CHAPTER ONE

"It may well be that it would take hundreds of generations for the progenitive instinct to develop in this way, but if it should do so, nature would have taken her revenge, and the variety *Homo contracipiens* would become extinct and would be replaced by the variety *Homo progenitivus*"

Charles Darwin

GENERAL INTRODUCTION

Parasitic diseases have shaped the course of human history and present a continual threat to the wellbeing of millions of people and domesticated animals across the world. They have for centuries ranked with war and disasters as the leading causes of death and disability and still present major challenges to human progress and survival (Morens *et al*. 2004). Parasitic infections can't be controlled or eradicated simply by the application of drugs or anti-vector measures after a parasite had been identified, its life cycle been demonstrated, and it been implicated as the causative agent of disease (Cox 1993). Careful consideration of recurrent lessons from history justifies the urgency of an understanding of the dynamic interactions between parasites, their hosts, and the environment. Emerging infectious diseases and the diversity and adaptability of pathogenic organisms are governed by evolutionary vigour, and associated with a range of underlying causal factors (Daszak *et al*. 2000; Morens *et al*. 2004). Most notably, these include a change in the ecology of the host, the parasite, or both, which is driven by human population expansion due to increasing population density and urbanisation, and expansion into previously natural habitats (Daszak *et al*. 2000). Thus, a variety of societal and cultural factors may contribute to increased host exposure or susceptibility to parasites. These factors induce changes that enhance the spread and transmission of parasitic diseases (Thompson 2001).

Background to spirocercosis

Spirocercosis is a canine disease caused by the nematode parasite *Spirocerca lupi* (Rudolphi, 1809) (Spirurida: Spirocercidae) (Van der Merwe *et al*. 2008) and is a potentially fatal condition in domestic dogs (*Canis familiaris*). This is a cosmopolitan parasite, though it is more commonly found in the warmer tropical and subtropical regions of the world (Bailey 1972). *S*. *lupi* parasitizes mainly domestic dogs but natural infections have been reported in other members of the family Canidae which serve as important reservoir hosts (Bailey 1972; Mazaki-Tovi *et al*. 2002). The larval life cycle of this parasite involves intermediate and paratenic (transport) hosts (Van der Merwe *et al*. 2008). Various species of coprophagous dung beetles (Scarabaeidae: Scarabaeinae) serve as the principle intermediate hosts after ingesting the embryonated eggs of *S*. *lupi* in the faeces of the definitive host (Bailey *et al*. 1963; Chhabra & Singh 1972; Chowdhury & Pande 1969). The nematode larvae encyst within the tissues of the dung beetle and reach communicability (Larval stage 3) within two months (Bailey 1972). Vertebrate paratenic hosts, including wild and domestic fowl, lizards, and certain mammals, may become infected only after ingestion of a suitable infective coprophagous dung beetle (Bailey 1972). Final hosts become infected after ingestion of either an infected scarabaeine or paratenic host (Bailey 1972; Van der Merwe *et al*. 2008).

Data on the prevalence of this disease in dogs is often cumbersome to interpret and can be misleading due a variety of factors. Limitations in diagnostic techniques employed by clinicians can lead to inaccuracies in the establishment of prevalence, such as false negative results given by faecal flotation tests, undetected variation in egg shedding by female worms, and challenges presented to clinical methods such as endoscopy and radiography (Dvir *et al*. 2010; Fisher *et al*. 2009; Van der Merwe *et al*. 2008). Furthermore, prevalence data on spirocercosis varies considerably between regions (countries), rural and urban areas, changes over time (seasonal), and must be interpreted in terms of the dog population sampled (feral dogs versus pets) (Van der Merwe *et al*. 2008). Differences in the prevalence of *S*. *lupi* have also been identified in pet dogs that show different behaviour in life and hunting styles (Mylonakis *et al*. 2001). Discovery of infection with *S*. *lupi* is often “coincidental”, during routine examinations for unrelated conditions or necropsies (Fisher et al. 2009; Van der Merwe et al. 2008). Moreover, a lack of awareness by the general public about spirocercosis, perhaps due to the large suite of clinical manifestations in dogs, and the scarcity of information in popular literature about the conditions that can lead to infection, may also contribute to underreporting of this parasitic infection in domestic dogs.

These factors have been clearly demonstrated in a study by Fisher *et al*. (2009) where they found a prevalence of 24% in apparently healthy dogs in St. Kitts, West Indies, brought to their clinic for neutering. This was found to be comparable with previous reports of infection with *S*. *lupi* in 22% of dogs in Kenya (Kagira & Kanyari 2000) and 28% of dogs in South Africa (based on surveys completed by privately practicing veterinarians) (Lobetti 2000). In Kenya, prevalence based on necropsy results was as high as 78% (85% in stray dogs and 38% in companion animals) (Brodey *et al*. 1977) while Minnaar & Krecek (2001) and Minnaar *et al*. (2002) reported infections of 14% and 13% in dogs belonging to people in two resource-limited communities in the provinces of Gauteng and the Free State, South Africa, respectively.

Treatment of spirocercosis

To date, the effectiveness of treatment with drugs or surgery and chemotherapy has been met with mixed success. A number of drugs have been used for the treatment and or prophylaxis of spirocercosis, but thus far none have been successful in killing both the adult and juvenile stages of this nematode without showing host side-effects (Van der Merwe et al. 2008). Doramectin, a cattle anthelmintic, and ivermectin were used as conventional treatment and have proved to be effective under clinical conditions over the last decade, although breed specific toxicity have been reported in in collies and other herding dog breeds following administration of both these treatments (Van der Merwe *et al*. 2008). Recently, Kok *et al*. (2011) tested the efficacy of Milbemycin oxime under clinical conditions against pre-adult *S. lupi*, which prevented the establishment and encapsulation of *S. lupi* in the oesophagus of experimentally infected dogs. Their results showed promising potential for the development of a prophylactic and therapeutic anthelmintic. Surgical removal of oesophageal sarcomas and surgery of the spinal cord to remove worms and the surrounding damaged tissue have been relatively unsuccessful up to date due to high post-surgical mortality rates (Dvir *et al*. 2010; Van der Merwe *et al*. 2008).

Despite extraordinary advances in biomedical research, it is unlikely that these alone will alleviate the burden of parasitic diseases. In fact, drug resistance in parasites will, in all likelihood, become more widespread due to an increase in the use thereof (Thompson 2001). Instead, an understanding of how human behaviour is influencing parasite transmission patterns, often sustaining such infection cycles, is essential if there is any hope in keeping emerging diseases in check. Spirocercosis is an emerging disease in several parts of the world (e.g. in Tel Aviv, Israel, where a sevenfold increase in incidence was reported in nine years (Van der Merwe et al. 2008)). Recently, there has also been growing concern over the upsurge in incidence and reported cases of spirocercosis in domestic dogs in South Africa. There is a plethora of literature on the clinical, diagnostic and epidemiological aspects of this disease in dogs, yet no study has aimed at fully understanding the dynamic interactions between the various hosts and *S*. *lupi*, governed by the consequences of their behaviour under different and ever-changing environmental conditions. It is most likely that the impact of this disease is accentuated by constant changes in human demographics and behaviour.

Interactions between the hosts, the parasite, and their environment

Humans and dogs share an ancient association that span nearly 14 000 years (Archer 1997; Daniels & Bekoff 1989). Viewed from an evolutionary perspective they resemble social parasites, manipulating human responses to ensure relationships for the procurement of resources. However, this statement would probably be refuted by most dog owners who would argue for the source of security and sense of wellbeing that they convey (Archer 1997). Domestic dogs are considered to be the most abundant extant terrestrial carnivore, and are found in every habitat that humans occupy (Daniels & Bekoff 1989). They show great behavioural and ecological plasticity: their social organisation being a response to the quantity and spatial distribution of food resources, and the strategies they have to employ to acquire it (Daniels & Bekoff 1989). This would account for the differences in social organisation and feeding behaviour encountered between dogs that are kept as companion animals and those that are free-ranging (feral).

Although dogs belong to the order Carnivora they are actually omnivores, because of their differences in food preferences and food selection behaviour to most members of the order, which they inherited from their ancestral association with humans (Bradshaw 2006). Furthermore, dogs are also known to be coprophagous, although the reasons for this practice have received little scientific attention (Soave & Brand 1991). The degree to which they are coprophagous should be similar in companion animals and feral dogs, although one would expect feral dogs to exhibit an increased frequency of coprophagy due to the factors that characterise their social organisation. Studies on spirocercosis in dogs have considered the consumption of the various paratenic hosts or the deliberate ingestion of dung beetles to be the main cause of the transmission of *S*. *lupi* to dogs. However this study suggests that the coprohagous behaviour of dogs and the subsequent accidental ingestion of coprophagous dung beetles in or on faeces are mainly responsible for the transmission of this parasitic nematode to dogs.

Urbanisation is increasing globally and more than half the world's population currently resides in cities and towns (Evans *et al*. 2009). In South Africa, about 17 million people (35% of the total population) live in informal settlements in urban and peri-urban areas. These are mostly very poor or low-income communities without access to any formal hygienic facilities such as sanitation. A further 20 million people are without on-site waterborne sanitation (Carden *et al*. 2008). Coupled to the enormous health risks posed by such absent, dysfunctional or inadequate sewage removal systems, is the accumulation of exposed human faeces. Moreover, dogs often become the most common large mammal in urban environments where a change in land use has led to the reduction or complete absence of grazing herbivores (Carpaneto *et al*. 2005) (e.g. where small holdings are converted into housing complexes). Pet owners are often reluctant to clean up after their dogs where they have defecated in their gardens or public areas, a habit that leads to the accumulation of dog faeces in public open spaces (e.g. parks) and on streets.

Dung beetles are mostly coprophagous and mediate several essential ecosystem services, such as the suppression of dung-dispersed nematodes and protozoa in the environment by removal of dung for feeding and breeding purposes (Nichols et al. 2008). They are known to colonise human faeces (Fincher et al. 1970) and dog dung (Wallace & Richardson 2005). Larger amounts of exposed faeces may lead to an increase in the abundance of certain species of coprophagous scarabaeines that are suitable intermediate hosts of *S*. *lupi*. Dogs do not seem to show any discrimination in the choice of dung they consume, and were observed on several occasions during this study to consume the dung of both humans and other dogs (Du Toit pers. obs.). The prevalence of infection with *S*. *lupi* in dung beetles and the subsequent infection of dogs with this nematode in any particular area depend in part on the abundance of susceptible beetles in that area and the contact rate between them and dogs (Bailey 1972). Changes in urban land use and subsequent changes along urban-rural gradients influence the nature of biological interactions partly due to changes in species assemblage structure and composition (Carpaneto *et al*. 2005; Evans *et al*. 2009). Such alterations in assemblage structure of species pose a particular risk to altered rates of parasitism and disease transmission (Evans *et al*. 2009). Higher rates of parasitism and disease are consistent in urban wildlife populations, in comparison to such populations in rural areas (Evans *et al*. 2009).

Rationale for the study

This study represents the first investigation into the dynamic interactions between *S. lupi* and its dung beetle intermediate hosts under natural conditions anywhere in the world. Although it was conducted under South African circumstances, it generated a novel understanding of the processes that govern the interactions between this parasitic nematode, the intermediate hosts, the definitive host, and humans, and should be representative for any region of the world where this disease is endemic. Furthermore, it is unique in that all previous studies on the intermediate dung beetle hosts were conducted in the laboratory or under experimental conditions.

There exists a real opportunity to prevent spirocercosis in dogs before it needs to be controlled or cured by veterinary intervention. But, who is responsible for preventing, or at least, managing an increase in the transmission rate of this disease to dogs?

The notion of treating spirocercosis in dogs with drugs or by means of surgery and chemotherapy is a member of the “no technical solution” problems (Hardin 1968). While progress in biomedical research is desirable and necessary, veterinary treatment of animals infected with this disease alone will not prevent this condition in uninfected dogs. People who are concerned about this emerging disease in dogs (with different perspectives on the problem ranging from personal to professional) are exploring new avenues of reducing infection in dogs without acknowledging (knowingly or unknowingly) the origin of the problem. This problem cannot be solved in a technical way.

In order to address this issue there must be a realisation of the actual problem, which is one of acknowledgement of personal responsibility. Such a responsibility would naturally extend to include a responsibility towards other humans in terms of their emotional well-being concerning the health of their dogs; their sense of pride and self-confidence with regards to having access to basic amenities of society; and their sense of community by cooperating with others in sustaining an agreeable way of life (living in an aesthetically appealing place). By adhering to this sense of self-responsibility, one is not necessarily conforming to altruism (for it is not truly attainable in our species), but rather ensuring self-preservation in terms of a preferred way of life.

All people want the maximum good, but as asked by Hardin (1968), what is this good? Perhaps it is survival. In order to attain an increased probability of survival (for dogs), there needs to be a common interest in managing the spread of this disease by decreasing the amount of exposed human and dog faeces. In this lies the “tragedy of the commons”. Rational man will find that his individual effort in fouling the commons (whether by him directly or indirectly, i. e. the dog) is less than the effort of cleaning the waste that goes into it. This is true for everyone and in a sense “we are fouling our own nest” as long as we act individually as rational free-riders (Hardin 1968). The problem of fouling is a consequence of population density:

as a population becomes denser, biological recycling of such waste becomes overburdened (Hardin 1968). As a function of population density, the problem of fouling discloses a principle of morality: "the morality of an act is a function of the state of the system at the time it is performed" (Hardin 1968). It calls for a redefinition of property rights and the betterment of basic human and societal needs.

Public open space, be it parks, streets or undeveloped urban land, is open to all. It is to be expected that dog owners would use this commons, to the mutual benefit of owner and dog, as often as possible. Crowding of the commons by dogs would not be an obvious problem, as long as the density of dogs is below a certain maximum. Such an arrangement will work reasonably well until that maximum capacity is reached. Being rational, every dog owner seeks to maximise his gain. This is the conclusion reached by every dog owner and therein is the tragedy. Of course, there are expected differences between a commons in an established neighbourhood and that in an informal settlement. All land is common in the "township" and there is no hindrance to dogs that frequent this commons. When the dogs are feral, there is no control over crowding. Privately owned land does not constitute a commons although the attitude of the owner with regards to crowding and fowling of his private property will contribute to the tragedy (dung beetles can fly some distance to a food resource and carry the parasite with them).

What will guide people's behaviour in terms of cleaning-up after their dogs or themselves? Formal institution's role in managing this problem is limited. It is not feasible to fence open spaces in informal settlements or impose fines on using this commons as latrines. A scenario more likely to succeed is to provide sanitation facilities to those who do not have such amenities (which would also contribute to uplifting basic human dignity) and to control the number of feral animals in these areas. In established public spaces a fine-system is more probable to aid in accomplishing this goal, although provision should be made for dog owners to have the opportunity to dispose of their pets' faeces (by e. g. providing plastic bags and bins). Here, formal institution can play a role by guiding land use (perhaps also by providing incentives for people to adhere to these principles). Unfortunately, formal institution will have little effect in privately owned property.

In the end it is the informal institution of moral values that will have the most effective solution to preventing the spread of this disease (and simultaneously contribute to community upliftment). Free-riders who refuse to conform to these values (either by not removing their dogs' faeces from public or private spaces, or by not disposing of their own (e.g. by burying it)) will ultimately be accountable for increased transmission and incidence of spirocercosis in dogs.

Aims of this research

This study aimed to investigate the dynamic associations between the parasitic dog nematode *Spirocerca lupi* and its intermediate dung beetle hosts. From these data generalities are explored by drawing conclusions about the interactions between this parasite and its intermediate hosts under natural conditions.

Chapter 2 investigates the prevalence of *S*. *lupi* in populations of its intermediate dung beetle hosts under natural conditions in two geographical regions of South Africa (Grahamstown in the Eastern Cape Province, and Pretoria in Gauteng). Specific objectives of this chapter are (1) to determine which species of dung beetles are hosts under natural conditions; and (2) to establish the proportion of infection with *S*. *lupi* in the samples of species collected from their populations in these geographical regions. The role of dung beetle feeding mechanisms in limiting their suitability as hosts for *S*. *lupi* is discussed in Chapter 3. A specific objective of this chapter is to exclude certain dung beetles as possible intermediate hosts of this nematode based on the size of ingested food particles. Chapter 4 investigates the effects of trophic preference and urbanization on dung beetle assemblage structure and transmission of *S*. *lupi* to dogs. Objectives of this chapter are to demonstrate the effect of location and food preference on dung beetle assemblage structure, and the effect those may have on infestation rates; and to indicate consequences of the effect of a larger suite of hosts on possible increased transmission rates of *S*. *lupi* to dogs. Chapter 5 serves as a conclusion to the study.