater areas before taking the necessary precautions. Eliminate animals within a herd which are tick 'taxi's and introduce oxpeckers (Bezuidenhout and Stutterheim, 1980) onto the farm if the habitat will accommodate them.

For control of endoparasites which is a huge problem in sheep on irrigated pastures, breed for resistance (the ability to suppress the establishment and/or subsequent development of a worm infection) and resilience (the ability to maintain relatively undepressed production while infected) as discussed by Bisset and Morris (1996). Diversify farming practices, for instance by alternating sheep and cattle. Create an environment where dung beetles (Bornemissza, 1960; Bryan, 1973; Grønvold et al., 1996) can propagate, as they aid helminth control by breaking open dung pats and pellets and in this way exposing worm eggs and larvae to the ravages of the elements.

No, Nature cannot manage on its own where Man has interfered with the ecosystem. Man therefore has the responsibility to use the tools invented by him, such as chemicals and vaccines that are slowly becoming available (Lightowlers, 1994; Opdebeeck, 1994; Emery, 1996) in a responsible and scientific way, so as to produce sufficient food for all the globe's people, but without exploiting Nature.

'Then God said, 'And now we will make human beings; they will have power over the fish, the birds, and all animals, domestic and wild, large and small. I am putting you in charge of the fish, the birds, and all the wild animals. God looked at everything he had made, and he was very pleased'' (Genesis 1: 27–31).

References

- Anderson, R.M., 1979. The influence of parasitic infection on the dynamics of host population growth. In: R.M. Anderson, B.D. Turner, and L.R. Taylor (Editors). *Population dynamics*. Blackwell, Oxford, pp. 245–281.
- Anderson, R.M. and May, R.M., 1978. Regulation and stability of host-parasite population interactions. I. Regulatory processes. *J. Anim. Ecol.*, 47: 219–247.
- Barger, I.A., 1978. Grazing management and control of parasites in sheep. In: A.D. Donald, W.H. Southcott, J.K. Dineen (Editors). *The epidemiology and control of gastrointestinal parasites of sheep in Australia*. Commonwealth Scientific and Industrial Research Organization, Australia (Shiels Printing, Mt Waverley), pp. 53–63.
- Barger, I.A., Lewis, R.J. and Brown, G.F., 1984. Survival of infective larvae of nematode parasites of cattle during drought. *Vet. Parasitol.*, 14: 143–152.
- Barger, I.A. and Southcott, W.H., 1975. Control of nematode parasites by grazing management. I. Decontamination of cattle pastures by grazing with sheep. *Int. J. Parasitol.*, 5: 39–44.
- Barnard, J.H. and Hassel, R.H., 1981. Rabies in kudus. *J. S. Afr. Vet. Ass.*, 52: 309–314.
- Barré, N., Uilenberg, G., Morel, P.C. and Camus, E., 1987. Danger of introducing heartwater onto the American mainland: potential role of indigenous and exotic *Amblyomma* ticks. *Onderstepoort J. Vet. Res.*, 54: 405–417.

- Bengis, R.G., Kriek, N.P.J., Keet, D.F., Raath, J.P., de Vos, V. and Huchzermeyer, H.F.A.K., 1996. An outbreak of bovine tuberculosis in a free-living African buffalo (*Syncerus caffer*, Sparman) population in the Kruger National Park: a preliminary report. Onderstepoort J. Vet. Res., 63: 15–18.
- Bezuidenhout, J.D. and Stutterheim, C.J., 1980. A critical evaluation of the role played by the red-billed oxpecker *Buphagus erythrorhynchus* in the biological control of ticks. Onderstepoort J. Vet. Res., 47: 51–75.
- Bisset, S.A. and Morris, C.A., 1996. Feasibility and implications of breeding sheep for resilience to nematode challenge. Int. J. Parasitol., 26: 857–868.
- Borgsteede, F.H.M., Roos, M.H., Smith, G. and Prichard, R.K., 1996. Workshop summary: Anthelmintic resistance. Vet. Parasitol., 64: 129–132.
- Bornemissza, G.F., 1960. Could dung eating insects improve our pastures? J. Aust. Inst. Agric. Sci., 26: 54–56.
- Braack, L.E.O., Maggs, K.A.R., Zeller, D.A. and Horak, I.G., 1995. Exotic arthropods in the Kruger National Park, South Africa: modes of entry and population status. Afr. Entomol., 3: 39–48.
- Brunsdon, R.V., 1980. Principles of helminth control. Vet. Parasitol., 6: 185–215.
- Bryan, R.P., 1973. The effects of dung beetle activity on the numbers of parasitic gastrointestinal helminth larvae recovered from pasture samples. Aust. J. Agric. Res., 24: 161–168.
- De Vos, V. and Imes, G.D., 1976. An outbreak of dermatophilosis in sable (*Hippotragus niger*) and roan antelopes (*Hippotragus equinus*) in the Kruger National Park. Koedoe 19: 1–15.
- De Vos, V., Bengis, R.G. and Coetzee, H.J., 1983. Population control of large mammals in the Kruger National Park. In: R.N. Owen-Smith (Editor). Management of large mammals in African conservation areas. HAUM Educational Publishers, Pretoria, pp. 213–231.
- Emery, D.L., 1996. Vaccination against worm parasites of animals. Vet. Parasitol., 64: 31–45.
- Fourie, L.J. and Vrahimis, S., 1989. Tick induced paralysis and mortality of gemsbok. S. Afr. J. Wildl. Res., 19: 118–121.
- Georgioui, G.P. and Lagunes, A.T., 1991. The Occurrence of Resistance to Pesticides in Arthropods. FAO-AGP-T5100-MISC/91-1, Rome.
- Gordon, H. McL., 1981. Epidemiology of helminthosis in sheep. Refresher course for veterinarians. Refresher course on sheep, August 10–14, 1981. University of Sydney. Proceedings No. 58: 551–556.
- Grønvold, J., Henriksen, S.A., Laisen, M., Nansen, P. and Wolstrup, J., 1996. Biological control. Aspects of biological control—with special reference to arthropods, protozoans and helminths of domesticated animals. Vet. Parasitol., 64: 47–64.
- Grootenhuis, J.G., 1979. Theileriosis of wild bovidae in Kenya with special reference to the eland (*Taurotragus oryx*). Ph.D. Thesis, State University, Utrecht.
- Gunn, A. and Sadd, J.W., 1994. The effect of ivermectin on the survival, behaviour and cocoon production of the earthworm *Eisenia fetida*. Pedobiologia, 38: 327–333.
- Harthoorn, A.M., 1977. Control of ticks in wildlife. Fauna and Flora, Pretoria, 27: 9.
- Holmes, J.C., 1982. Impact of infectious disease agents on the population growth and geographical distribution of animals. In: R.M. Anderson and R.M. May (Editors). Population biology of infectious diseases. Dahlen Konferenzen 1982. Springer-Verlag, Berlin, pp. 37–51.
- Horak, I.G., 1978. Parasites of domestic and wild animals in South Africa. IX. Helminths in blesbok. Onderstepoort J. Vet. Res., 45: 55–58.
- Horak, I.G., 1981. Host specificity and the distribution of the helminth parasites of sheep, cattle, impala and blesbok according to climate. J. S. Afr. Vet. Ass., 52: 201–206.
- Horak, I.G., de Vos, V. and Brown, M.R., 1983. Parasites of domestic and wild animals in South Africa. XVI. Helminth and arthropod parasites of blue and black wildebeest (*Connochaetes taurinus* and *Connochaetes gnou*). Onderstepoort J. Vet. Res., 50: 243–255.
- Horak, I.G., de Vos, V. and Braack, L.E.O., 1995. Arthropod burdens of impala in the Skukuza region during two droughts in the Kruger National Park. Koedoe, 38: 65–71.
- Jordan, E.E., Phillips, W.A., Morrison, R.D., Doyle, J.J. and McKenzie, K., 1988. A 3-year study of continuous mixed grazing of cattle and sheep: Parasites of offspring. Int. J. Parasitol., 18: 779–784.
- Keet, D.F., Kriek, N.P.J., Penrith, M.L., Michel A., Huchzermeyer, H.F.A.K., 1996. Tuberculosis in buffaloes (*Syncerus caffer*) in the Kruger National Park: spread of the disease to other species. Onderstepoort J. Vet. Res., 63: 239–244.

- Krecek, R.C., Malan, F.S., Reinecke, R.K. and de Vos, V., 1987. Nematode parasites from Burchell's zebras in South Africa. *J. Wildl. Dis.*, 23: 404–411.
- Lawrence, J.A. and Norval, R.A.I., 1979. A history of ticks and tick-borne diseases of cattle in Rhodesia. *Rhod. Vet. J.*, 10: 28–40.
- Lightfoot, C.J. and Norval, R.A.I., 1981. Tick problems in wildlife in Zimbabwe. 1. The effects of tick parasitism on wild ungulates. *S. Afr. J. Wild. Res.*, 11: 41–45.
- Lightowers, M.W., 1994. Vaccination against animal parasites. *Vet. Parasitol.*, 54: 177–204.
- Mansvelt, P.R., 1956. Rabies in the northern Transvaal (1950) outbreak. *J. S. Afr. Vet. Med. Ass.*, 27: 167–178.
- May, R.M. and Anderson, R.M., 1983. *Coevolution*. Sinauer Associates, Sunderland, MA, pp. 186–206.
- McKenzie, A.A., 1990. The ruminant dental grooming apparatus. *Zool. J. Linn. Soc.*, 99: 117–128.
- McKenzie, A.A., 1993. Biology of the black-backed jackal *Canis mesomelas* with reference to rabies. *Onderstepoort J. Vet. Res.*, 60: 367–371.
- McGaughey, W.H. and Whalon, M.E., 1992. Managing insect resistance to *Bacillus thuringiensis* toxins. *Science*, 258: 1451–1455.
- Michel, J.F., 1969. The epidemiology and control of some nematode infections of grazing animals. In: B. Dawes (Editor). *Adv. Parasitol.*, 7: 211–282.
- Michel, J.F., 1976. The epidemiology and control of some nematode infections in grazing animals. In: B. Dawes (Editor). *Adv. Parasitol.*, 14: 355–397.
- Minshull, J.I. and Norval, R.A.I., 1982. Factors influencing the spatial distribution of *Rhipicephalus appendiculatus* in Kyle Recreational Park, Zimbabwe. *S. Afr. J. Wildl. Res.*, 12: 118–123.
- Morley, F.F.W. and Donald, A.D., 1980. Farm management and systems of helminth control. *Vet. Parasitol.*, 6: 105–134.
- Nansen, P., Steffan, P., Monrad, J., Grønvald, J. and Henriksen, S.A., 1990. Effects of separate and mixed grazing on trichostrongylosis in first—and second—season grazing calves. *Vet. Parasitol.*, 36: 265–276.
- Opdebeeck, J.P., 1994. Vaccines against blood-sucking arthropods. *Vet. Parasitol.*, 54: 205–222.
- Padaiga, V.I. and Marma, B.B., 1970. [Invasion of the roe deer with parasites related to population density and conditions of life.] *Zool. Zh.*, 49: 283–287 (in Russian). Cited in *Helminth Abstracts (Series A)*, 40: 27.
- Rechav, Y. and Kostrzewski, M.W., 1991. Relative resistance of six cattle breeds to the tick *Boophilus decoloratus* in South Africa. *Onderstepoort J. Vet. Res.*, 58: 181–186.
- Reinecke, R.K., 1960. A field study of some nematode parasites of bovines in a semi-arid area, with special reference to their biology and possible methods of prophylaxis. *Onderstepoort J. Vet. Res.*, 28: 365–464.
- Reinecke, R.K., 1974. Studies on *Haemonchus contortus*. 1. The influence of previous exposure to *Trichostrongylus axei* on infestation with *H. contortus*. *Onderstepoort J. Vet. Res.*, 41: 213–215.
- Roush, R.T., 1993. Occurrence, genetics and management of insecticide resistance. *Parasitol. Today*, 9: 174–178.
- Sommer, C., Grønvald, J., Holter, P. and Nansen, P., 1993. Effects of ivermectin on two Afrotropical dung beetles, *Onthophagus gazella* and *Diastellopalpus quinque-dens* (Coleoptera: Scarabaeidae). *Vet. Parasitol.*, 48: 171–179.
- Southcott, W.H. and Barger, I.A., 1975. Control of nematode parasites by grazing management. II. Decontamination of sheep and cattle pastures by varying periods of grazing with the alternate host. *Int. J. Parasitol.*, 5: 45–48.
- Spickett, A.M., de Klerk, D., Enslin, C.B. and Scholtz, M.M., 1989. Resistance of Nguni, Bonsmara and Hereford cattle to ticks in a Bushveld region of South Africa. *Onderstepoort J. Vet. Res.*, 56: 245–250.
- Spickett, A.M., Horak, I.G., van Niekerk, A. and Braack, L.E.O., 1992. The effect of veld-burning on the seasonal abundance of free-living ixodid ticks as determined by drag-sampling. *Onderstepoort J. Vet. Res.*, 59: 285–292.
- Stevenson-Hamilton, J., 1912. *Animal life in Africa*. William Heinemann, London.
- Stevenson-Hamilton, J., 1929. *The Lowveld: its wildlife and its people*. Cassel, London.
- Stevenson-Hamilton, J., 1947. *Wild life in South Africa*, 5th edn. Cassel, London.
- Swanepoel, R., Barnard, B.J.H., Meredith, C.D., Bishop, G., Brückner, G.K., Foggin, C.M. and Hubschle, O.J.B., 1993. Rabies in Southern Africa. *Onderstepoort J. Vet. Res.*, 60: 325–346.
- Utech, K.B.W., Seifert, G.W. and Wharton, R.H., 1978. Breeding Australian Illawarra Shorthorn cattle for resistance to *Boophilus microplus*. 1. Factors affecting resistance. *Aust. J. Agric. Res.*, 29: 411–422.

- Van Wyk, J.A., Malan, F.S., Gerber, H.M. and Alves, Regina, M.R., 1989. The problem of escalating resistance of *Haemonchus contortus* to the modern anthelmintics in South Africa. *Onderstepoort J. Vet. Res.*, 56: 41–49.
- Van Wyk, J.A., 1990. Integrated worm control as a strategy in the control of gastro-intestinal nematodes of sheep and cattle. *J. S. Afr. Vet. Ass.*, 61: 141–145.
- Van Wyk, J.A., van Schalkwyk, P.C., Bath, G.F., Gerber, H.M. and Alves, R.M.R., 1991. The threat of wide dissemination of anthelmintic resistance by veld ram performance testing units. *J. S. Afr. Vet. Ass.*, 62: 171–175.
- Van Wyk, J.A., Malan, F.S. and Randles, J.L., 1997. How long before resistance makes it impossible to control some field strains of *Haemonchus contortus* in South Africa with any of the modern anthelmintics? *Vet. Parasitol.* (in press).
- Waller, P.J. and Larsen, M., 1996. Workshop summary: Biological control of nematode parasites of livestock. *Vet. Parasitol.*, 64: 135–137.
- Young, E., 1969. The significance of infectious diseases in African game populations. *Zool. Afr.*, 4: 275–281.
- Young, E. and Kruger, S.P., 1967. *Trichinella spiralis* (Owen, 1835) Railliet, 1895 infestation of wild carnivores and rodents in South Africa. *J. S. Afr. Vet. Med. Ass.*, 38: 441–443.
- Young, E., 1975. Some important parasitic and other diseases of lion, *Panthera leo*, in the Kruger National Park. *J. S. Afr. Vet. Ass.*, 46: 181–183.