CHAPTER FOUR

EFFECTS OF TROPHIC PREFERENCE AND URBANIZATION ON DUNG BEETLE ASSEMBLAGE STRUCTURE AND TRANSMISSION OF *Spirocerca lupi* TO DOGS

Introduction

Mammalian faeces represent very patchy and ephemeral habitats. They are patchy due to the distribution of the producer from which it is excreted and ephemeral as a result of the activities of a variety of dung colonisers (Dormont *et al*. 2007; Scholtz *et al*. 2009; Tshikae *et al*. 2008). However, dung is a highly sought-after and nutritious resource that, under favourable conditions, is quickly colonised by coprophagous beetles belonging to the subfamily Scarabaeinae, for the purposes of feeding and breeding (Scholtz *et al*. 2009). It constitutes a combination of characters such as age, size, water content, physico-chemical attributes, seasonality, and temporal and spatial distribution, which can be regarded as important niche dimensions for dung beetles (Scholtz *et al*. 2009; Sowig & Wassmer 1994; Tshikae *et al*. 2008). As these factors influence its species-specific attractiveness, selection of a particular dropping that is to be colonised results in differences between species assemblages in different dung types (Scholtz *et al*. 2009; Sowig & Wassmer 1994).

The physical and chemical composition of dung varies considerably between that of herbivores, omnivores and carnivores (Dormont 2007; Martin-Piera & Lobo 1996). There can also be substantial variation in the dung produced by different mammalian herbivores, since grazers and browsers produce quite different dung types (Scholtz *et al*. 2009). An additional complexity is whether the herbivore is a ruminant, producing fine-textured faeces, or a non-ruminant producing coarse dung, as well as variation in dung quality arising from such factors as disparities in pasture quality or the season when the dung is produced (Gittings & Giller 1998; Scholtz *et al*. 2009).

The assumption is often made that most dung beetles are polyphagous and colonise the faeces of several vertebrates without any discrimination between dung types (Dormont 2007). Although most species of dung beetles are indeed opportunistic without discriminating between various types of dung, specialist coprophages with clear trophic preferences have been documented (Davis 1994; Dormont *et al*. 2007; Fincher *et al*. 1970; Hanski & Cambefort 1991; Martin-Piera & Lobo 1996; Tshikae *et a*l. 2008). Moreover, some studies have empirically shown that dung beetles do display differences in colonisation activity among the dung of various herbivorous mammals (Dormont *et al*. 2007).

Urbanisation is increasing worldwide, and it is expected that more than 66% of the global human population will reside in cities within the next three decades (Bradley & Altizer 2006). Changes in urban land use influence shifts in the geographical ranges and densities of host species, interspecific interactions (Bradley & Altizer 2006), and more specifically, the structure of dung beetle species assemblages (Carpaneto *et al*. 2005). These changes in urban environments may lead to a reduction or complete absence of grazing herbivores. Dogs, both pets and feral animals, often then become the most common large mammal in these urban environments (Carpaneto *et al*. 2005). Dog dung may provide a temporary refuge for species of coprophagous dung beetles that do not prefer omnivore dung (the dog was treated as an omnivore in this study), but would otherwise encounter local extinction in these urban environments (Carpaneto *et al*. 2005).

The aims of the present study were to assess abundance, diversity, and trophic preference of dung beetles across three dung types along an urban-peri-urban-rural gradient in Grahamstown (Eastern Cape, South Africa). This area was found to be a focal area of high incidence of spirocercosis in domestic dogs by the ClinVet International Research Organisation, South Africa. The selection of specific sites for trapping was based on information obtained from a local veterinarian on patient records pertaining to dogs that were infected by *S*. *lupi* and consultation with dog owners on where dogs had been taken for daily exercise. Furthermore, this study served to identify omnivore dung beetle specialists which could potentially act as vectors for *S*. *lupi* under natural conditions in these environments. A specific objective of this chapter is to understand whether changes in dung beetle species assemblages and trophic choice due to changes in landscape use, can lead to altered transmission rates of *S*. *lupi* to dogs.

Materials and Methods

Sampling localities

Dung beetles were collected at three localities along an urbanisation gradient in Grahamstown, a medium-sized town with 57 030 inhabitants (McConnachie *et al*. 2008), in the Eastern Cape Province of South Africa (33°18'S, 26°32'E). Locality one was situated within an urban environment in an open field adjacent to a military base. This urban site was severely degraded in terms of having reduced woody vegetation cover, and most of the flora comprised of alien invasive and non-invasive species.

Locality two was situated on the periphery of the town in a peri-urban greenspace area and was less transformed by human activity than the urban site. The current landscape of this study site consists of grassland, dotted by a mosaic of evergreen shrubs and low woody plants. The area is used by urban dwellers for a variety of activities, such as hiking, horse riding, bird watching, and harvesting of fuel-wood (Du Toit pers. comm.). During the sampling period, dogs were regularly encountered in both the urban and peri-urban sites, as these areas were used extensively by dog owners for exercising their pets (either restricted on a leash or by letting the animals run freely) (Du Toit pers. obs.).

Locality three was situated on a sheep farm, approximately 5 kilometres outside Grahamstown. This rural study site was characterised by indigenous vegetation that forms part of the Grahamstown Grassland Thicket vegetation type (McConnachie *et* *al*. 2008). Dogs were conspicuously absent from the site and the area was grazed by mainly sheep, although a few indigenous antelope were observed during the study.

By comparing the abundance, trophic associations, and assemblage structure of dung beetles between these three localities, this study may identify potential effects of changes in landscape use and composition on the transmission rate of *S*. *lupi* to dogs.

Sampling design

Dung beetle assemblage structure and trophic associations with bait type were studied using three different types of mammalian dung. The three dung types consisted of (1) relatively smooth and rancid-smelling pig dung as a surrogate for dog dung (2) fine-fibred dung of a ruminant herbivore (cattle); and course-fibred dung of a hay-fed, non-ruminant herbivore (horse). Pig dung served as a surrogate for dog dung because it is also an omnivore and strong smelling, and due to difficulties in obtaining sufficient quantities of dog dung for baiting purposes. Dung for baits were collected from a commercial pig farm, from pasture-grazing cattle on a small holding West of Pretoria (Gauteng), and from stabled horses on a small holding in Grahamstown (Eastern Cape).

Trapping was conducted during November 2009, which coincides with high dung beetle activity (Davis 2002) in summer rainfall areas of South Africa. As dung beetle activity is strongly influenced by insolation (Tshikae *et al*. 2008), pitfall traps were placed in predominantly sunny situations to standardise sampling design according to microhabitat. In each locality, 30 pitfall traps were set 10 m apart along three transect lines. Transects were separated by 50 m intervals. All traps in a specific transect were baited with one of the three dung types. The plastic buckets used as traps had a 1 L capacity (11 cm in diameter and 12 cm deep) and were sunk into the ground so that the rims of the buckets were level with the soil surface. They were filled to about one-third of their volume with a water and soap solution to immobilise trapped beetles. On each trapping occasion the 0.5 L dung baits were suspended on u-shaped metal wire supports, which were placed over the buckets at ground level. Baits were wrapped in chiffon to allow for the diffusion of volatile compounds but at the same time exclude beetles from the dung baits. Traps were covered with lids supported on wire legs to prevent flooding of the buckets by rain.

Trapping was carried out in all sites simultaneously for a continuous 48 h period. Traps were baited between 06h00 and 08h00 and re-baited between 16h00 and 18h00 to ensure that diurnal as well as crepuscular/nocturnal species were presented with fresh baits. The trap contents were collected on each baiting occasion and samples were preserved in absolute ethanol for species-level identification and counting in the laboratory. Voucher specimens were deposited at the University of Pretoria Insect Collection.

Data analysis

The data were analysed using methods similar to Davis (1994) and Tshikae *et al*. (2008). Rank abundance curves were generated and used to compare abundance patterns and species evenness (Krebs 1999) across the three different dung types along an urban-peri-urban-rural gradient. Furthermore, species were classified along a gradient that ranges from specialist to generalist with regard to trophic niche width. A value for niche width across the three dung types was calculated for each species using the Shannon-Wiener diversity index (Krebs 1999) and niche width indices were standardised by dividing all values by -1.029, which was the most generalist value generated by the data set (Davis 1994). This provided an index scale for trophic niche width (W) where zero represented the most specialist species and one the most generalist.

Patterns of trophic associations (omnivore, ruminant-herbivore, and non-ruminant-herbivore) were classified by arranging the trap data as a matrix of eight species by total numbers attracted to each of the three dung types. The data matrix only included the eight most abundant species, which comprised 90% of all individuals collected. A cluster analysis with Bray-Curtis Similarity Index (**PRIMER** v5.0) was used to investigate differences in dung beetle assemblage structure between the three localities along the urban-peri-urban-rural gradient. The results were summarised and presented as a dendogram (Figure 3) from which groups of species with similar trophic associations were defined. For the eight most common dung beetle species Kruskal-Wallis tests (STATISTICA 10) were conducted to evaluate differences in abundance per trap between the three dung types (horse, cattle, and pig) and the three study sites (urban, peri-urban, and rural).

Results

In total, 2396 dung beetles were collected in the study representing 29 species in 16 genera and eight tribes (Appendix 1). Of the 29 species, 26 (90%) were sampled from pig dung, 24 (83%) from cattle dung, and 12 (41%) from horse dung (Figure 1a; Appendix 1). Omnivore dung attracted more beetles than the two types of herbivore dung combined. Pig dung baits attracted 1539 (64.2%) individuals, followed by cattle dung with 740 (30.9%). Only 115 (4.8%) dung beetles were collected from horse dung baits (Figure 1b, Appendix 1). Three species were collected exclusively from only one dung type (Appendix 1), and 15 species of dung beetles were attracted to two of the three dung types, while 11 species were attracted to all three dung types (Appendix 1).

Table 1 summarises trophic preference and abundance for the eight most abundant species, which comprised 90% of the total number of dung beetles sampled from three different dung types along the Grahamstown urbanisation gradient. *Onthophagus* spp. showed a strong trophic preference for pig dung (Table 1) and were most abundant in the urban and peri-urban sites. A similar pattern was observed for *Sarophorus striatus*. The most abundant species on cattle dung was *Drepanocerus kirbyi*, which reached peak numbers in the rural site furthest from the town (Table 1).

Rank abundance curves (Figure 2) of dung beetles trapped along the urban-peri-urban-rural gradient in Grahamstown show clear patterns of species diversity in the dung baits. The curves for species sampled from pig and cattle dung show a similar assemblage structure and indicate higher species diversity than that for species assemblages on horse dung. Species diversity was highest in the cattle dung assemblage, even though more dung beetle species were attracted to pig dung baited traps (a few species were much more abundant in pig dung baited traps than they were in cattle). Greatest evenness is observed in the curves for pig and cattle dung among species with intermediate and low abundance.

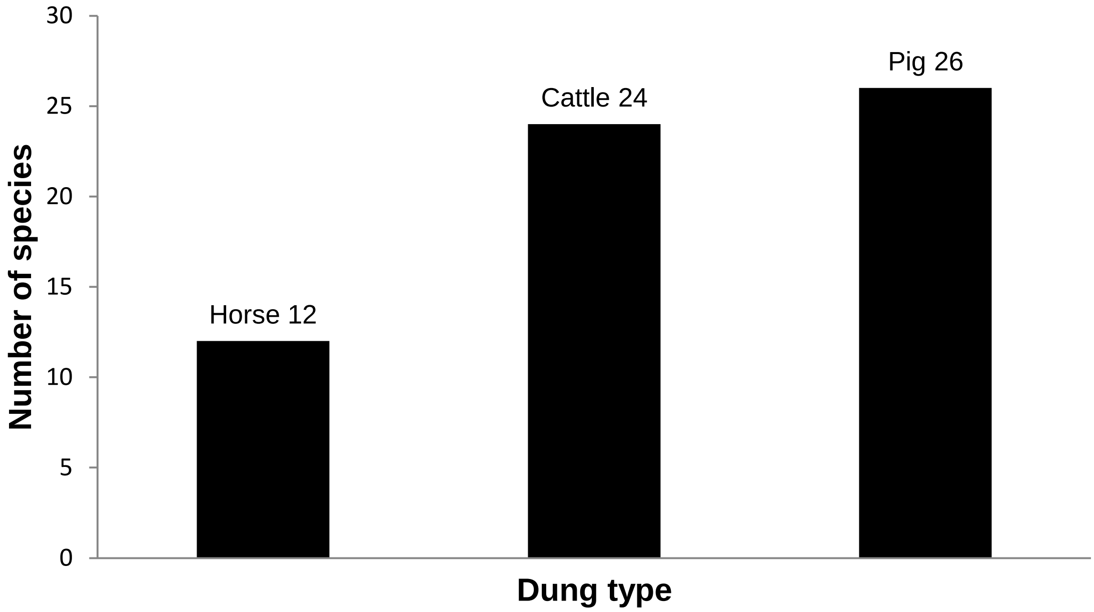

Figure 1a. Number of species trapped on different dung types.

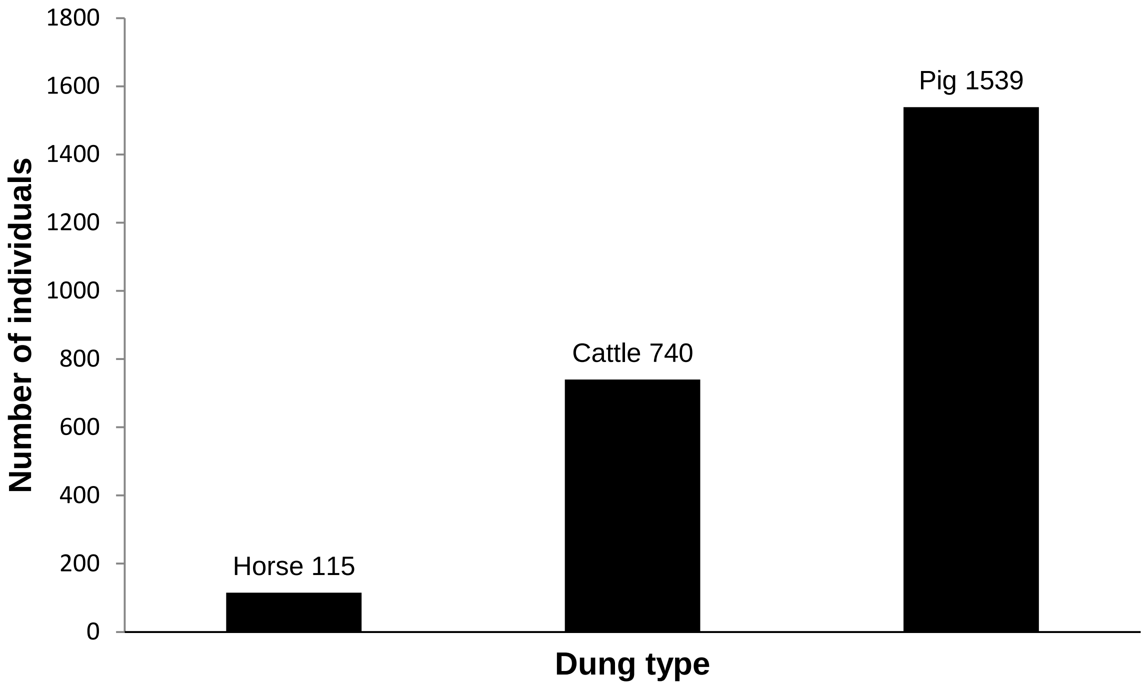

Figure 1b. Number of individual dung beetles trapped on different dung types.

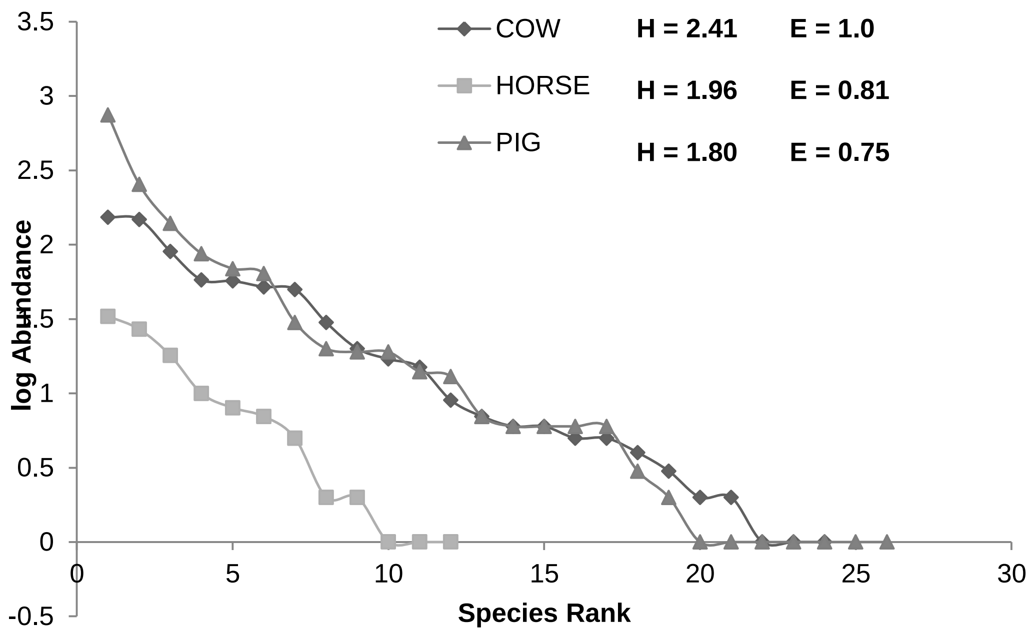

Figure 2. Rank-abundance curves for dung beetle species on three dung types (H, Shannon-Weiner; E, evenness).

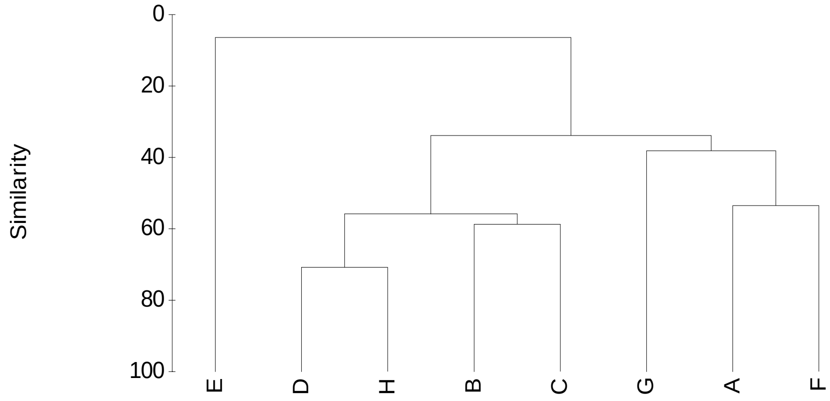

Figure 3. Dung beetle trophic associations of the eight most abundant species between the three localities along an urbanisation gradient. A= *Sarophorus striatus*; B= *Drepanocerus kirbyi*; C= *Euoniticellus africanus*; D= *Onthophagus asperulus*; E= *Onthophagus fritschi*; F= *Onthophagus lugubris*; G= *Onthophagus sugillatus*; H= *Sisyphus alveatus*

Table 1. Numbers showing trophic association of the eight most abundant dung beetle species collected along an urban-peri-urban-rural gradient in Grahamstown, Eastern Cape.

		Numbers on bait type										H
Species	Code	Horse 1	Horse2	Horse 3	Cattle 1	Cattle 2	Cattle 3	Pig 1	Pig 2	Pig 3	Total	(2, N=90)
Sarophorus striatus	A	0	6	2	18	24	15	78	112	65	320	33.21*
Drepanocerus kirbyi	B	0	0	1	9	27	117	1	18	20	193	26.61*
Euoniticellus africanus	C	0	0	0	7	13	28	5	19	41	113	22.31*
Onthophagus asperulus	D	0	6	1	5	14	71	0	11	76	184	8.17**
Onthophagus fritschi	E	0	0	0	57	1	0	1	0	0	59	11.96**
Onthophagus lugubris	F	1	16	1	0	21	9	1	68	15	132	6.32***
Onthophagus sugillatus (sp. 3)	G	2	18	13	32	75	41	185	365	196	927	26.97*
Sisyphus alveatus	H	0	3	26	0	0	52	1	11	127	220	5.44
Total		3	49	44	128	175	333	272	604	540	2148	

*P < 0.001, **P < 0.03, ***P < 0.05

4.4 Discussion

This study investigated trophic preferences in dung beetles along an urbanisation gradient to ascertain whether changes in species assemblages and trophic choice could lead to altered transmission rates of *S*. *lupi* to dogs. The prevalence of infection in dung beetles and the epidemiology of spirocercosis in any particular area depend in part on the abundance of these beetles and the degree of contact between them and domestic dogs (Bailey 1972). Higher contact rates with the faeces of infected dogs by coprophagous beetles lead to an increased probability of infection in dung beetles, and higher abundance and population density of susceptible dung beetle species on dog scats may lead to an increased transmission rate of *S*. *lupi* to dogs. Several factors influence the population density of scarabaeines in any specific region: vegetation cover; soil type and pH; dung type diversity (carnivore/ omnivore, and herbivore); temporal patterns such as successional processes associated with dung (age, size, water content), diel activity and seasonality; and physico-chemical attributes of the dung itself (Bailey 1972; Hanski & Cambefort 1991).

Eight out of a total of 29 species collected during the sampling effort, constituted 90% of the individual beetles trapped in the Grahamstown area (Appendix 1; Table 1). The most abundant species in terms of individuals trapped, belonged to the genus *Onthophagus*. Three of these, *O*. *sugillatus*, *O*. *lugubrus*, and *O*. *asperulus*, have been found positive for infection with *S*. *lupi* in a separate study. (Chapter 2). Although *Onthophagus cyaneoniger* was also found to harbour this nematode

(Chapter 2) it is excluded from analyses in this study because only one individual was collected. In a recent study on the prevalence of this nematode in populations of its intermediate dung beetle hosts in the Pretoria Metropole (Chapter 2), Du Toit *et al*. (2008) have shown *O*. *sugillatus* to be a vector of *S*. *lupi* in that region too, along with four other species, three of which also belonged to the genus *Onthophagus*. Gottlieb *et al*. (2011) identified *O*. *sellatus* as the main intermediate host of this parasite in an endemic urban area in central Israel. Therefore, it seems that *Onthophagus* spp. could be regarded as a major vector of *S*. *lupi* and the preferred host to support larval development and transmission to paratenic and definitive hosts (Gottlieb *et al*. 2011) under natural conditions, at least in urban environments where this disease in dogs is considered to be endemic. However, since *Onthophagus* is the largest dung beetle genus, the preference of a few species for dog dung may simply be a factor of large numbers of species of which some have niches wide enough to encompass dog dung as food source.

Species showing a preference for omnivore dung and a higher abundance in urban environments, can be expected to be more active in spreading *S*. *lupi* to dogs. Within urban and peri-urban areas in Grahamstown, the replacement of grazing herbivores by a single omnivorous species (domestic dog) may account for the high numbers of *Onthophagus* spp. and *Sarophorus striatus*. The dominance of domestic (sheep and cattle) and indigenous herbivores (kudu (*Tragelaphus strepsiceros*) and grey duiker (*Sylvicapra grimmia*)) in in the rural agro-ecosystem may explain both lower abundances in dung beetle species associated primarily with pig dung and much higher numbers in cattle dung frequenting species, such as *Drepanocerus kirbyi*.

Differences in beetle numbers between sites one (urban) and two (peri-urban) (Table1) could be a result of the differences in disturbance between those sites. Site one was situated on the edge of a military base golf course, which was more transformed in terms of the proportion of natural vegetation still intact, while site two served as an urban greenbelt area.

Landscapes modified by humans lead to altered local species assemblage structures (Radtke *et al*. 2008; Carpaneto *et al*. 2005). Of particular concern to this study, is the conversion of land previously used as pastures into urban parks, built-up residential areas, or informal, high density human settlements ("townships"). Where this takes place, grazing herbivores are often replaced by a single large omnivore, the domestic dog, which may be kept either as pets or roam freely as feral animals (Carpaneto *et al*. 2005). This leads to an increase in the numbers of dogs and the density of dog faeces. In turn, this may lead to a higher abundance of dung beetles that show a preference for carnivore/ omnivore dung. Another factor to consider is the socio-economic attributes of a particular area. Lower income level communities are significantly negatively correlated with the quality of public green spaces in towns in the Eastern Cape (McConnachie *et al*. 2008). This situation may arise because of a lack of proper sanitation, which is a consequence of the low income level of such a community. This would result in decreased hygienic conditions and an abundance of exposed human faeces often associated with socio-economic inequalities encountered in poorer communities (Du Toit pers. obs.).

Under such conditions, human faeces may serve as an additional food resource to dung beetles, which may play a pivotal role in their ability to persist under unfavourable conditions (in terms of trophic preference) in urban areas. Moreover, dog dung (and human faeces (Du Toit pers. comm.)) may provide a temporary refuge to dung beetles that do not primarily prefer this resource, but will otherwise encounter local extinction in urban environments (Carpaneto *et al*. 2005). In fact, species assemblages occurring in dog and human dung in India, were found to be distinct from those associated with herbivore dung (Carpaneto *et al*. 2005). This holds important implications for the suite of dung beetle species that can be considered as suitable intermediate hosts for *S. lupi* under natural conditions. See Chapter 3. Few data exist on the colonisation of dog faeces by coprophagous dung beetles in any world region (Carpaneto *et al*. 2005), although Wallace and Richardson (2005) have compiled an inventory of scarabaeines observed to utilise the dung of domestic dogs in Austin, Texas. Changes in traditional grazing regimes have been shown to lead to declines in several dung beetle species in that particular region (Nichols *et al*. 2009). A myriad of other examples exist on the dramatic effects that a reduction in large mammal diversity (and thus, a reduction in the diversity of dung types available to Scarabaeine dung beetles) has had on the structure of dung beetle assemblages (Nichols *et al*. 2009; Scholtz *et al*. 2006).

Dung quality in terms of water content varies widely between different dung types and is an important factor affecting patch choice. Larger droppings, such as those produced by cattle, differ in their water retention qualities from smaller droppings, such as those produced by sheep, which are able to rehydrate by dew or during rainfall (Sowig & Wassmer 1994). Almost all adult dung beetles feed exclusively on the minute particles in the micro-organism-rich, liquid fraction of dung (Holter 2000; Holter *et al*. 2002). Thus, since there is considerable variation in the size of dung produced by different mammals, it might play an important role in niche separation (Sowig & Wassmer 1994). Canine dung undergoes a more rapid change of microclimate conditions because of its coarse structure (Carpaneto *et al*. 2005). Furthermore, changes in the quality of available dung resources (when one dung type is substituted with another) cause shifts in dung beetle communities with regards to competition within and between ecological guilds (Lumaret *et al*. 1992). In warmer climates competition is exacerbated by factors such as dryness and temperature (Lumaret *et al*. 1992).

4.5 Conclusion

It is imperative to have a comprehensive understanding of the incidence of species persisting in dynamic equilibriums between local extinction and colonisation events (Roslin & Koivunen 2001). At the landscape scale such events are expected to be higher in a dense network of patches than in a sparser one. Differences in the densities of patch networks cause differences in population densities. Thus, higher densities of suitable habitat patches in the landscape translate into higher local population densities (Roslin & Koivunen 2001). This necessitates the study of urban dung beetle assemblage structures because they indicate ecological changes in the local environment (Radtke *et al*. 2008). Dog dung (Carpaneto *et al*. 2005) and human faeces (Du Toit pers. comm.) are the most abundant resources for dung beetles in urban environments and pose major hygiene problems if not removed. Furthermore, dog and human faeces may favour certain rare species of dung beetles, or provide temporary refuge to species that do not usually show a preference for omnivore dung, which could allow for the persistence of their metapopulations in urban areas (Carpaneto *et al*. 2005). However, coprophagous dung beetles provide essential ecological services through their feeding and nesting activities, which not only allow for the recycling of faeces in urban environments (Wallace & Richardson 2005), but also serve to control the abundance of dung-dispersed nematodes and protozoa (Spector et al. 2008). These ecological services hold enormous implications for the health and wellbeing of humans and their companion animals.